

# Rock-Paper-Scissor Dynamics and Intransitive Competition link Ecology and Evolution

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## Abstract

Rock-paper-scissors (RPS) dynamics have been shown to affect the evolutionary relationships within populations. These processes are analogous to the ways in which intransitive competition modifies ecological outcomes and the co-existence between species within communities. Here we explore the similarities between rock-paper-scissor dynamics and intransitive competition and how this link opens new avenues of research into eco-evolutionary processes. Intransitivity can drive the stable coexistence of phenotypes within species, as well as the diversity of species within communities. In addition, the links between these dynamics highlight possible feedback mechanisms that might operate across these evolutionary and ecological scales. Using simulations, we show that greater intraspecific intransitivity within a population can lead greater levels of intransitivity at the community-level, with direct implications for community diversity and stability. As such, RPS dynamics and intransitivity can serve as an ideal conceptual framework to understand the feedback mechanisms that drive diversity across evolutionary and ecological scales.

Dear Dr. Thrall,

We are pleased to be submitting our *Perspectives* paper for the Ecology Letters special issue “Exploring the Border between Ecology and Evolution”. We were in correspondence with Dr. Hello and yourself in May and were invited to submit this manuscript. We thank you for your time and consideration.

Rock-paper-scissors dynamics have been shown to affect the evolutionary dynamics at play within species and populations and are analogous to the ways in which intransitive competition modifies competitive outcomes and the co-existence of species. While these processes are studied by both ecologists and evolutionary biologists in a growing body of literature, there is an absence of research into how these processes may be working simultaneously across both ecological and evolutionary scales. The continued separation of ecological and evolutionary research has led to an incomplete and fragmented understanding of both rock-paper-scissor dynamics and intransitive competition.

In our *Perspectives* article we explore the similarities between rock-paper-scissor dynamics and intransitive competition and how this link opens new avenues of research into eco-evolutionary processes. We begin by investigating how rock-paper-scissor dynamics and intransitive competition have each been used in past research to explore the diversity and stability of systems. In particular, intransitive dynamics have been shown to drive the stable coexistence of different phenotypes within species. At the same time, these dynamics clearly operate at the community level to maintain diversity across species. In doing so, we argue that this phenomenon (intransitivity) occurs simultaneously in both ecological and evolutionary contexts, and represents an exciting new avenue of research linking these disciplines. Our review of the literature highlights not only the presence of intransitive dynamics in both ecological and evolutionary contexts, but

the potential existence of feedback mechanisms that operate between them. Using simulations adapted from Maynard et al. (2019), we provide mathematical support for the idea that greater intraspecific intransitivity between phenotypes within a population can lead to greater levels of intransitivity between species at the community-level, with direct implications for community diversity and stability.

**Novelty of this work:** This is the first paper that explicitly makes this connection, and we hope that our conceptual framework will strengthen our understanding of how non-hierarchical interactions shape both evolutionary and ecological outcomes. We provide promising directions for future research and our work creates a path towards an improved interpretation of natural systems that is more dynamic, integrative, and holistic.

We hope that you would consider this for possible publication in Ecology Letters. No part of this has been submitted elsewhere.

Yours sincerely,

Giacomo Delgado

Rock-Paper-Scissor Dynamics and Intransitive Competition link Ecology and Evolution

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Abstract

Rock-paper-scissors (RPS) dynamics have been shown to affect the evolutionary relationships within populations. These processes are analogous to the ways in which intransitive competition modifies ecological outcomes and the co-existence between species within communities. Here we explore the similarities between rock-paper-scissor dynamics and intransitive competition and how this link opens new avenues of research into eco-evolutionary processes. Intransitivity can drive the stable coexistence of phenotypes within species, as well as the diversity of species within communities. In addition, the links between these dynamics highlight possible feedback mechanisms that might operate across these evolutionary and ecological scales. Using simulations, we show that greater intraspecific intransitivity within a population can lead greater levels of

intransitivity at the community-level, with direct implications for community diversity and stability. As such, RPS dynamics and intransitivity can serve as an ideal conceptual framework to understand the feedback mechanisms that drive diversity across evolutionary and ecological scales.

## INTRODUCTION

In nature, systems that lack a purely hierarchical structure can mimic the children’s game Rock-Paper-Scissors (RPS). In this analogy, there are three possible “strategies” each of which “beats” one other; rock beats scissors, scissors beat paper and paper beats rock (Figure 1a). A system like this is said to be perfectly intransitive and lacks a single best competitor. Due to this inherent lack of hierarchy, RPS dynamics and intransitive interactions can lead to stable (albeit dynamic) co-existence in a population of phenotypes of a single species (Sinervo and Lively 1996) and in communities of different species (May and Leonard 1975, Buss and Jackson 1979).

In the late 20<sup>th</sup> century, evolutionary biologists described a unique oscillating population dynamic in a natural system (Sinervo and Lively 1996). Coined “Rock-Paper-Scissors” (RPS) dynamics these systems give rise to the development of distinct evolutionary trajectories (Sinervo and Lively 1996, Gray and McKinnon 2006). Within a population, RPS dynamics have the potential to increase genetic diversity (San-Jose et al. 2014, Huang et al. 2012), genetic stability (Liao et al. 2019), and even lead to speciation (Gray and McKinnon 2006). At the same time, ecologists noticed that competitive interactions among species can also be highly intransitive (May and Leonard 1975, Buss and Jackson 1979) and that these interactions increase the stability and even diversity of their communities (Gallien et al. 2017, Maynard et al. 2017). By ensuring that no single species dominates, such intransitive interactions can help to maintain co-existence of competitors (Buss and Jackson 1979, Soliveres et al. 2015, Soliveres et al. 2018, Gallien et al. 2017), encourage parasite and host co-evolution (Cameron et al. 2009, Liao et al. 2019) and give insights into entire community assemblages (Soliveres and Allan 2018, Levine et al. 2017). As extensions of both game theory and negative frequency density-dependent selection, these patterns have broad implications for the maintenance of diversity at both evolutionary and ecological scales. Moreover, it is likely that these ecological and evolutionary processes may be working synergistically to shape and stabilize natural systems in a wide variety of contexts.

Ecology and evolution have largely remained two separate disciplines with experts in either field leveraging unique explanatory models, invoking their own theories, and publishing in separate journals. However, with the development of increasingly sophisticated genetic analysis tools at the end of the 20<sup>th</sup> century, a growing body of research suggested that evolutionary dynamics can take place over ecologically relevant timescales (Thompson 1998, Hairston et al. 2005, Hendry and Kinnison 1999). This “rapid evolution” suggested that genetic changes could happen quickly enough to affect ecological outcomes, potentially driving feedbacks to influence evolutionary dynamics again in turn (Pelletier et al. 2009, Garant et al. 2007). Despite a large amount of interest in these “Eco-evolutionary feedbacks” serious questions, issues and knowledge gaps remain (Hendry 2019). As such, there remains a need for the development of conceptual frameworks that leverage both ecological and evolutionary theory to understand the diversity and stability of natural systems under current and future climate scenarios. Given the highly dynamic, integrative, and stabilizing nature of intransitive systems across both ecology and evolution, we propose that intransitivity may provide a valuable framework to study eco-evolutionary dynamics in natural systems.

At their most basic level RPS dynamics and intransitive interactions, whether working within populations or across communities, help to explain the incredible diversity of life, a goal that ecologists and evolutionary biologists both share. However, perhaps even more importantly, they represent unique mathematical modeling approaches that go beyond pair-wise interactions and hierarchical models. In addition, the potential for eco-evolutionary feedbacks that operate to promote diversity within and across species mean that intransitive dynamics represent a wealth of possible new approaches to studying stability mechanisms within natural systems. Here, we propose that RPS dynamics and intransitive competition work in tandem to shape populations and communities. In this context, we review the development of mathematical frameworks (Allesina and Levine 2011, May and Leonard 1975, Vandermeer 2011, Laird and Champ 2018) and ecological tools to study intransitivity across populations and communities, highlighting that the similarities across fields

may represent an ideal opportunity for establishing feedbacks between ecology and evolution. We use model simulations adapted from Maynard et al. (2019) to evaluate the potential for feedbacks between intransitivity within and between species. Such feedbacks may potentially be linked to the stability of entire communities suggesting that intransitive relationships play a critical role in maintaining stability within natural systems.

## EVOLUTIONARY DYNAMICS: EXPLAINING POLYMORPHISM

Genetic diversity within populations is confounding in the face of classic evolutionary theory. Many mechanisms of natural selection and genetic drift should work to decrease the amount of genetic diversity by moving populations towards a “most fit” genotype (Brisson 2018, Gray and McKinnon 2006). As such, models of balancing selection must be introduced to accommodate for the large genetic diversity seen in nature. Such models include host-parasite coevolution, niche theory, spatial or temporal habitat heterogeneity, heterozygote advantage and negative frequency dependent selection (NFDS). NFDS is particularly powerful as it can work alongside other mechanisms of selection such as host-parasite coevolution (Koskella and Lively 2009), sexual selection and reproductive investment strategies (Iserbyt et al. 2013, Takahashi et al. 2010), plant-pollinator interactions (Gigord et al. 2001), competition (Le Gac et al. 2012, Huang et al. 2012) and predator-prey dynamics (Brisson 2018).

RPS dynamics can maintain genetic diversity and polymorphisms through a modification of the same logic. Critically, rather than a rare allele (say allele C) enjoying a fitness advantage due to its low absolute frequency (as in NFDS) its advantage comes from its relative frequency compared to a dominant allele (allele A) which it outcompetes. Adding in a third allele (allele B) leads to a scenario in which no allele holds a competitive advantage in the population for long enough to cause a competitive exclusion. In other words, alleles or phenotypes that exist at low frequencies can be “rescued” from extinction time and time again. Thus, this mechanism can maintain a stable coexistence between the three alleles or phenotypes through a dynamic cycling of allele frequencies. Sinervo and Lively (1996) showed this exact scenario plays out in a population of the common side-blotched lizard (*Uta stansburiana*). In this system, RPS dynamics have led to the evolution of three throat-color morphs (orange, blue and yellow) in males of this species, each employing its own mating strategy. The high heritability of throat color and the reproductive advantage that each mating strategy enjoys over one another leads to stable cycling between the three morphs (Figure 1c-d).

Similar patterns of stable coexistence of phenotypes resulting from RPS dynamics have been shown in populations of *Zootoca vivipara* (San-Jose et al. 2014), *Escherichia coli* (Kerr et al. 2002, Lewis-epstein and Hadany 2020, Liao et al. 2019) and computer simulated populations (Reichenbach et al. 2007). Interestingly, RPS dynamics go beyond simply explaining coexistence but can accommodate other processes such as dispersal (Reichenbach et al. 2007, Kerr et al. 2002) and cooperation (Lewis-epstein and Hadany 2020). Additionally, spatially, or temporally heterogenous habitats in populations with low mobility are known to encourage RPS dynamics and polymorphism (Reichenbach et al. 2007), which may set the stage for new species to arise via assortative mating or allopatric speciation (Gray and McKinnon 2006). It’s clear that the flexibility and explanatory power of the RPS model makes it a useful tool for understanding evolutionary processes in real systems. However, the ubiquity of these dynamics within populations remains in question as many studies investigating RPS dynamics have been conducted in experimental laboratory conditions. Nonetheless, work with natural populations (Sinervo and Lively 1996, San-Jose et al. 2014) and the roles that similar selective processes (such as NFDS) play in natural systems, indicate that RPS dynamics may be more prevalent than previously thought.

Clearly RPS dynamics are a powerful tool in explaining evolutionary phenomena such as genetic diversity, polymorphism and even speciation. Even over short time periods, RPS dynamics can influence the genetic variation in a population, leading to diverse evolutionary outcomes. However, the same non-hierarchical interaction model can also be adapted to explain ecological patterns.

## ECOLOGICAL DYNAMICS: INTRANSITIVE COMPETITION

Many of the ecological theories that attempt to explain coexistence such as resource partitioning/niche differentiation (Tilman 1982) or models invoking invasibility (Lotka-Volterra models; Lotka 1925, Volterra

1926) approach coexistence in a pairwise fashion and begin to struggle with increasing levels of community complexity. Real systems contain many more species than there are limiting resources and interactions occur between multitudes of species simultaneously rather than just two at a time. The key limitation of these models is that they regard competition as purely hierarchical and binary, such that in more complex systems one superior competitor should displace all others (or perhaps one competitor for each limiting resource). This is unlikely to be realistic, as many species exist that are competitively similar and even species that are competitively distinct have been shown to coexist (Maynard et al. 2017). Therefore, it is possible – and perhaps even likely – that competition is more often intransitive in nature, whereby there is no single best competitor, but rather competitive outcomes are determined by environmental variables and community/population compositions (Soliveres et al. 2018, Soliveres et al. 2015, Gallien 2017). Like the RPS dynamics described above, intransitive relationships result in an oscillating or dynamic equilibrium.

Multiple factors influence the stability of an intransitive system. Most basically, system stability increases with increasing intransitivity (Laird and Schamp 2006) such that a purely hierarchical or transitive competitive system results in the competitive exclusion of all but one competitor. A purely intransitive system – in which all competitors are part of an intransitive loop and coexistence is impossible in the absence of the loop – is particularly powerful in allowing for coexistence. In fact, models of such systems show that coexistence is possible even in the absence of any niche differences (Allesina and Levine 2011, Laird and Schamp 2006). However, pure intransitivity is also unlikely. Complete intransitivity requires an unlikely scenario in which all species are present at the moment of community establishment (Gallien et al. 2017). Natural systems most likely exist along a gradient from purely transitive to purely intransitive competition (Laird and Schamp 2006, Soliveres and Allan 2018, Gallien et al. 2017).

Intransitive competition also allows for the co-existence of not just three species (as in the classic RPS scenario), but a theoretically limitless number of competitors where each beats the following and is beaten by the previous (Figure 2). Therefore, the length of the intransitive loop also stabilizes a system, with longer loops exhibiting more stable coexistence, by reducing the impact that any single species has on the stability of the loop (Gallien et al. 2017). As the number of species increases, so too does the number of possible competitive interactions and intransitive loops. The existence and/or outcomes of these interactions can also influence the stability of the system (Allesina and Levine 2011, Vandermeer 2011, Gallien et al. 2017, Gallien 2017). As interactions increase within the intransitive loop nested loops are formed which further stabilize the system (Figure 2b), similar to the effects seen in food webs (Stouffer and Bascompte 2011) and plant-animal mutualistic networks (Bascompte et al. 2003). Gallien et al. (2017) note that the stabilizing effects of nested loops becomes increasingly harder to quantify as they increase in length and complexity. This may be because they depend on the length of the inner loop(s) and the fitness differences between loop members. However, evidence across five major taxonomic groups indicate that intransitivity in natural systems is commonly nested, with interactions occurring more frequently between species with similar competitive abilities (Soliveres et al. 2018). There is also evidence to suggest that intransitive loops in highly diverse communities not only enable coexistence but promote additional diversity (Maynard et al. 2017). Nonetheless, stability of the loops is contingent on an odd number of species. An even numbered loop leads to the benefit of half the species to the exclusion of the other half (Vandermeer 2011), as is the case in a two species system where one outcompetes the other.

Intransitive competitive networks quickly become highly complex. A seven species network with all species interacting with each other (Figure 2b) already contains 49 possible competitive interactions in which the outcomes of any given interaction may be influenced by the identity of the species, environmental variables, the nestedness of the loops and the outcomes of other interactions within the network (Allesina and Levine 2011). This complexity makes studying intransitivity in natural systems difficult. Empirical support for intransitivity's role in maintaining coexistence and shaping community structure remains relatively scarce. Additionally, the research that does exist is complicated by the lack of a commonly accepted index or methodology to measure intransitivity (Table 1: See Laird and Schamp 2018 for a review). The methods chosen to measure intransitivity make different assumptions about the nature of the competitive system and may quickly increase the complexity and the feasibility of studying natural systems. For example, a common

method of measuring intransitivity is via competitive reversals. Competitive reversals occur when a species that would be “lower” in a purely hierarchical system beats a species that would be “higher”, thereby creating a loop. However, measuring the number of competitive reversals quickly becomes computationally intensive. For an  $n$ -species system, the number of competitive reversals needed to reach a possible pure hierarchy must be calculated for all  $n!$  possible hierarchies. This means the 7 species system mentioned above involves calculating the number of competitive reversals across 5040 possible hierarchies, but an 11 species system requires  $11! = 39,916,800$  (Laird and Schamp 2018, Slater 1961).

Despite the challenges, intransitive competition has emerged as a popular avenue of research for explaining ecological phenomena such as coexistence and community structure. Work with plants, coral and fungi suggests that intransitive competition is the rule rather than the exception (Buss and Jackson 1975, Soliveres et al. 2018, Soliveres et al. 2015, Browne and Karubian 2016). An analysis by Soliveres et al. (2018) of hundreds of plant communities across Europe showed that intransitivity was present in almost 70% of dryland and over 80% of grassland plant communities. Furthermore, a review by Gallien (2017) found evidence of intransitivity in a diverse set of taxa including aquatic invertebrates, microorganisms, ants and lizards. Studies also show that intransitivity can work in tandem with other diversity promoting mechanisms such as habitat spatial heterogeneity or species mobility (Soliveres et al. 2018, Allesina and Levine 2018, Reichenbach et al. 2007, Levine et al. 2017, Soliveres and Allan 2017).

While intransitivity has the potential to explain both coexistence and community structure, fundamental weaknesses in the current body of research makes interpreting its effects on natural systems difficult. For example, questions remain about how to accommodate other theories of coexistence alongside intransitive competition. However, research indicates that intransitive competition alone is unlikely enough for stable coexistence (Vandermeer 2011, Levine et al. 2017, Gallien et al. 2017, Soliveres and Allan 2017) indicating that pairwise mechanisms of coexistence and intransitive competition may work together to maintain diverse communities in nature. Another problem is the lack of a universally accepted index or methodology for measuring intransitivity (Table 1), and therefore the strength (along the gradient from a pure hierarchy to pure intransitivity) and even the presence of intransitivity in most communities remains unknown or underestimated. Finally, natural communities are incredibly complex and contain dozens if not hundreds of species. This complexity leaves open questions as to how intransitive competition patterns function across different spatial (Reichenbach et al. 2007, Levine et al. 2017) and temporal (Gallien et al. 2017, Laird and Schamp 2018, Le Gac et al. 2012) scales, trophic levels (Levine et al. 2017, Cameron et al. 2009, Soliveres and Allan 2018) and functional groups (Gallien 2017, Kassen 2002) In addition to these ecologically oriented questions there is also a need to investigate how these intransitive ecological interactions may be altering evolutionary outcomes. Despite these uncertainties, the potential explanatory power, and the existing evidence for the prevalence of intransitivity provides a case for these dynamics playing a pivotal role in coexistence theory.

## ECO-EVOLUTIONARY APPLICATIONS: BRIDGING THE DIVIDE

RPS dynamics and intransitivity represent the same underlying logic, that interactions within a system are conditional on each other and thus outcomes may differ from those observed in pair-wise interactions. Therefore, these theories represent a unique theoretical tool for exploring eco-evolutionary processes as the same mechanistic approach can be used to explain competition, selection, and coexistence on multiple levels of organization. With research interest in both intransitive interactions and eco-evolutionary theory growing, we propose that intransitivity can be used as a framework to continue to explore feedbacks between ecology and evolution.

Some previous research has also begun to provide direct or indirect evidence for the interactive effects of intransitivity in eco-evolutionary processes (Cameron et al. 2009, Huang et al. 2017, Koskella and Lively 2009). While Cameron et al. (2009) do not explicitly show evolution happening over the course of their experiment, they do show that intransitivity along with certain environmental conditions can stabilize a hemi-parasite, host, and resistant species system. This RPS-enabled coexistence could lead to coevolution, as other host-parasite systems have previously shown (Koskella and Lively 2009, Brown and Tellier 2011,

Ebert 2008). While co-evolution in this specific instance is only speculative, it points to the need to move towards a broader eco-evolutionary understanding of natural systems, as ecologically orientated studies often fail to track the genetic changes needed to identify evolution in action.

The flexibility of intransitivity and RPS dynamics to work within and between species, as well as to emerge in a variety of scenarios further showcase the potential that intransitivity has in connecting ecology and evolution. Research has shown that intransitivity is found across the living world in a variety of taxa and in a diverse set of circumstances (Soliveres et al. 2018, Gallien 2017). Many of the scenarios which commonly or theoretically produce intransitivity (Figure 3) are ecological in nature and allow for stable coexistence and long-term interaction between species (or genetic variants within a species). In this way, intransitivity sets the stage for either co-evolution or unidirectional evolution of one species (or morph) in response to selective pressures created by other members of the intransitive loop. These evolutionary changes can in turn change the ecological interactions or the population dynamics of phenotypes within the system. The ubiquity of these patterns, their potential as powerful stabilizing forces and their flexibility to work across both ecology and evolution lead us to believe that intransitivity functions across complete eco-evolutionary feedback loops. Establishing the presence and mechanisms of such feedbacks remain a major goal within eco-evolutionary research (Fussman et al. 2007, Pelletier et al. 2009, Hendry 2019) and we believe that intransitivity represents an ideal framework for these investigations. Yet, no studies have provided direct empirical support for this hypothesis.

To test the potential for such eco-evolutionary intransitivity feedbacks, we have adapted a set of simulations to examine whether intransitivity at the population-level leads to greater stability between species at the community level. Using the model of Maynard et al. (2019) we explored the effects of within-species intransitive relationships on community-level intransitivity by simulating the dynamics of a zero-sum competitive communities with phenotypic variation. This model is a generalization of the replicator-mutator equation, allowing for competitive interactions among phenotypes nested within species (Hofbauer 1985). The dynamics are described by two key parameters: phenotypic similarity ( $\rho$ ), which ranges from 0 to 1, quantifying the average correlation between phenotypes' competitive abilities within a species; and phenotypic memory ( $\phi$ ) which ranges from  $\frac{1}{m}$  to 1 (with  $m$  being then number of phenotypes within a species), capturing the probability that the offspring of an individual have the same phenotype as the parent. Using this model, we randomly generated 15 million interaction matrices across a gradient of  $\rho$  and  $\phi$  values, with the number of species fixed at  $n = 5$  and the number of phenotypes fixed at  $m = 3$  per species (see Maynard et al. 2019 for details). For each random set of matrices, we implemented two different scenarios: (1) where all of the 3x3 intraspecific sub-matrices of  $H$  are perfectly intransitive rock-paper-scissor matrices, and (2) where all of the 3x3 intraspecific sub-matrices are perfectly hierarchical. We then integrated the dynamics of the community, under each of the two scenarios, until they reached equilibrium. To quantify the effect of intraspecific intransitivity on interspecific intransitivity, we calculated the species-level intransitivity of the initial and final communities using Kendall and Babington Smith's  $d$  (Kendall and Babington Smith 1940, Laird and Schamp 2018), and then calculated the relative difference between the two scenarios (perfectly intransitive vs. perfectly transitive intraspecific relationships). The resulting difference gives the net effect of intraspecific intransitivity on interspecific intransitivity across a gradient of  $\rho$  and  $\phi$  values (Fig 4).

We found clear evidence for a positive correlation between the intransitivity of phenotypes within a population, and the resulting intransitivity between species within a community. In all cases, intransitive (rock-paper-scissors) relationships among the three phenotypes led to an average increase in community-level intransitivity between species ( $3.6\% \pm 0.009\%$  across all combinations,  $p < 0.001$ ), demonstrating clear positive feedbacks between intra- and inter-specific intransitivity. This effect was largest under high values of  $\rho$  and low values of  $\phi$  (low similarity but high memory), exhibiting upwards of 10% increase in community-level intransitivity due to intraspecific intransitivity. These results demonstrate that this benefit is strongest when phenotypes have unique interactions with other species and that there is a strong benefit to being more competitive. Interestingly, this is the same general region where Maynard et al. (2019) observed that phenotypic variation provided the strongest stabilizing force on the dynamics of the system, suggesting that the intransitivity and stability of the system may be partially linked. This relationship only declines at

the extreme, as  $\rho=1$  and  $\gamma=0$ , where communities have high dynamical stability to begin with (Maynard et al. 2019), suggesting that differences in intraspecific interactions have little effect when the dynamics are already globally stable. At the other extreme, intraspecific intransitivity had a negligible effect when there were no competitive differences among phenotypes to begin with ( $\gamma=1$ , Fig. 4, top black line), highlighting that intraspecific dynamics have no effect on community-level dynamics when there is no variation in fitness among phenotypes (i.e., phenotypes differ in name only). Collectively, these simulation results show proof-of-concept of feedbacks between intra- and interspecific intransitivity, while demonstrating that the same conditions which promote stability and robustness in these communities are the same conditions whereby intraspecific intransitivity promotes interspecific intransitivity.

Given the potential for feedbacks between intransitivity within and across species, these dynamics provide a conceptual framework for linking ecological and evolutionary dynamics. As the emerging fields of RPS and intransitive dynamics continue to grow, we highlight the need for future empirical research to focus on evaluating the presence of such feedback mechanisms within different ecological contexts. The possibility of these frameworks to help us find tangible linkages between the mechanisms driving diversity within and across species represents a valuable research avenue for developing a more holistic understanding of stability within ecological systems.

## DISCUSSION

We propose that intransitivity represents a unifying mechanism to advance eco-evolutionary theory. This work does not represent a comprehensive evaluation of all intransitivity research, but rather aims to collect the conceptual building blocks needed to use intransitivity as a framework for investigating feedbacks between ecology and evolution. While our results support the feasibility of intransitive eco-evolutionary feedback loops, more research will be needed to determine if these phenomena are at play in real systems. Empirical studies showing RPS dynamics and intransitive interactions at work remain relatively rare, especially in larger and more complex systems like metapopulations, communities and ecosystems. However, recent research has increasingly recognized the potential that RPS dynamics and intransitive competition have in explaining foundational questions of both ecology and evolution. Even without realizing it, parallels between the two disciplines via these mechanisms have already been drawn. In talking about intransitive competition and the ecological dynamics of coexistence in complex communities, Levine et al (2017) cite RPS dynamics within a single species (such as the example in *U. stansburiana*) as the best empirical evidence for these dynamics at work in natural systems. Furthermore, even the evolutionary orientated studies (Sinervo and Lively 1996, San-Jose et al. 2014, Kerr et al. 2002) are centered around the ecological processes of competition, reproductive strategies, and behavior. Incorporating both disciplines into future intransitivity studies can only serve to improve the strength of research and theory.

While there is much more work on eco-evolutionary theory than presented here, there remains a lack of research that empirically establishes full feedbacks between ecology and evolution. Hendry (2019) cites the need to conduct more empirical experiments in non-laboratory settings to show how contemporary evolution may influence the ecological dynamics at play in natural populations, communities, and ecosystems. We suggest that increasingly sophisticated mathematical models to measure intransitivity and improved genetic tools to track evolutionary changes will show that intransitivity works simultaneously across both ecology and evolution to shape and stabilize natural systems. Nevertheless, finding empirical support for such feedbacks remains a considerable challenge. The lack of long-term empirical studies investigating both RPS enabled polymorphisms and intransitive competition, makes determining the conditions that permit these patterns hard to determine. These mechanisms seem to operate on longer temporal scales than those of the pair-wise interactions that are often investigated. However, whether these dynamics can assemble quickly and spontaneously or whether they require long periods of co-existence and adaptation remains unclear. Additionally, the circumstances under which intransitivity or RPS-dynamics begin to breakdown are also unknown as even unstable even-numbered intransitive loops can decay into stabilized odd-numbered loops (Levine et al 2017). Research into these boundary conditions and the maintenance of intransitive loops across larger spatial and temporal scales are necessary to solidify their role in both ecological and evolutionary

processes.

Even studies that do attempt to measure intransitivity in natural systems may underestimate its effects given that many of the commonly used indices rely on pair-wise measures of competitive outcomes which may incompletely capture the complexity of these inherently multispecies interactions (Table 1). Clearly, there is a need for an improved and standardized measure of intransitivity which can be used in both ecological and evolutionary contexts. While our model relied on Kendall and Babington Smith's  $d$  (Kendall and Babington Smith 1940, Laird and Schamp 2018), which does measure the number of three-species intransitive triads, this measure may quickly become too computationally intensive in larger systems.

## CONCLUSIONS

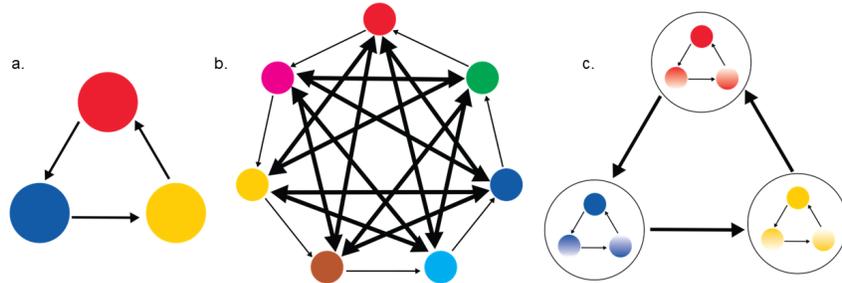
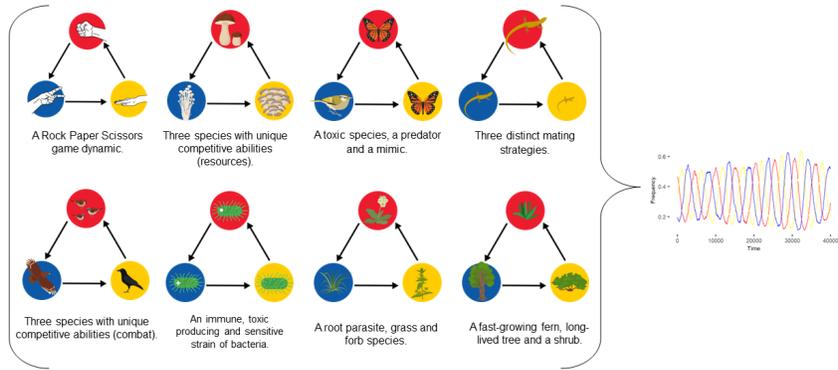
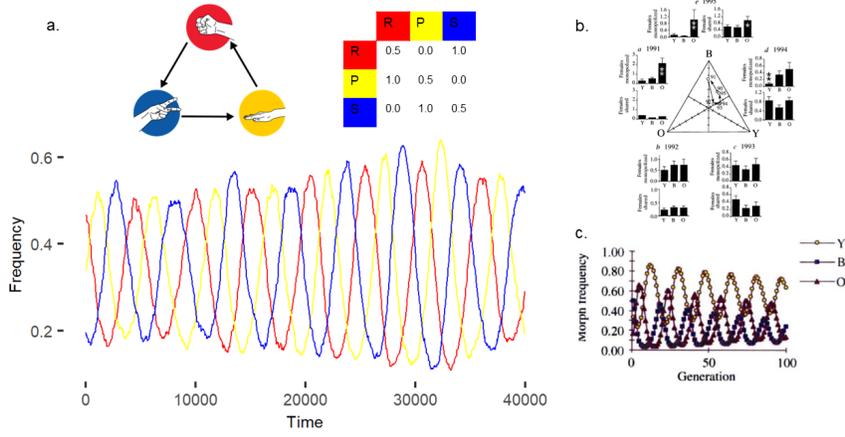
Overall, a growing body of research highlights the tangible linkages between the intransitive dynamics of phenotypes within populations as well as between species within a community, and how these can give rise to the stable maintenance of diversity across scales. The potential for feedback mechanisms to operate between these scales means that intransitivity may present a valuable framework for enhancing our understanding of eco-evolutionary dynamics. Our simulations provide some initial support for the potential existence of such feedbacks, but we propose that future empirical research should strive to test the strength of such linkages within natural systems. Given the prevalence of intransitivity, and the importance of such stabilizing mechanisms across evolutionary and ecological scales, this research has the potential to provide insights into some of the fundamental questions in ecology and evolution. Questions like; How can we explain genetic variation within populations? Or why is there such an abundance of biodiversity on our planet? We propose that intransitivity can also provide a conceptual framework for explaining the complexity of natural systems and shifting our understanding towards more holistic interpretations. In so doing, it might allow us to better understand the natural world, giving us insights into the connections that are fundamental in shaping natural systems.

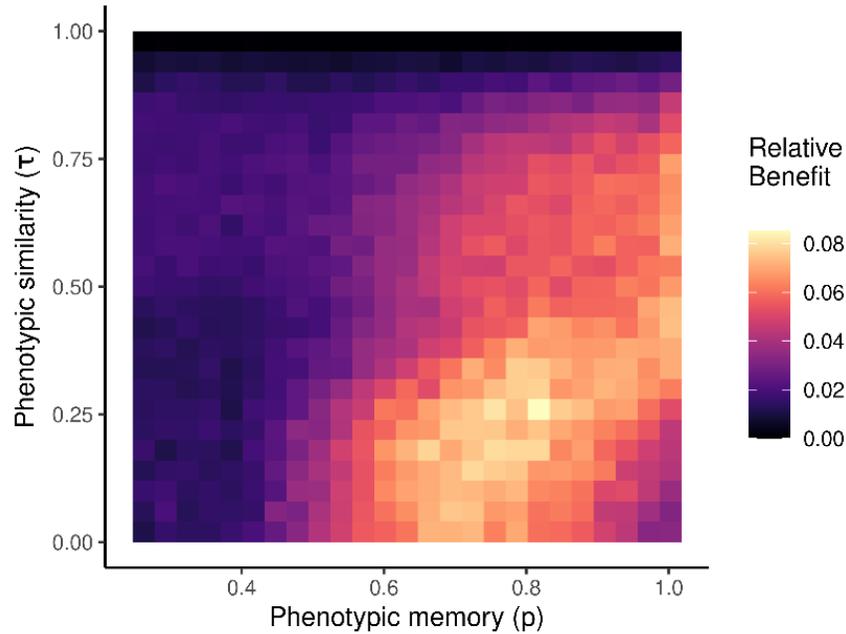
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**Figure Legend 1** The most basic Rock-Paper-Scissors Dynamic. (a) Modelled dynamics of a population of 900 “players” with perfectly intransitive competitive interactions. Players “tie” with themselves, winning and losing with equal probability. The model begins with Rock, Paper and Scissors players at 0.5, 0.33 and 0.17 proportional frequencies respectively and simulates their competitive interactions over 40,000 time steps (c and d) Figures adapted from Sinervo and Lively 1996. Similar RPS dynamics play out in a real population between three color morphs Yellow (Y), Blue (B,) and Orange (O) of *U. stansburiana*.

**Figure Legend 2** Extending the logic of intransitive loops. (a) A classic RPS scenario, with three competing species each with an advantage over one other (b) Intransitivity can scale up to larger ecological communities. In this case seven species interact with every other species within the outermost loop, creating several inner (or nested) loops. (c) We suggest that these intransitive relationships happen simultaneously both intra and interspecifically to influence both ecological and evolutionary outcomes. Here three phenotypes of three species interact between and amongst themselves in overlapping intransitive loops.

**Figure Legend 3** Intransitive or RPS loops can occur in a wide variety of scenarios, across unique temporal scales and across many taxa. The flexibility of these dynamics leads us to believe that they are widespread in nature and important stabilizing forces for both ecological and evolutionary outcomes. Some of these scenarios have been observed in nature and others represent systems where intransitivity may play an important role.

**Figure Legend 4** The relative benefit of intraspecific intransitivity on interspecific intransitivity across a gradient of phenotypic similarity (?) and phenotypic memory (p) values. Scenarios in which relative benefit is highest (high p and low ?) are the same conditions that promote stability and robustness in the community. For model details see Maynard et al. (2019).

Intransitivity Index	Formula or Derivation
$i$	Minimum number of competitive reversals separating the competitive system from a pure hierarchy
$d$	$d = \binom{n}{3} - \sum_{i=1}^n a_i \binom{a_i-1}{2}$
$v$	$v = \frac{1}{2} \ out(R) - \langle 0, 1, 2, \dots, n-1 \rangle\ _1$

Intransitivity Index	Formula or Derivation
$\delta'$	$\delta' = \delta_n \frac{(n-1)}{2}$
$u$ or $a$	$u =$ unbeatability $a =$ always-beatability
$\Delta r_i$	$r_i = \frac{\sum_{j \neq i}^S r_i - r_{i,-j}}{S-1}$

**Table Legend 1** Indices used to measure intransitivity. Many indices have been used to calculate the degree of intransitivity present in a system. Some have been proposed by ecologists specifically for use in competition and coexistence theory, while others were originally developed for other calculations and later repurposed for ecological studies.