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LETTER

The three-species problem: Incorporating competitive asymmetry and intransitivity in modern coexistence theory

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Abstract

While natural communities can contain hundreds of species, modern coexistence theory focuses primarily on species pairs. Alternatively, the structural stability approach considers the feasibility of equilibria, gaining scalability to larger communities but sacrificing information about dynamic stability. Three-species competitive communities are a bridge to more-diverse communities. They display novel phenomena while remaining amenable to mathematical analysis, but remain incompletely understood. Here, we combine these approaches to identify the key quantities that determine three-species competition outcomes. We show that pairwise niche overlap and fitness differences are insufficient to completely characterize competitive outcomes, which requires a strictly triplet-wise quantity: cyclic asymmetry, which underlies intransitivity. Low pairwise niche overlap stabilizes the triplet, while high fitness differences promote competitive exclusion. The effect of cyclic asymmetry on stability is complex and depends on pairwise niche overlap. In summary, we elucidate how pairwise niche overlap, fitness differences and cyclic asymmetry determine three-species competition outcomes.

KEYWORDS

communities, competition, intransitive competition, Lotka–Volterra competition, modern coexistence theory, multispecies coexistence, structural stability

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INTRODUCTION

Modern coexistence theory (MCT) is a widely used theoretical framework for understanding species coexistence. MCT has two strands (Song et al., 2019), with roots in either the Lotka–Volterra competition model (Chesson, 1990) or invasion analysis (Barabás et al., 2018; Chesson, 2000, 2018). Both strands define two quantities that determine the outcome of competition: niche overlap and fitness differences. Niche overlap is thought to measure resource-use overlap and fitness differences to measure differences in innate competitive ability. Lower niche overlaps promote coexistence, while higher fitness differences lead to competitive exclusion.

Despite its success, MCT has focused primarily on pairwise competition. Extension to multispecies competition has proven challenging, which first becomes apparent when moving from two to three species. In multispecies competition, the term ‘fitness difference’ is a misnomer: unlike usual difference operations, the fitness differences within two pairs of species (A & B; B & C) do not determine the fitness difference between A and C. Therefore, fitness differences as defined in MCT are relative and meaningful only in the context of specific pairs of species, which impairs their application to more-diverse communities. This issue holds for niche overlaps, which are also specific to pairs. Further, the invasion-analysis strand of MCT is based on mutual invasibility (Barabás et al., 2018; Chesson, 2000, 2018). In a community of \mathcal{N} species, mutual invasibility requires a positive invasion rate of each species when rare into the long-term attractor of the community of $\mathcal{N} - 1$ remaining species (Armstrong & McGehee, 1976; Hofbauer & Schreiber, 2022). However, this requires that all of the resident communities with $\mathcal{N} - 1$ species persist without the invader present. While this is easy to achieve in species pairs, where resident communities are simple monocultures, more sub-communities are likely to be infeasible in diverse communities. Thus, the application of invasion-based techniques to more diverse communities is challenging (Barabás et al., 2018; Hofbauer & Schreiber, 2022).

Three-species competition represents a significant jump in complexity, both in terms of the number of parameters and dynamical phenomena. The addition of just one more species to the pairwise Lotka–Volterra competition model increases the number of parameters from six to twelve. In a triplet, intransitive competition can occur where each species can exclude one species but is excluded by the other (rock–paper–scissors), resulting in either stable three-species coexistence or a stable heteroclinic cycle (a trajectory that connects the boundary equilibria, approached with ever-slowing oscillations) (Gilpin, 1975; May & Leonard, 1975). Since no pair of species can coexist in isolation in intransitive competition, invasions are cyclic in nature and traditional invasion analysis cannot determine the outcome of competition

(Hofbauer, 1994; Hofbauer & Schreiber, 2022). Besides heteroclinic cycles, three-species competition can result in other novel phenomena such as limit cycles (Hofbauer & So, 1994) and various flavours of alternative stable states. Figure 1 summarizes twenty-three distinct outcomes of three-species LV competition (Zeeman, 1993). Three-species communities are the simplest that can exhibit indirect effects, yet remain amenable to mathematical analysis, so we focus on them as a stepping stone to understanding more complex communities and to illustrate the challenges of scaling up pairwise approaches.

An alternative approach to multispecies communities focuses on the *structural stability* of equilibria (Cenci & Saavedra, 2018; Saavedra et al., 2017). Structural stability considers the feasibility of the equilibria (all species have positive abundance)—a necessary condition for coexistence—and how this depends on environmental parameters. Calculating the feasibility of equilibria is easy in Lotka–Volterra systems, where it requires only inverting the community matrix, allowing this approach to scale readily to larger communities. However, it ignores the dynamic stability of a community, which is of great ecological relevance: if a feasible community is dynamically unstable, it is unlikely to be seen in nature. Further, the dynamical stability of a community may even change within the structurally stable range of parameters. Therefore, the structural stability approach may overstate the range of environments where species coexist.

Due to the limitations of both invasion-based and structural stability frameworks, a full understanding of how multispecies communities persist remains elusive. In this study, we fill this gap by combining the perspectives of MCT, structural stability and dynamical systems theory to more fully characterize three-species competition. We first partition pairwise fitness differences in MCT into two quantities: absolute fitness differences and competitive asymmetry. Next, we identify cyclic competitive asymmetry as the basis of intransitivity, a novel outcome possible in triplets but not in pairs. We then systematically explore how cyclic asymmetry, pairwise niche overlap and fitness differences combine to determine the outcome of three-species competition. We start with symmetrical interactions but later remove this assumption to show the generality of our results. We conclude by showing that the three-species competition outcome can largely be predicted using only six parameters, massively reducing the dimensionality of the problem. All-in-all, this work develops a nearly complete map of three-species competition outcomes as a function of cyclic asymmetry, niche overlaps and fitness differences.

MODEL AND ANALYSIS

We study the \mathcal{N} -species Lotka–Volterra (LV) competition model ($\mathcal{N} = 2$ or 3)

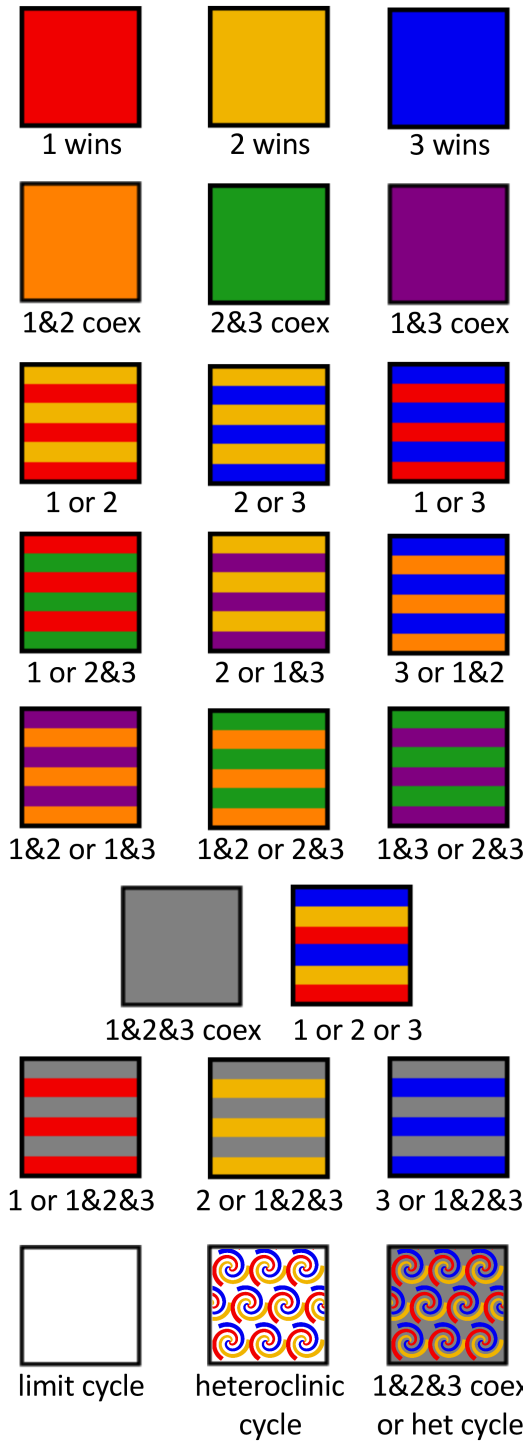


FIGURE 1 Colour coding for the 23 different outcomes of the three-species Lotka–Volterra competition. Monocultures are represented by primary colours, and coexisting pairs are shown by mixing the constituent species' colours. Alternative stable states are shown as stripes corresponding to colours of the constituent stable states. Dark grey represents the coexistence of all three species. Heteroclinic cycles are shown as spirals, and white space represents limit cycles.

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

where N_i is the density of species i . The intrinsic growth rate of species i is its growth rate when alone at low density, denoted by r_i . We assume $r_i > 0$ so that each species can persist in the absence of competition. The competition coefficients α_{ij} measure the per-capita competitive impact of species j on species i , which is then summed across all species.

Two-species competition

We start with a brief summary of two-species LV competition (Chesson, 2020). The invasion rate $\lambda_{i,j}$ of species i into the monoculture equilibrium of species j and vice versa ($\lambda_{j,i}$) are:

$$\lambda_{i,j} = r_i - \frac{r_j \alpha_{ij}}{\alpha_{jj}} \quad (2)$$

$$\lambda_{j,i} = r_j - \frac{r_i \alpha_{ji}}{\alpha_{ii}} \quad (3)$$

For pairwise coexistence of i and j , both invasion rates must be positive ($\lambda_{i,j} > 0$ and $\lambda_{j,i} > 0$), which results in the coexistence conditions

$$\sqrt{\frac{\alpha_{ii} \alpha_{jj}}{\alpha_{ij} \alpha_{ji}}} > \frac{r_i}{r_j} > \sqrt{\frac{\alpha_{jj} \alpha_{ii}}{\alpha_{ij} \alpha_{ji}}} \quad (4)$$

MCT defines the niche overlap between species i and j as $\rho_{ij} = \sqrt{\frac{\alpha_{ij} \alpha_{ji}}{\alpha_{ii} \alpha_{jj}}}$, and their relative fitness difference (technically, their fitness ratio) as $F_{ij} = \frac{r_i}{r_j} \sqrt{\frac{\alpha_{jj} \alpha_{ii}}{\alpha_{ij} \alpha_{ji}}}$. Therefore, species i and j coexist if $0 \leq \rho_{ij} < 1$ and

$$\frac{1}{\rho_{ij}} > F_{ij} > \rho_{ij} \quad (5)$$

Conversely, there is founder control ($\lambda_{ij} < 0$ and $\lambda_{ji} < 0$), also called priority effects, if $\rho_{ij} > 1$ (hyper-niche-overlap) and

$$\rho_{ij} > F_{ij} > \frac{1}{\rho_{ij}}. \quad (6)$$

(Chesson, 2020; Ke & Letten, 2018)

Expanding on MCT, we decompose the fitness difference between species i and j , F_{ij} , into the product of the ratio of intrinsic growth rates $R_{ij} = r_i / r_j$ and a combination of the competition coefficients that measures *competitive asymmetry* A_{ij} :

$$F_{ij} = R_{ij} A_{ij}, \text{ where } A_{ij} = \sqrt{\frac{\alpha_{jj} \alpha_{ii}}{\alpha_{ij} \alpha_{ji}}} \quad (7)$$

Because each species' intrinsic growth rate depends only on its fit to the abiotic environment, we call R_{ij} the *absolute* fitness difference between species i and j . For fixed r_i values, competitive asymmetry can change the outcome of competition, but across the range of fitness differences, it has only a quantitative effect, recentring the range of fitness differences that result in coexistence or founder control at $R_{ij} = 1/A_{ij}$. However, it will prove key in understanding three-species competition below.

Three-species competition: The dimensionality of parameter space

How much more complex is three-species competition compared to two-species? The two-species LV model has six parameters—two intrinsic growth rates and four competition coefficients—which can be reduced to three through nondimensionalization (Appendix D), two of which can be effectively combined by recentring. This leaves a two-dimensional space of outcomes, which can be parameterized by either the invasion growth rates $\lambda_{i,j}$ and $\lambda_{j,i}$, or by niche overlap ρ_{ij} and fitness difference $F_{ij} = R_{ij}A_{ij}$ (Equations 5–7). A large competitive asymmetry within a pair can be offset by an inverse absolute fitness difference, leading to a relative fitness difference close to 1, which is at the centre of the pairwise coexistence region.

Adding a third competitor illustrates a subtlety in the definition of fitness differences in MCT. One might suppose that the fitness difference F_{ij} is the difference (technically, the ratio) between the fitness of species i and j , that is, $F_{ij} = F_i/F_j$ for some appropriate definition of F_i . If that were true, then knowing the fitness difference between species 1 and 2 (F_{12}) and that between species 2 and 3 (F_{23}) would dictate the fitness difference between species 1 and 3 to be $F_{13} = \frac{F_1}{F_3} = \frac{F_1}{F_2} \cdot \frac{F_2}{F_3} = F_{12}F_{23}$. Yet, the definition of fitness differences in Equation (7) shows that this is not generally true due to the competitive asymmetries A_{ij} . Therefore, fitness differences between two species must be seen as relative to that particular pair of species and not reflecting the difference between any species-specific fitnesses—an apparent contradiction. On the other hand, the absolute fitness differences $R_{ij} = r_i/r_j$ are based on species-specific fitness (r_i) and have the desirable property that $R_{13} = R_{12}R_{23}$. Thus, following Saavedra et al. (2017), we will use the intrinsic growth rates r_i as a measure of a species' match to the abiotic environment.

Following Equations (5)–(7), the outcomes of the three *pairwise* competitions among the three species are determined by six invasion growth rates ($\lambda_{1,2}, \lambda_{2,1}, \lambda_{2,3}, \lambda_{3,2}, \lambda_{1,3}$ and $\lambda_{3,1}$) or equivalently, by three niche overlaps (ρ_{12}, ρ_{23} and ρ_{31}) and three relative fitness differences (F_{12}, F_{23} and F_{31})—six parameters (note the cyclic ordering of subscripts). However, if we use the absolute fitness r_i for the reasons described above, then we lose a degree of freedom since $R_{12}R_{23}R_{31} = \frac{r_1}{r_2} \cdot \frac{r_2}{r_3} \cdot \frac{r_3}{r_1} = 1$, leaving only five

independent parameters. What is the missing parameter encoded in the three relative fitness differences F_{ij} that cannot be found in the two independent r_i 's? Inspired by Klimentko (2015), we suggest the missing parameter is the geometric mean of the competitive asymmetries A_{ij} ,

$$\bar{A} = \sqrt[3]{A_{12}A_{23}A_{31}} = \sqrt[6]{\frac{\alpha_{21}}{\alpha_{12}} \frac{\alpha_{13}}{\alpha_{31}} \frac{\alpha_{32}}{\alpha_{23}}} \quad (8)$$

which we term the *cyclic asymmetry* of the triplet.

The cyclic asymmetry \bar{A} measures the nonadditivity of competition among the three species. When $\bar{A} = 1$, $F_{12}F_{23}F_{31} = 1$ and intransitivity is impossible. Deviation of \bar{A} from 1 signals that the triplet is potentially intransitive, and higher deviations signal higher potential intransitivity. Intransitivity can go in one direction ($1 \rightarrow 2 \rightarrow 3 \rightarrow 1$) or the other ($1 \rightarrow 3 \rightarrow 2 \rightarrow 1$), reflected by $\bar{A} > 1$ or $\bar{A} < 1$, respectively. Thus, permuting species labels replaces \bar{A} with its reciprocal, but has no effect on the outcome.

Moving beyond the pairwise competitive outcomes discussed above to consider the full three-species competition, the total number of parameters of three-species Lotka–Volterra competition is twelve—three intrinsic growth rates and nine competition coefficients. This can be reduced to eight through nondimensionalization (Appendix D), but an exhaustive exploration of parameter space remains challenging. We will present our results in terms of three intrinsic growth rates (r_1, r_2 and r_3), three pairwise niche overlaps (ρ_{12}, ρ_{23} and ρ_{31}) and three competitive asymmetries (A_{12}, A_{23} and A_{31}). To facilitate comparison with the structural stability framework (Saavedra et al., 2017), we assume without loss of generality $r_1 + r_2 + r_3 = 1$, which reduces the total number of parameters to eight ($3+3+3-1=8$), consistent with the nondimensionalization. We assume that the r_i 's represent species responses to the underlying environment and that the competition coefficients/measures of niche overlap and competitive asymmetry are constant for a set of species.

Three-species competition: Analysis

Following Saavedra et al. (2017), we present our results in the unit simplex $r_1 + r_2 + r_3 = 1$ to illustrate how species' intrinsic growth rates influence the outcomes of competition (see Appendix B for details about how to interpret the simplex). Saavedra and colleagues focused on the *structural stability* of an equilibrium, that is, the environmental range under which the equilibrium is feasible. For simplicity, they assumed that the matrices of competition coefficients are either positive definite or Volterra-dissipative, which implies $\rho_{ij} < 1$ for all pairs and global stability of all coexisting communities and subcommunities (Saavedra et al., 2017, Appendix S1). Under this assumption, the feasibility

of an equilibrium implies its global stability. However, $\rho_{ij} > 1$ results in alternative stable states in pairs (Ke & Letten, 2018). Therefore, focusing solely on feasibility as in the structural stability framework may overestimate the environmental conditions under which species coexist. Thus, a fuller understanding of the outcome of three-species competition requires consideration of *dynamical* stability.

We numerically evaluate the feasibility and stability conditions of all equilibria (see Appendix A for details), consisting of the full community (the unique three-species equilibrium) and all of its subcommunities (three one-species and three two-species equilibria), using local stability analysis. In the case of subcommunities, this can be simplified to invasion analysis, combining Equations (5)–(7) with the invasion growth rate of missing species ($\lambda_{inv, res}$ for species *inv* invading resident community *res*). We apply Routh–Hurwitz criteria to check the local stability of the three-species equilibrium if it is feasible. Finally, if a heteroclinic cycle exists from species $i \rightarrow j \rightarrow k \rightarrow i$ ($\lambda_{j,i} > 0 > \lambda_{i,j}$, $\lambda_{k,j} > 0 > \lambda_{j,k}$ and $\lambda_{i,k} > 0 > \lambda_{k,i}$), we check its stability using the Hofbauer criterion (Hofbauer & Sigmund, 1998). We evaluate these conditions numerically across the simplex for different values of pairwise niche overlap and cyclic asymmetry.

We summarize the outcome of competition across the $r_1 + r_2 + r_3 = 1$ simplex. There are at least twenty-three qualitatively different outcomes possible, with a large number of alternative stable states (Zeeman, 1993). To visually communicate this, we use a colour scheme based on the traditional red–yellow–blue colour model (Figure 1). Monocultures are shown as primary colours. The stable coexistence of a pair is shown as the secondary colour formed by mixing the corresponding monocultures' primary colours. Alternative stable states are shown with stripes whose colours correspond to the alternative outcomes. Stable equilibrium three-species coexistence is denoted by grey, stable heteroclinic cycles are denoted by spirals and limit cycles are denoted by white. Colourblind-friendly versions of key figures are given in Appendix G.

Three-species competition: Results

Due to the eight-dimensional parameter space, we present various special cases that embed various symmetries in the parameters. We begin by varying the number of stably coexisting pairs ($\rho_{ij} < 1$) versus those with founder control ($\rho_{ij} > 1$). We then examine the role of cyclic asymmetry by considering equal asymmetry between species ($A_{12} = A_{23} = A_{31} = \bar{A} > 1$). We then investigate the combined role of niche overlap ($\rho_{12} = \rho_{23} = \rho_{31} = \rho$) and cyclic asymmetry (\bar{A}). Finally, we present more cases that break these symmetries, and provide code as a supplement for readers to explore further.

Pairwise coexistence versus founder control

Depending on the pairwise niche overlap among species, structural and dynamical stability can have a complex relationship (Figure 2). The left column of Figure 2a,c,e,g shows the feasibility regions of the three-species equilibrium (dark grey triangle) and of the three pairwise equilibria, with colour indicating their pairwise stability (coexistence in orange and founder control in lavender). See Appendix B for a detailed explanation of the construction and interpretation of these plots. The right column shows the outcome of competition. Note that we chose an especially symmetrical case for demonstration, where all the feasibility regions are centred on the centroid of the simplex ($r_1 = r_2 = r_3 = 1/3$); we will see below that this case has no cyclic asymmetry ($\bar{A} = 1$). There are four different combinations of stability between the pairs: 0 (Figure 2a,b), 1 (Figure 2c,d), 2 (Figure 2e,f) and all 3 (Figure 2g,h) pairs with founder control.

The distinction between the feasibility plots and the competitive outcome plots is immediately apparent (Figure 2) (see Appendix C for more details). Only in the first row (Figure 2a,b), where all three pairs can potentially coexist, does three-species feasibility translate into three-species coexistence (grey in both Figure 2a,b). In cases with more pairwise founder control (Figure 2c–h), the relationship between feasibility and competitive outcomes becomes more complex. Pairwise founder control impacts even the region where the three-species equilibrium is feasible (grey region in the centre, left column), where the competitive outcome is a variety of alternative stable states (striped regions, right column), not three-species coexistence. When all three species show founder control (Figure 2g,h), the competitive outcome at the centre of the simplex is a three-way founder control between the three monocultures (red, yellow and blue stripes in the centre). Surprisingly, this occurs over a much larger region than the grey feasibility region of the three-species equilibrium in the feasibility plot. Therefore, the competitive outcome in this case is not directly related to the feasibility of the three-species equilibrium.

Cyclic asymmetry and intransitivity

In pairwise competition, competitive asymmetry A_{ij} only recentres the range of absolute fitness differences R_{ij} that lead to coexistence or founder control (Equation 8). However, in three-species communities, this recentring is not completely possible when $\bar{A} \neq 1$.

When there is no cyclic asymmetry ($\bar{A} = 1$, Figures 2 and 3a,b), the stabilizing pairwise niche overlap plays the dominant role in determining the competition outcome. Each pair can coexist when the environment favours neither species in the pair. Similarly, the triplet can coexist stably when the environment is relatively balanced between all three species. The lack of cyclic asymmetry can

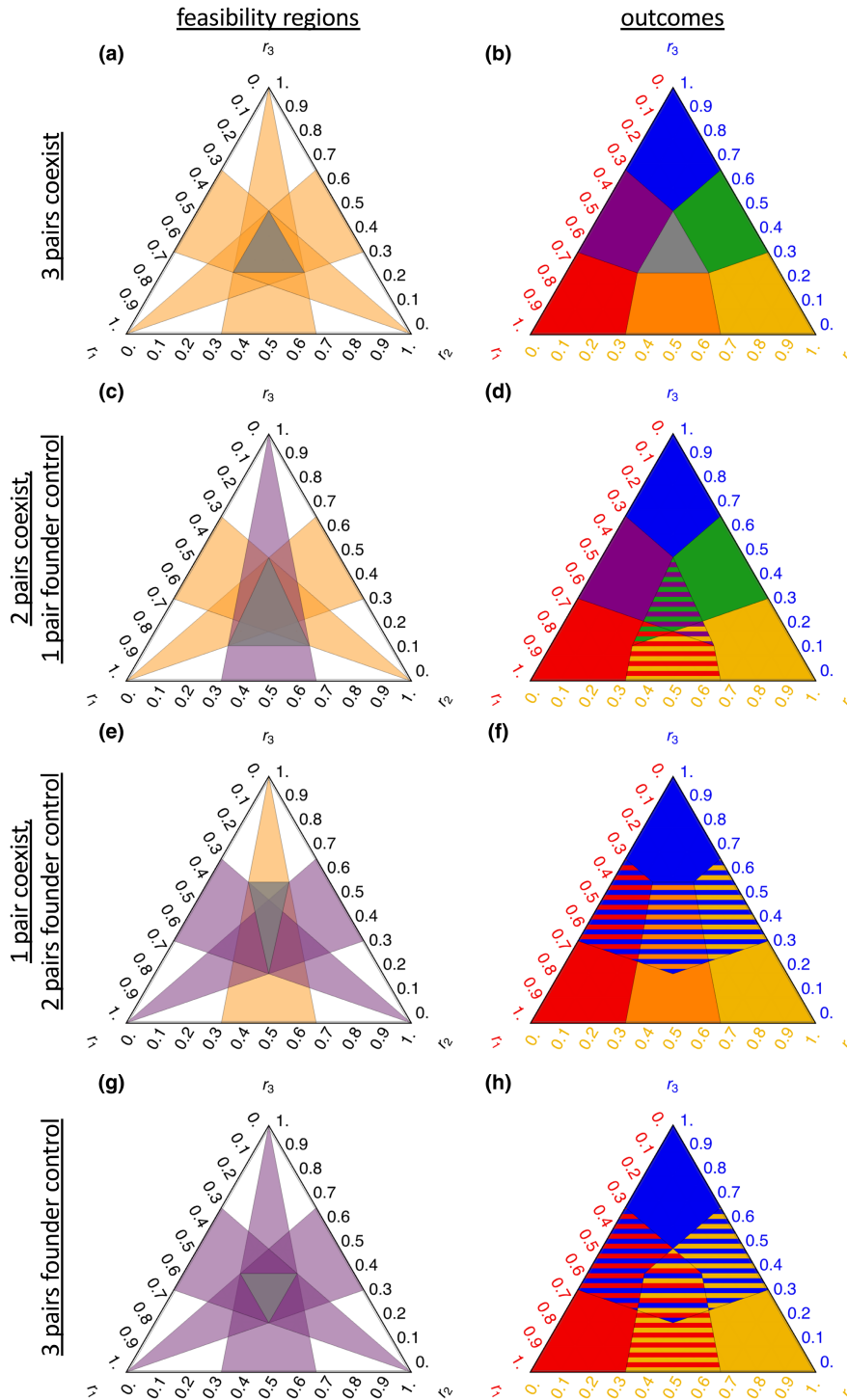


FIGURE 2 The effect of pairwise coexistence versus founder control on the outcome of competition. The left column shows the feasibility regions for the pairwise equilibria and their stability (stable in orange, unstable in lavender) and the feasibility regions for the three-species equilibrium (grey). The right column shows the corresponding competitive outcomes. The legend for the different colours for outcomes is shown in Figure 1, and the parameter values are provided in Appendix E. (a, b) All pairs coexist. (c, d) Two pairs coexist; one pair shows founder control. (e, f) One pair coexists; two pairs show founder control. (g, h) All pairs show founder control.

be seen in Figure 3a, where all three pairwise equilibria regions (orange triangles) intersect at the same location, maximizing their overlap. Consequently, the three-species equilibrium is both feasible (grey triangle, Figure 3a) and stable (grey triangle, Figure 3b) at the centre.

Intermediate cyclic asymmetry (Figure 3c,d) promotes the conditions for an intransitive rock–paper–scissors cycle: a parameter region where the three-species equilibrium is feasible but none of the pairwise equilibria are (shown with a dashed border in Figure 3c). However,

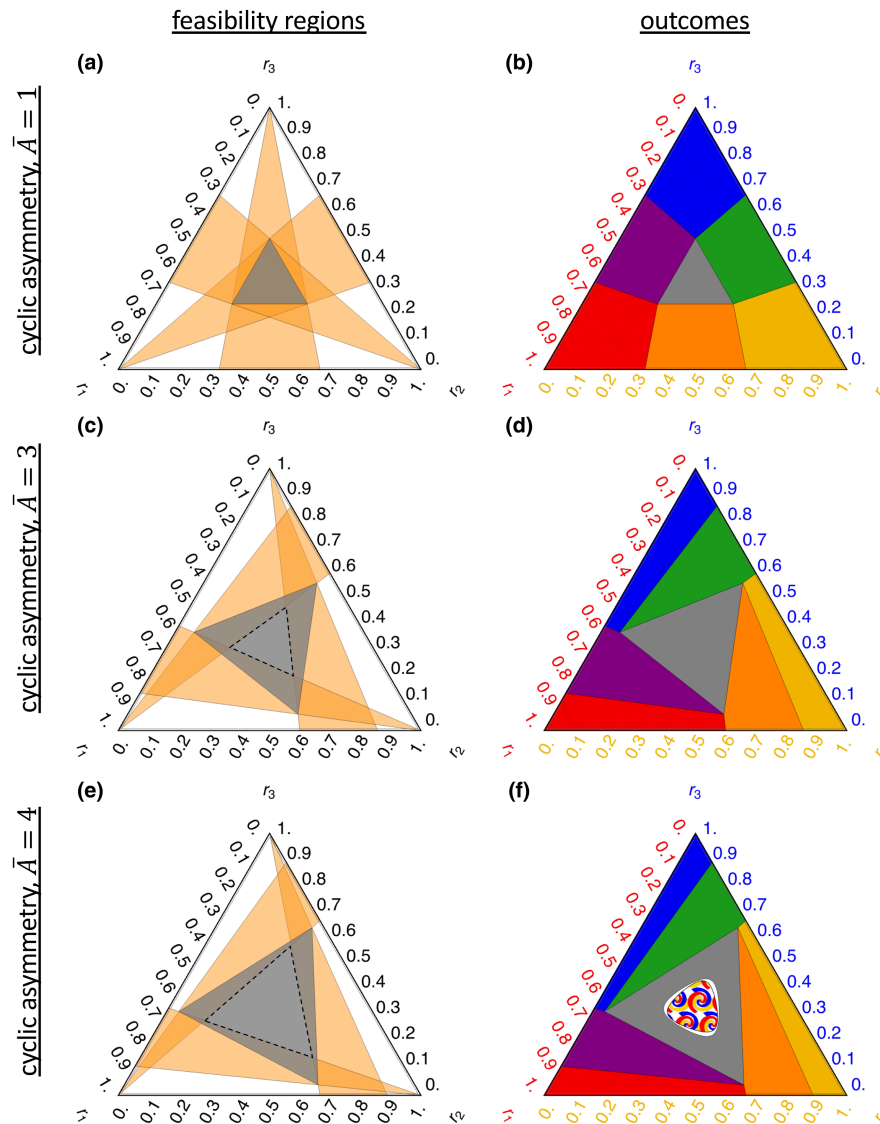


FIGURE 3 The effect of cyclic asymmetry on the outcome of competition. The left column shows the feasibility regions for the pairwise equilibria and the feasibility regions for the three-species equilibrium (grey). The right column shows the corresponding competitive outcomes. All pairs have identical niche overlap $\rho = 0.5$. The legend for the different colours for outcomes is shown in Figure 1 and the parameter values are provided in Appendix E. (a, b) When there is no cyclic asymmetry ($\bar{A} = 1$), the pairwise stability regions and the regions with different outcomes are all symmetrical. The central region where the three-species equilibrium is feasible (dark grey in a) leads to the stable coexistence of all three species (dark grey in b). (c, d) At intermediate levels of cyclic asymmetry ($\bar{A} = 3$), the pairwise stability regions are twisted. This gives rise to a range of parameters in the centre of c, where the three-species equilibrium is stable but all pairwise equilibria are not feasible (bounded by a dashed line). However, the competitive outcome continues to be a stable three-species equilibrium (dark grey region in d). (e, f) At high levels of cyclic asymmetry ($\bar{A} = 4$), the parameter region where the three-species equilibrium is stable but all pairwise equilibria are not becomes larger (central region in e). The competitive outcome at the centre of unit simplex switches to a mix of heteroclinic cycles (spirals), limit cycles (white) and stable three-species (dark grey) equilibrium.

cyclic asymmetry interacts with the low pairwise niche overlap so that the competitive outcome in this region remains stable three-species coexistence (grey region, Figure 3d). Graphically, the competitive asymmetry within each pair twists the orange feasibility regions away from the centroid of the simplex, representing the indirect positive effect of species 1 on species 3 due to inhibiting species 2.

At high cyclic asymmetry (Figure 3e,f), the orange pairwise feasibility regions twist even further, expanding the region where intransitivity occurs (Figure 3e).

For some values of the intrinsic growth rates, the three-species equilibrium loses stability, resulting in a stable heteroclinic cycle that is approached with ever-slower oscillations (Figure 4a). In natural communities, these cycles would result in monocultures due to finite population sizes. However, even at high cyclic asymmetry, the parameter regions with heteroclinic cycles are surrounded by regions of stable three-species coexistence (grey region in Figures 3f and 4c) due to the stabilizing pairwise niche overlaps in all pairs. In a narrow range of parameters in between stable equilibria and stable

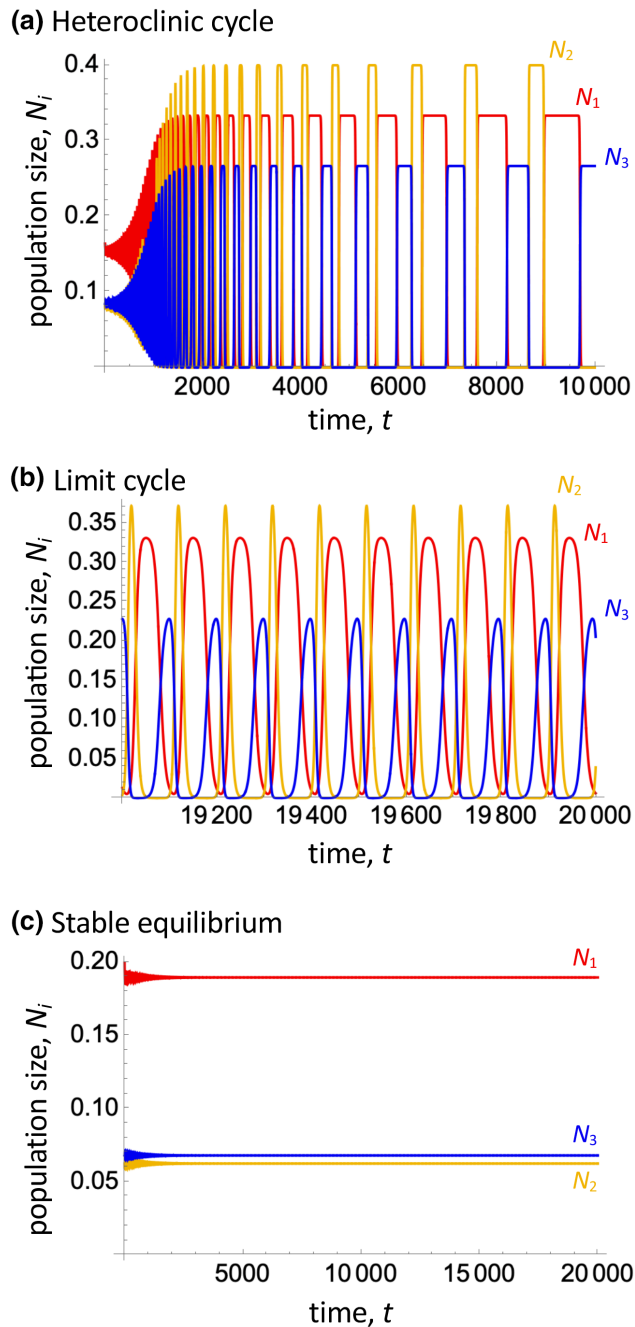


FIGURE 4 Population dynamics for three cases from Figure 3. (a) A heteroclinic cycle. (b) A limit cycle. (c) A stable equilibrium. Parameter values are provided in Appendix E.

heteroclinic cycles, there is a limit cycle where the three species oscillate with a fixed period (the narrow white region around the region with heteroclinic cycles in Figures 3f and 4b).

Interaction of cyclic asymmetry and niche overlap

In a triplet, higher cyclic asymmetry increases the proportion of environments where heteroclinic cycles occur

(Figure 3). How is this influenced by pairwise niche overlap and fitness imbalances? For a more complete picture of how these three quantities interact, we plotted a series of outcome plots simultaneously varying pairwise niche overlap and cyclic asymmetry (Figure 5). We omit cyclic asymmetry values lesser than one because the results are symmetric.

Read Figure 5 beginning at the centre of the bottom row. The case of no cyclic asymmetry ($\bar{A} = 1$) and complete niche overlap ($\rho = 1$) represents competition for a single resource: coexistence is impossible and the winner is the species with the highest r_i value (Tilman, 1985). Moving to the left represents decreasing niche overlap between species, which increases the likelihood of pairwise coexistence (left half of the bottom row). This is also a stabilizing influence on the triplet, where the stable three-species equilibrium is found in a region that increases in size with decreasing niche overlap, making the coexistence of all three species more likely. In contrast, increasing niche overlap between pairs destabilizes the triplet, resulting in no three-species coexistence. Further, the likelihood of alternative stable states increases due to the presence of founder control in the pairs, as can be seen in the increased area of the striped regions as niche overlap increases towards the right in the bottom row (Figure 5).

Next, return to $\rho = 1$, $\bar{A} = 1$ and now move up to see the role of cyclic asymmetry in isolation in the absence of niche overlap. As shown in Figure 3, increased cyclic asymmetry results in the development of a region of parameter space with heteroclinic cycles (spiral regions). Higher cyclic asymmetry leads to larger proportions of the environment where the competitive outcome is heteroclinic cycles. At extremely high cyclic asymmetry ($\bar{A} = 8$), competition results in heteroclinic cycles in almost all environments.

Overall, as in pairwise competition, low niche overlap stabilizes the triplet, while high niche overlap destabilizes it by creating alternative stable states. Cyclic asymmetry can destabilize the system in a different way, creating environments where heteroclinic cycles occur. How do these two forms of destabilization interact? At low values of niche overlap and high cyclic asymmetry, the stabilizing influence of low niche overlap counteracts the destabilizing effect of cyclic asymmetry (towards the left in the top row of Figure 5). Thus, the parameter space resulting in heteroclinic cycles reduces in area and is replaced by a stable three-species equilibrium. Hyper-niche-overlap ($\rho > 1$) also reduces the likelihood of heteroclinic cycles, albeit by replacing them with alternative stable states that are also destabilizing (towards the right in the top row of Figure 5). Figure S1 shows the stability of the symmetric $r_1 = r_2 = r_3 = 1/3$ equilibrium, as shown in Figure 1 of May and Leonard (1975), in terms of our parameters ρ and \bar{A} , which supports these conclusions.

For a more complete picture of the interaction of pairwise niche overlap and cyclic asymmetry on the likelihood of three-species coexistence, we plotted the proportion of the $r_1 + r_2 + r_3 = 1$ simplex that results in

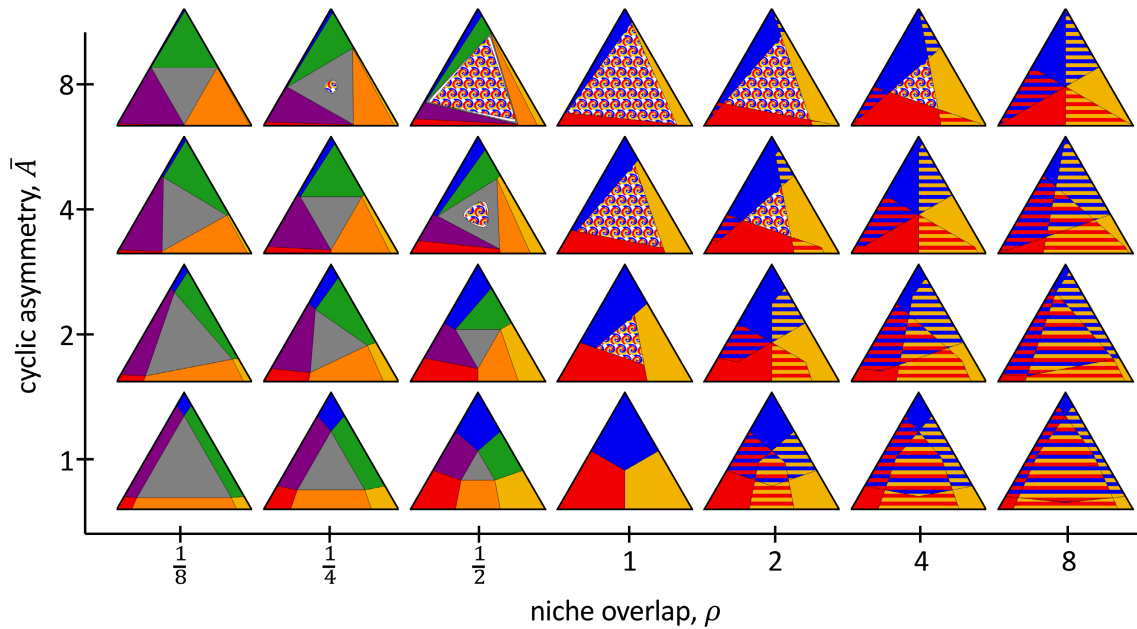


FIGURE 5 Competitive outcome as niche overlap, cyclic asymmetry and absolute fitness vary. The x-axis represents pairwise niche overlap, which is assumed to be the same for all three pairs. Niche overlap goes from very low (pairs can coexist) on the left to very high on the right (pairs can show founder control). The y-axis represents cyclic asymmetry in the triplet, which goes from non-existent to high. The legend for the different colours for outcomes is shown in Figure 1 and the parameter values are provided in Appendix E. Low niche overlap (bottom left corner) in the pairs stabilizes the community, leading to three-species coexistence. High niche overlap (bottom right corner) in the pairs leads to alternative stable states. Cyclic asymmetry, when combined with niche overlaps close to 1, destabilizes the community and leads to heteroclinic cycles.

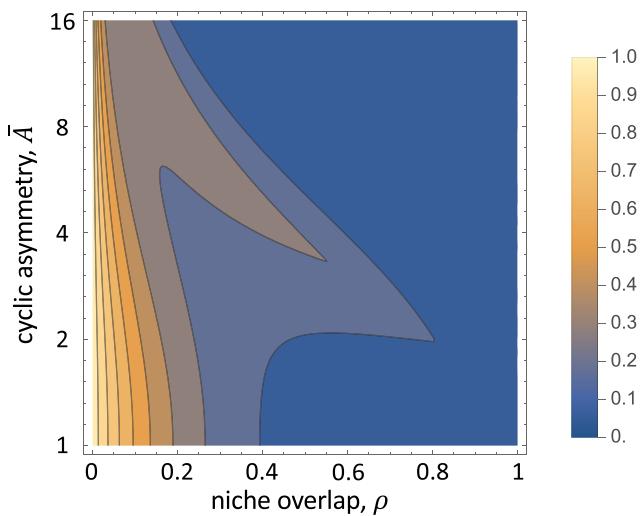


FIGURE 6 The interactive effect of pairwise niche overlap and cyclic asymmetry on the probability of three-species coexistence (the proportion of environments in the unit simplex $r_1 + r_2 + r_3 = 1$, resulting in three-species coexistence). Warmer colours represent higher proportions of environments, resulting in three-species coexistence.

stable three-species coexistence (Figure 6). The dependence of three-species coexistence on cyclic asymmetry and pairwise niche overlap is surprisingly complex. At low niche overlap ($\rho < 0.25$), increasing cyclic asymmetry decreases the likelihood of three-species coexistence. At intermediate niche overlap ($0.25 < \rho < 0.75$),

the likelihood of three-species coexistence is maximized at intermediate cyclic asymmetry. At higher niche overlap ($\rho > 0.75$), three-species coexistence is unlikely. In all cases, increasing cyclic asymmetry increases the proportion of environments that result in heteroclinic cycles.

Relaxing assumptions of symmetry

Aside from Figure 3, we have assumed that all three pairs within the triplet have the same niche overlap ($\rho_{12} = \rho_{23} = \rho_{31} = \rho$) and equal competitive asymmetry ($A_{12} = A_{23} = A_{31} = \bar{A}$). Thus, Figure 5 represents only a four-dimensional slice through the full eight-dimensional parameter space of the three-species LV competition model. We now relax these assumptions in two ways.

Numerical exploration

To illustrate some of the further possible outcomes of three-species competition, we break the symmetry of the ρ_{ij} 's by allowing one pair (1 and 3) to have a different niche overlap than the other two. We choose the third pair's niche overlap to be the reciprocal of the first two ($\rho_{12} = \rho_{23} = 1/\rho_{31}$), as to change the stability of the feasibility regions while keeping their extent unchanged (as in Figure 2). In Figure S2, we reconstruct the outcome

plots while varying both cyclic asymmetry and pairwise niche overlap. We find more complex transitions along outcomes. We find the same general result as in Figure 5, that heteroclinic cycles occur with balanced intrinsic growth rates, large cyclic asymmetry and intermediate niche overlap. We also identified novel outcomes, such as alternative stable states between one species and three-species coexistence (yellow–grey striped regions). Finally, we see that three-species coexistence can be stable even when one pair of species experiences founder control in isolation ($\rho > 1$) if there is also cyclic asymmetry (grey regions for $\bar{A} > 1$).

Recentring

Despite having three free parameters, the outcome of two-species LV competition can be described by only two quantities (relative fitness difference F_{ij} and niche overlap ρ_{ij}) by recentring the absolute fitness difference $R_{ij} = r_i / r_j$ by the competitive asymmetry A_{ij} (Equation 7). Can the dimensionality of three-species LV competition be reduced from its eight parameters in a similar way? The answer is a qualified “yes”: we can recover the feasibility regions completely and most of the outcomes, but the stability of the three-species equilibrium can change.

Our approach to recentring the growth rates is suggested by the pairwise coexistence conditions

$$\frac{1}{\rho_{ij}} > A_{ij} R_{ij} > \rho_{ij} \quad (9)$$

To isolate the effect of cyclic asymmetry $\bar{A} = \sqrt[3]{A_{12}A_{23}A_{31}}$ from other aspects of competitive asymmetry, we factor it out from the relative fitness difference $A_{ij}R_{ij}$:

$$\begin{aligned} \frac{1}{\rho_{ij}} &> \bar{A} \frac{A_{ij}^{2/3}}{A_{ki}^{1/3} A_{jk}^{1/3}} R_{ij} > \rho_{ij} \\ \frac{1}{\rho_{ij}} &> \bar{A} A'_{ij} R_{ij} > \rho_{ij} \end{aligned} \quad (10)$$

Note that $A'_{12}A'_{23}A'_{31} = 1$, so that \bar{A} captures all of the cyclic asymmetry of the triplet. Breaking up A'_{ij} as $A'_{ij} = \left(\frac{A_{ij}}{A_{ki}}\right)^{1/3} / \left(\frac{A_{jk}}{A_{ij}}\right)^{1/3}$, we see that by rescaling the r_i 's and using a different constraint on them:

$$r_1 \left(\frac{A_{12}}{A_{31}}\right)^{1/3} + r_2 \left(\frac{A_{23}}{A_{12}}\right)^{1/3} + r_3 \left(\frac{A_{31}}{A_{23}}\right)^{1/3} = 1 \quad (11)$$

effectively recentres the feasibility plots (see also Saavedra et al., 2017; Appendix S5).

Figures S3 and S4 illustrate the effect of this recentring procedure on feasibility regions and outcome plots. In both cases, the feasibility regions are identical to those with equal $A_{ij} = \bar{A}$ after recentring (Figures S3 and S4, compare c vs. e). The outcome plots are also largely the same after recentring (Figures S3 and S4, compare

d vs. f), with the exception of the stability region of the three-species coexistence equilibrium (grey vs. white regions in Figure S4d,f). The case with unequal asymmetries (Figure S4d) presents a new outcome: alternative stable states between three-species coexistence and a heteroclinic cycle, which we have verified numerically (Figure S5a,b), along with limit cycles in the white region of Figure S4d (Figure S5c). Recentring effectively causes the units of time in each species' equation to be different, therefore changing the parameter ranges of time-dependent quantities such as limit cycles but not of static quantities such as equilibria, which remain unaffected.

However, these residual effects of unequal asymmetries after recentring are largely irrelevant to the question of species persistence: triplets that coexist at a stable equilibrium or on a limit cycle still coexist, and a stable heteroclinic cycle still presents the risk of extinction in a finite world. Therefore, recentring effectively preserves the outcome of competition, although the dynamics may change. Thus, the outcome of three-species LV competition can be largely captured using six parameters: three pairwise niche overlaps, two rescaled fitness ratios and cyclic asymmetry \bar{A} .

DISCUSSION

Modern coexistence theory primarily relies on models of pairwise competition to understand species coexistence. However, the extent to which insights from pairwise models extend to more diverse communities remains unknown. In this study, we analysed a three-species competition model to demonstrate the limitations of applying insights from pairwise models to more diverse communities that lack symmetry (Chesson, 2000), as in the case of intransitive competition. Intransitivity is defined as a cyclic ranking of species' competitive ability, where no pair coexists but there is no strict competitive hierarchy. In our three-species setting, intransitivity is equivalent to a rock–paper–scissors configuration. Just as MCT does not incorporate non-hierarchical competition, existing studies of intransitivity do not consider cases of pairwise coexistence or founder control. Our framework extends MCT to three-species competition using three quantities: absolute fitness differences, pairwise niche overlap and cyclic asymmetry, which quantifies the potential for intransitivity. Together, these quantities determine the outcome of three-species competition (but possibly not the dynamics).

Among the three quantities determining the competition outcomes, only low pairwise niche overlap stabilizes the entire community. Hyper-niche-overlap ($\rho > 1$) destabilizes the community towards alternative stable states (Ke & Letten, 2018). Large fitness differences tend to result in the dominance of the species with the higher intrinsic growth rate, and perhaps counterintuitively, small relative fitness differences can promote heteroclinic cycles. Increasing cyclic asymmetry expands the parameter region where heteroclinic cycles are possible.

Intransitivity has often been thought of as a diversity-promoting force (Soliveres & Allan, 2018). In our three-species model, intransitivity occurs in the region between pairwise coexistence regions in feasibility plots, shown with dashed triangles in Figure 3c,e. As seen in the corresponding outcome plots, intransitivity sometimes leads to stable coexistence but can also result in heteroclinic cycles where species reach arbitrarily low densities (Figure 4a) and would go extinct in the real world (May & Leonard, 1975). In fact, this is always the case in the absence of niche differences ($\rho = 1$ in Figure 5; Figure S1). Therefore, intransitivity does not allow three-species coexistence by itself but can interact with niche differences to expand the size of the coexistence region (Figures 5 and 6). However, note that in contrast to our well-mixed system, in spatially extended systems, heteroclinic cycles can be stabilized through asynchronous fluctuations that prevent global extinction (Kerr et al., 2002; Laird & Schamp, 2006).

Since large fitness differences, high niche overlap and cyclic asymmetry all destabilize three-species communities, three-species coexistence only occurs in a limited proportion of environments in the model. Similar results can be seen across a range of empirical and theoretical work where communities only consist of a subset of the species pool (May, 1973; Medeiros et al., 2021; Song & Saavedra, 2018). Typically, regional species pools are fairly large, and the assembly process eliminates some species, resulting in a sub-community. Mathematically, this is an example of the ‘curse of dimensionality’. For all species to coexist in a high-dimensional system like a diverse community, every species has to be stabilized by the processes acting in the system. In contrast, destabilization in any of these species results in destabilization of the entire community.

By building on pairwise models and characterizing three-species competitive outcomes, our work naturally invites the question “what next?” The importance of intransitivity could be studied by measuring cyclic asymmetry in addition to fitness differences and pairwise niche overlap in natural communities. Godoy et al. (2017) found that intransitivity was uncommon in annual plant communities. Alternatively, resource-competition models could be used to illuminate the ecological mechanisms that lead to competitive asymmetry and intransitivity (Huisman & Weissing, 1999).

One theoretical extension would be to predator–prey and mutualistic interactions [see Bomze (1983, 1995) for a catalogue of outcomes in the general two-species Lotka–Volterra model]. Concerning diversity, incrementally increasing the number of species is clearly not a sustainable approach to understanding coexistence since model complexity increases too fast for a complete analysis to be feasible. However, the transition from two to three species is unique since it involves the addition of indirect effects (Appendix F) that result in a fundamentally different ecological process: intransitivity. Understanding three-species competition also allows us to use triplets instead of pairs as a unit while investigating diverse communities in the future. This gives us additional explanatory power

by accounting for intransitive competition. Finally, a range of other notable approaches to investigate coexistence in diverse communities exist: focusing on networks of species (Allesina & Levine, 2011; Allesina & Tang, 2012, 2015; May, 1973), the permanence of large communities (Hofbauer & Schreiber, 2022; Patel & Schreiber, 2018), trait-based approaches (Klausmeier et al., 2020) and techniques inspired by statistical mechanics (Advani et al., 2018; Barbier et al., 2018). Fruitfully combining these theoretical approaches with empirical work will further the coexistence research program.

AUTHOR CONTRIBUTIONS

RR, TK and CAK jointly developed the theory. RR performed initial analyses using code written by CAK and RR, and TK and CAK contributed substantially to further analyses. RR wrote the first draft of the manuscript, which TK and CAK revised. CAK obtained funding and supervised.

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DATA AVAILABILITY STATEMENT

The study uses no data. The code is available at <https://doi.org/10.5281/zenodo.10806689>.

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SUPPORTING INFORMATION

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