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1   **Competition modes determine ecosystem stability in rock–paper–scissors games**

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Abstract

Identification of the mechanisms which permit ecological communities to maintain high

levels of biodiversity is of both theoretical interest and practical importance. Intransitive

competition, in which there is no single superior competitor, is known to play an

important role in this problem. In this study, we undertake a systematic comparative

analysis of how different competition modes and ranges affect community stability in

paper-rock-scissors games. We confirm that short-ranged interactions, in combination

with cyclic competition, permits relatively stable coexistence. However, in contrast to

previous studies, we show that long-range interactions can also produce stable

communities. This stability emerges when competition interactions create asymmetries

in the opportunities for population growth depending on the abundance of the species.

Our findings demonstrate that small differences in the way species compete can

qualitatively change dynamic behaviors of the system, and therefore emphasize the

importance of correctly identifying these competition modes when designing

conservation actions.

Keywords: cyclically competing ecosystems; negative frequency dependence (NFD);

interaction modes; interaction range; symmetric and asymmetric competition.

1. Introduction

Exploring how a multitude of species can coexist in a community is a long-standing

issue in ecology [1-5]. Many mechanisms have been proposed (e.g. niche and neutral

theories), and significant progress has been made in understanding community

maintenance [2-7]. Among them, intransitive competition has been a classic paradigm to

explain species coexistence, as it can prevent the emergence of a dominant species [5,

7-12]. Moreover, there is a substantial body of empirical evidence which supports the

presence of intransitive competition across a broad range of natural communities [7, 9,

12-16].

The classic game of rock-paper-scissors provides a paradigmatic model for

intransitive competition. Models of communities with this sort of competition structure

typically produce neutrally stable limit cycles, in which species abundances oscillate

without converging to a stable equilibrium point. However, adding so-called

higher-order interactions (HOIs), i.e. interactions where the effect of one species on

another is modulated by a third, has been shown to stabilize these systems, resulting in

the convergence to an equilibrium steady state [17-20]. Furthermore, Reichenbach *et al.*

[21] have demonstrated the importance of population mobility in mediating ecosystem

stability in rock-paper-scissors games, specifically with low mobility promoting species

diversity while high mobility jeopardizing biodiversity. Similarly, it has been shown that

embedding such communities in space stabilizes their dynamics when species interact

only over short distances [22, 23]. When interactions are long-ranged, such

49   communities become unstable, producing large oscillations in species abundance and,

50   ultimately, stochastic extinctions [23-26]. This theoretical outcome has also been

51   confirmed in controlled microcosm experiments [9, 27]. Later, Szolnoki & Perc [28]

52   have additionally found that zealots are very effective in taming the amplitude of

53   oscillations arising from mobility and/or long-range interactions. Thus, these efforts

54   have greatly promoted our understanding of ecosystem stability and biodiversity

55   maintenance in spatial rock-paper-scissors games (see reviews in [29, 30] and

56   references therein).

57   However, these results do not tell the full story. In a theoretical study, Laird and

58   Schamp [11] found that short-range intransitive competition reduced community

59   diversity compared to long-range competition. This suggests the existence of an

60   opposed mechanism which can stabilize cyclic competition at longer spatial scales.

61   Rojas-Echenique & Allesina [31] suggest a candidate for this mechanism. Specifically,

62   where the spatial interaction rules are asymmetric, species fitness can vary depending

63   on its abundance, stabilizing the community for long-range interactions. Whether this

64   mechanism applies to other competition rules (e.g. competing for an empty site [19, 23])

65   remains unclear. Additionally, existing analysis of the effects of competition mode and

66   range on community stability is fragmented, with specific cases being considered in

67   separate studies. In this study, we seek to address this gap, by undertaking a systematic

68   comparative analysis of community stability using four typical competition modes

69   across a wide range of spatial scales.

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70   **2. Methods**

71   We consider a system of 3 species in a rock-paper-scissors game, with a large fixed

72   number of individuals (*N*) arranged in a 2D-lattice (i.e. regular distribution of

73   individuals). Each site can only accommodate one individual. Similar to previous

74   studies [10, 11, 31], we simply assume the competitive matrix

75   $\mathbf{H} = \begin{bmatrix} 0 & 0 & 1 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix}$,

76   with elements H_{ij} denoting the probability of species *i* winning against species *j*. In

77   particular, when there is an interspecific competition event occurring between species *i*

78   and *j*, H_{ij}=1 represents that species *i* is always the winner while species *j* being the loser.

79   When members of the same species compete, neither has an advantage [32]. Thus, we

80   set the diagonal elements H_{ii}=0, i.e. disregarding intraspecific competition throughout.

81   Such a simple competition matrix **H** can avoid the enormous numerical difficulties we

82   face at the specific matrix where the values of H_{ij} are highly heterogeneous [33].

83   We perform simulations of the community dynamics as follows: (1) we have a

84   square lattice of *N*= *L*×*L*=100×100 sites (or 200×200 sites in Fig. S1, *Appendix*) with

85   periodic boundaries; (2) we populate the lattice with individuals randomly drawn from

86   three species; (3) In each time step, we perform a competition event using the four

87   interaction modes specified below; (4) we repeat step (3) for a long time, finding that

88   10,000 generations (i.e. 1×10^8 steps) are sufficient for those systems with linear size

89   *L*=100 (while 20,000 generations for *L*=200) to achieve the steady state; (5) we record

90   the number of individuals for each species and their spatial patterns at every generation.

91   To explore the effect of competition range on community stability, we consider a

92   variety of interaction ranges. We define these ranges in terms of the number of sites that

93   are considered to be in the neighbourhood of a focal site. Specifically, at the extremes of

94   this scale we have: *local* interactions, for which the neighbourhood consists of the four

95   sites directly adjacent to a focal site; and *global* interactions, for which the

96   neighbourhood consists of all sites within the lattice. Between these extremes, a range

97   of X means that the X sites closest to the focal site constitute the neighbourhood.

98   **Mode 1:** In each time step, a focal site is randomly selected along with four sites

99   within interaction range of it. According to the competitive matrix **H**, we then check if

100   any of the individuals of these four invader sites can outcompete the resident of the

101   focal site: (i) if none of them can outcompete the resident, then the resident is

102   unchanged; (ii) if there is at least one superior competitor (relative to the focal resident),

103   then we randomly select one of the superior competitors to replace the focal resident.

104   Note for local competition, the invader sites are the four sites directly adjacent to the

105   focal site. This algorithm is similar to that used by Laird & Schamp [11].

106   **Mode 2:** This type of interaction is similar to Mode 1. The only difference is that if

107   none of the invaders can outcompete the focal resident, then one of them is chosen at

108   random to be replaced by the resident of the focal site.

109   **Mode 3:** In each step, the resident of a randomly chosen site dies. Two invader

110   sites are chosen randomly within the interaction range to compete for the empty site,

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111   with the winner occupying this site. Note for local competition, the invader sites are

112   chosen randomly from the four directly adjacent sites. This algorithm is similar to that

113   used by Grilli *et al.* [19] and Calleja-Solanas *et al.* [23].

114   **Mode 4:** In each time step, two sites within interaction range are chosen at random.

115   If one of the two individuals is able to outcompete the other, then the losing individual

116   is replaced by the winner [34]. Note that for local competition, the sites must be directly

117   adjacent. This algorithm is similar to that often used by previous studies [31, 35-39].

118   **3. Results**

119   We begin by investigating the temporal population dynamics of this three-species

120   system with linear size L=100 (Fig. 1) and L=200 (Fig. S1 in *Appendix*). Species

121   abundances fluctuate around the equilibrium point $\rho^* = \left(\frac{1}{3}, \frac{1}{3}, \frac{1}{3}\right)$, as is expected in a

122   stochastic rock-paper-scissors system. These fluctuations have an underlying structure;

123   in particular, they form loops around ρ^* in phase space (Fig. 1I-P). These loops result

124   from the succession cycles which are a typical characteristic of communities with

125   rock-paper-scissors games. A species increases in abundance by displacing the species

126   which it outcompetes and then declines as it is displaced in turn by the species which

127   outcompetes it.

128   The mode and range of competition affect the magnitude of these fluctuations. With

129   local competition, the variation in fluctuation size among the four interaction modes is

130   small (Fig. 1A-D). Mode 1 produces the smallest fluctuations (Coefficient of Variation

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131   C.V.=0.034), while Modes 2-4 produce somewhat larger fluctuations (with C.V.≈0.087);

132   in all cases the system remains close to the equilibrium point. In contrast, global

133   competition may yield a large or small variation in fluctuation size, depending on the

134   interaction mode. Specifically, modes 1 & 2 (Fig. 1E-F & M-N) produce small

135   fluctuations (C.V.=0.02 and 0.027 respectively) comparable to, or even smaller than

136   those obtained under local competition. Under Modes 3 & 4 (Fig. 1G-H & O-P),

137   fluctuations become very large, and stochastic extinctions occur, eventually leading to

138   monoculture.

139   Competition mode and range also influence the spatial organization of the

140   community (Fig. 2). With local competition, the species aggregate into spatial clusters

141   excluding the other species from these regions of space. The cluster size can be

142   measured using the intraspecific clumping degree, i.e. the density of pairs of adjacent

143   sites occupied by the same species is divided by the global density of that species (see

144   Fig. S2 in *Appendix*). These clusters are relatively small for Mode 1 but are clearly

145   identifiable for Modes 2-4. By contrast, with global competition, no spatial

146   self-organization emerges, instead the species remain well-mixed. Fluctuations in

147   cluster sizes mirror those seen for species abundances, with small fluctuations for local

148   competition and global competition under Modes 1 & 2 while large fluctuations for

149   global competition under Modes 3 & 4 (Fig. S2 in *Appendix*).

150   The two competition ranges (i.e. the number of neighbours surrounding a focal site)

151   considered so far lie at the two extremes of interaction range. We observe that

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152   competition mode influences how the magnitude of fluctuations in abundance varies

153   between these extremes (Fig. 3). For Modes 1 & 2, fluctuation size decreases

154   monotonically but later levels off, as interaction range increases. In contrast, for Modes

155   3 & 4, fluctuations generally increase in size as interaction range increases, though the

156   minimum fluctuation size for Mode 4 is achieved at an intermediate interaction range of

157   around 8 neighbours for a focal site. We also note that Modes 1 & 3 generally produce

158   the smallest and largest fluctuations in population abundances respectively.

159   Finally, we observe that increasing the number of available habitat sites generally

160   increases community stability (Fig. 4). Specifically, with local competition, increasing

161   system size results in a linear decline in the magnitude of fluctuations in abundance

162   regardless of competition mode (Fig. 4A). For global competition, the same linear

163   decline in fluctuation magnitude is obtained for Modes 1 and 2 (Fig. 4B). Under Modes

164   3 & 4, succession cycles continue to expand and, ultimately, result in monoculture due

165   to stochastic extinctions. However, it takes longer for these extinctions to occur in larger

166   systems.

167   **4. Discussion**

168   Our results confirm that cyclic dominance alone is not sufficient to maintain

169   biodiversity [9, 27]. In particular, despite a cyclic competition structure, global

170   competition with Modes 3 and 4 results in monoculture in the long term (Fig. 1; Fig. S1

171   in *Appendix*). Previous empirical and theoretical studies concluded that local

172   interactions promote ecosystem stability relative to global competition, in line with our

173 predictions in Modes 3 & 4. However, in stark contrast to this conclusion, we find that

174 with Modes 1 & 2, fluctuations decrease in magnitude for global competition,

175 producing a more stable community. The rule governing competition appears to play an

176 important role in determining how the interaction range affects community stability. In

177 particular, small changes in the way competitors interact can reverse how local vs.

178 global competition modify ecosystem stability. As such, to avoid misleading predictions,

179 the competition rules must be identified and accurately characterized before modelling a

180 given community.

181   Local competition permits the emergence of self-organized spatial structure within

182 the habitat which is not possible under global competition (Fig. 2). Specifically, when

183 interactions are short range, chance aggregations of a single species tend to expand as: 1)

184 the species with the highest local density has the greatest chance to occupy nearby sites;

185 and 2) intraspecific competition events do not change the composition of the local area.

186 This results in the formation of relatively large conspecific clusters. In turn, this slows

187 down the community dynamics (Fig. S3 in *Appendix*), as only competition events

188 occurring at the boundaries of these clusters result in changes in species abundances and

189 such boundaries represent a relatively small proportion of the total habitat. With global

190 competition, all sites are equally far apart, as such, the results of competition are

191 predicted by the total, rather than the local, abundances of each species. This means that,

192 when one species gains a population advantage, it will tend to increase in abundance by

193 displacing its weaker competitor. However, this reduces competition pressure on its

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194 stronger competitor, which is then able to increase in abundance by displacing it in turn.

195 Thus global competition produces global scale succession cycles and large fluctuations

196 in abundances.

197   However, this does not explain the stability of communities under Modes 1 & 2

198 with long-range interactions. This can be attributed to the emergence of frequency

199 dependence selection under these competition modes. We find that, under Modes 1 & 2,

200 the average fitness of individuals decreases as they become more common (negative

201 frequency dependence, NFD; see *System Analysis* in *Appendix*). In particular, we

202 analyze the expected growth of a given species relative to its abundance in a simplified

203 system with global competition. As shown in Fig. S4 (*Appendix*), Modes 1 & 2 induce

204 NFD, i.e. the expected growth is positive when species abundance is below the

205 equilibrium level (1/3) and negative when species abundance is above this level. In

206 contrast, Modes 3 & 4 do not induce NFD, instead the expected growth is always equal

207 to zero regardless of species abundances. NFD acts as a restoring force; by reducing the

208 growth rate of any species which becomes dominant, it damps oscillations and biases

209 the system dynamics towards returning to the equilibrium state.

210   We note further that the effect of NFD is stronger for longer range interactions.

211 This results, again, from the formation of conspecific clusters for short range

212 competition. Recall that, when competition is localized, species abundances change

213 only at the boundary of these clusters. Since the majority of sites occupied by a species

214 are likely to lie within a cluster, they are protected from competition and so do not

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215   experience NFD as noted by Rojas-Echenique & Allesina [31]. Our results suggest that

216   NFD plays a greater role in stabilizing the community dynamics than the formation of

217   conspecific clusters. In particular, variation around the equilibrium state is lower with

218   global competition (permitting NFD) than with local competition (permitting

219   conspecific cluster formation) for Modes 1 & 2. This contradicts the claim that reducing

220   the range of species interaction is always beneficial to community stability [9, 21, 23].

221   The emergence of negative frequency dependence arises from the symmetry, or

222   asymmetry, of the competition rules. In particular, Modes 3 and 4 permit only pairwise

223   interactions, which are inherently symmetric in the rock-paper-scissors game. This

224   means that, a given species wins half of its interactions with other species and loses the

225   other half. By contrast, Modes 1 & 2 allow interactions to occur between the occupants

226   of five sites (one focal individual competing with four competitors). This benefits

227   species at low abundance and disadvantages those at high abundance. Specifically, this

228   rule gives a species with low abundance more frequent opportunities to compete than it

229   would obtain under a pairwise competition rule. This can allow its population to grow

230   quickly if the species it outcompetes is high abundance. By contrast, a high abundance

231   species is involved in proportionately fewer competition events than it would be under a

232   pairwise competition rule. Note that this asymmetry is stronger for Mode 1 (i.e. higher

233   NFD) than for Mode 2 (Fig. S4, *Appendix*), explaining why Mode 1 produces the most

234   stable communities for long-range competition.

235   It seems likely that different types of real-world ecosystems will correspond to

236   different interaction modes and scales. Asymmetric long-range interactions, like Modes

237   1 & 2, might be more appropriate for animal communities, where competition is more

238   diffuse. On the other hand, where individuals compete directly for substrate on which to

239   grow, and can grow over a competitor (e.g. lichens, corals or sponges), a symmetric

240   short-range interaction, like Mode 4, would be more appropriate. Similarly, Mode 3

241   might be appropriate to describe competition in forests, where the death of an individual

242   creates a gap in the canopy for which seedlings compete. In this case, the interaction

243   range would depend on the range of seed dispersal in the community. Despite the

244   diversity of possible applications, microbial experiments would be most appropriate to

245   test our modelling predictions, as they are easy to control and manipulate [14]. In

246   particular, microcosm experiments have the key advantage that the rapid microbial

247   reproduction allows multigenerational community dynamics to be studied within short

248   time frames. For instance, using toxin-producing (colicinogenic) *E. coli* to construct the

249   rock-paper-scissors system has proved useful for studying the generation and

250   maintenance of biodiversity [9].

251   This study adopts a simple lattice-structured model where three species with

252   rock-paper-scissors games compete for space under diverse interaction modes and

253   ranges. We find that competition rules determine the effect of interaction range on

254   ecosystem stability. Specifically, where spatial competition is limited to nearest

255   neighbours, the formation of conspecific clusters leads to more stable species

256   coexistence. This is in good agreement with empirical evidence that the self-organizing

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257   patterns created by local competition play a vital role in maintaining biodiversity [9, 22,

258   27]. However, asymmetry induced by higher-order interactions can induce negative

259   frequency dependence in competition outcomes, thereby stabilizing communities with

260   long-range interactions. This result is in contrast to prior studies which omitted this

261   mechanism and consequently concluded that long-range interactions were always

262   destabilizing. Our findings highlight the importance of identifying the modes of

263   competition present in an ecosystem prior to developing models for it, as apparently

264   small differences in these modes can produce qualitatively different system behaviors.

265   **Declaration of interests**

266   The authors declare that they have no known competing financial interests or personal

267   relationships that could have appeared to influence the work reported in this paper.

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273   **Data accessibility statement**

274   This theoretical study has no data.

275   **Supplementary materials**

276   *Appendix* is available for this manuscript.

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380

381   **Figure captions**

382   **Figure 1.** Panels (A-H): Dynamics of the abundance of a 3-species system in

383   rock-paper-scissors games, comparing different interaction modes under both local and

384   global competition. In each panel, the ecosystem is represented by a 2D-lattice of linear

385   size $L=100$ ($N=L\times L=10^4$ sites). Panels (I-P): Trajectories in the phase space represented

386   by the 3-simplex (sum of three species' abundances equal to one) with different

387   interaction modes and ranges (local and global), corresponding to the dynamics of the

388   panels (A-H). The colour bar represents time evolution (generations). Larger

389   oscillations around the equilibrium point cover boarder areas, indicating a more

390   unstable system.

391   **Figure 2.** Snapshots of the spatial organization of a 3-species ecosystem at the 1000th

392   generation in a 2D-lattice of linear size $L=100$ ($N=L\times L=10^4$ sites) for different

393   competition modes under local and global interactions. Individuals of each species are

394   painted in a different color. Panels (A-D): local competition within the four nearest

395   neighbours. Panels (E-H): global competition across the whole lattice.

396   **Figure 3.** Effect of interaction range (i.e. increasing the number of neighbours for each

397   site) on ecosystem stability (defined as the coefficient of variation C.V. in the size of

398   fluctuations in species abundances) in a 3-species ecosystem with a total number of

399     $N=L^2=10^4$ individuals, again under different competition modes (see *Methods*). The

400   points represent the mean of 20 replicates with standard deviation (error bar).

21

401   **Figure 4.** Effect of system size ($N=L^2$) on ecosystem stability under local and global

402   competition of three species in four different interaction modes. Stability is

403   characterized by the coefficient of variation (C.V.) in fluctuations around the mean of

404   species abundances, or the time (generations) required for the first species being extinct.

405   As such, higher C.V. or less time required for the first species extinction indicates a

406   more unstable ecosystem. Each point is the mean of 20 replicates (error bar – standard

407   deviation).

Figure 1
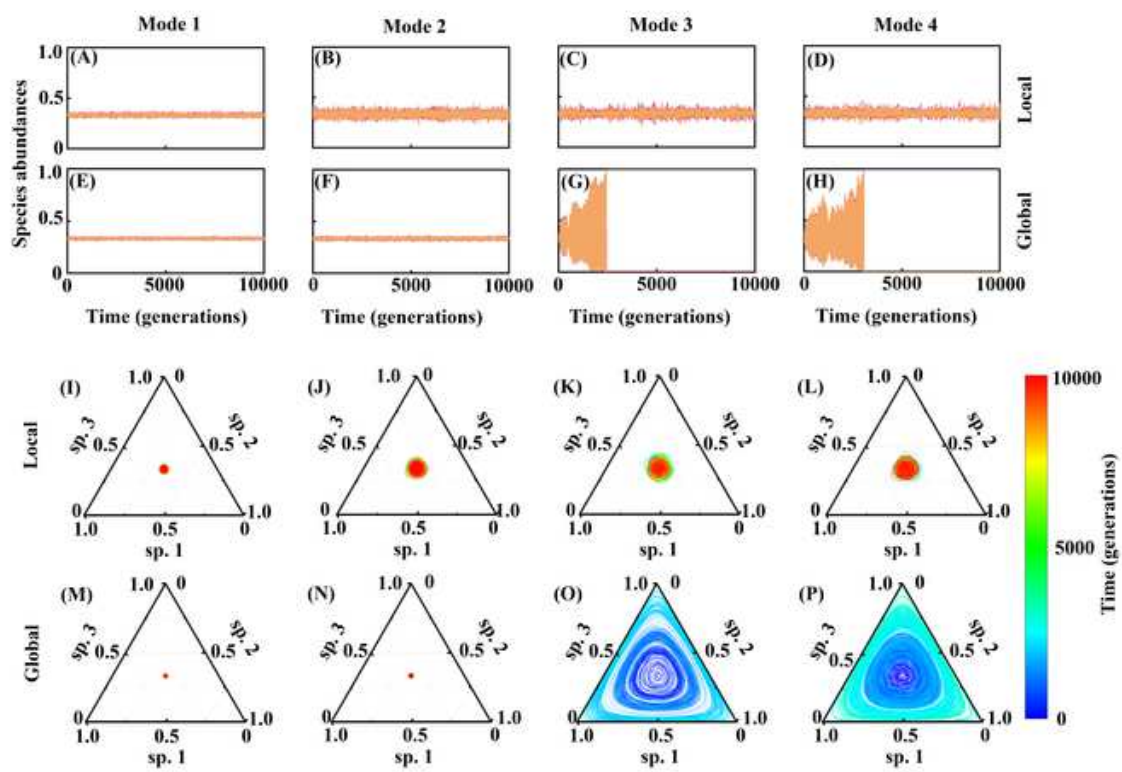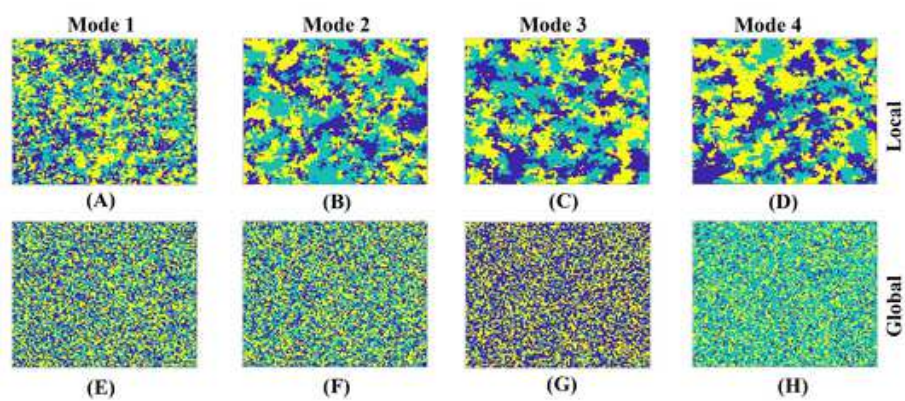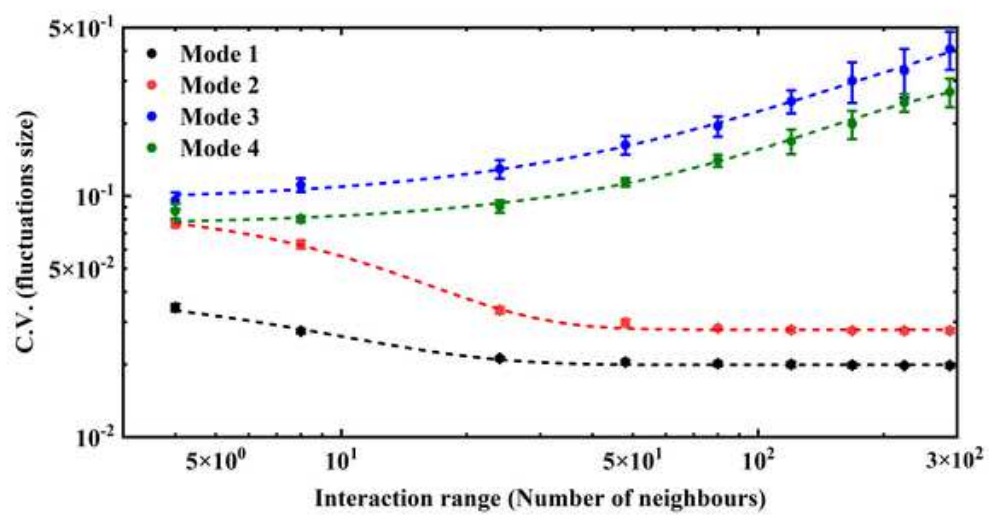
Figure 2

Figure 3

Figure 4
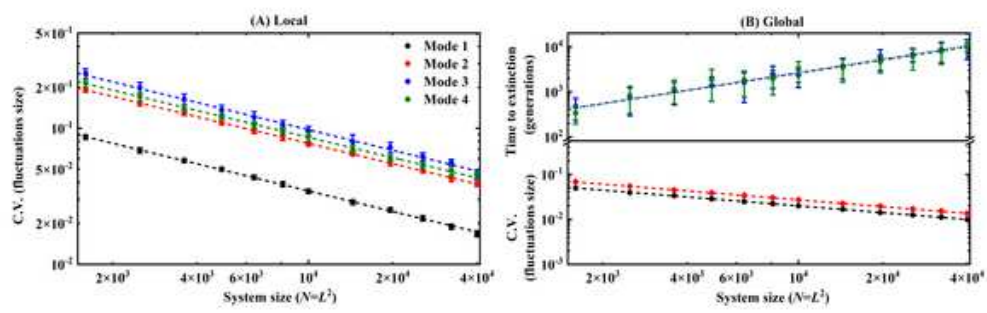
Cover Letter

Journal name: Physica A: Statistical Mechanics and its Applications
Manuscript ID: PHYSA-22659
Title: Competition modes determine ecosystem stability in rock-paper-scissors games

Dear Prof. Dr. Kenneth A. Dawson,

Thank you for giving us the opportunity to revise this manuscript. We have addressed the comments from both reviewers, and list the responses and corrections in *Response to Reviewers*.

In *Response to Reviewers*, we additionally submit a *revised version with track changes* in which we have inserted line numbers ourselves. Using these line numbers, we indicate the exact positions of all changes.

The manuscript has been resubmitted to your journal. We thank you for the helpful comments and look forward to your response.

Yours sincerely,
Jinbao Liao* on behalf of other co-authors
*Corresponding author: Dr. Jinbao Liao (Email: jinbaoliao@163.com)

Highlights

- We compare system stability among four interaction modes in cyclic competition

- We find that long-ranged competition can also produce stable coexistence

- Small differences in interaction modes qualitatively change dynamic behaviors

- We emphasize the importance of correctly identifying species competition modes

Credit author statement:

Zeyu Zhang: Methodology, Software, Data curation, Visualization, Investigation.

Daniel Bearup: Writing - Review & Editing.

Guanming Guo: Formal analysis, Software, Visualization.

Helin Zhang: Formal analysis, Software, Visualization.

Jinbao Liao: Conceptualization, Methodology, Formal analysis, Supervision, Funding acquisition, Writing- Original draft preparation.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: