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Intransitive stability collapses

under the influence of dominant competitors

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ABSTRACT

Intransitive competition has received much attention over the past decade. Indeed, these cyclic arrangements of species interactions have the potential to promote and stabilise species coexistence. However, the importance of intransitive interactions in real-world species-rich communities containing a mixture of hierarchic and intransitive interactions remains unknown.

Here, using simulations, we explore the behaviour of intransitive loops when they interact with outer competitors, as would be expected in real-world communities. Our results show that dominant competitors often cancel the beneficial effects of intransitive loops of inferior competitors. These results call for caution when inferring beneficial effects of intransitivity on species coexistence. Although intransitive loops are a frequent motif in competition networks, their positive effects on species coexistence may be less important than previously thought. The specific properties of a sub-network - such as stabilisation by intransitive loops - should thus not be interpreted outside the context of the global network.

INTRODUCTION

Understanding the mechanisms by which multiple species interact and coexist is one of the central quests of ecologists. In recent decades, we have moved from studying pairs
40 of species to studying species-rich communities with complex direct and indirect interactions (Godoy et al., 2018; Levine et al., 2017; Losapio et al., 2021). In this context, one specific type of indirect interaction has (re)gained much attention: intransitive competition (Gilpin, 1975; May and Leonard, 1975; Soliveres and Allan, 2018).

Intransitive competition, sometimes also called cyclic competition, emerges when there
45 is no strict hierarchy between competitors and when the competitive interactions of species form a loop, as in the rock-paper-scissors game (rock beats scissors, which beat paper, which beats rock). The mechanisms underlying intransitive competition and its potential consequences for species coexistence have been explored in theoretical models (Fig. 1; Alcántara et al., 2017; Allesina and Levine, 2011; Gallien et al., 2018; Vander-
50 meer, 2011). It has notably been shown that intransitivity can stabilise coexistence in loops containing an odd number of species. In an odd-loop, each competitor directly reduces the abundance of the next species in the loop, which indirectly regulates its own abundance at the end of each cycle, creating a mechanism of negative frequency dependence. Conversely, in even-loops cyclic interactions will destabilise coexistence (Allesina
55 and Levine, 2011; Vandermeer, 2011). In systems that contain multiple intransitive loops nested within each other, their overall effects on coexistence can be highly variable and hard to predict (Gallien et al., 2017). In the end, most of what we know about the effects of intransitive competition comes from the study of single loops, independently of their interactions with the rest of the community (but see Vandermeer, 2011;
60 Muyinda et al. 2020).

Species-rich real-world communities potentially contain a mixture of both transitive and intransitive competition, yet little is known about the dynamics of systems with this type of mixed architecture (Muyinda et al., 2020). It has been proposed that since species-rich systems are likely to harbour a large number of interaction loops, these loops
65 must have a general stabilisation effect for the whole community richness and persistence; and that the more loops there are in the system, the more stable it should be (Soliveres et al., 2015; Wootton, 2001; but see Godoy et al., 2017). However, these hypotheses and the stability of coexistence within those systems remain to be tested.

A necessary first step to improve our understanding of mixed systems is to test whether
70 species outside the intransitive loops can modify the intransitive stabilisation effects. In fact, a species outside of an intransitive loop (“outer competitor” in the following) that imposes competition on a species inside the loop may alter the stabilising effect of the loop by dampening the oscillations in species abundances over time and thus reducing the negative frequency dependence mechanism. But does the competition imposed by
75 the outer species have to be strong to affect the intransitive dynamics, or can a mild interaction also interfere? What happens when not just one species in the intransitive loop is affected but several species, do the outer competitors have additive effects or do they counteract each other? And does the loop length affect the way an intransitive loop responds to outer competitors?

80 Here, we propose to test the influence of outer (dominant) competitors on the stabilising effects of (inferior) intransitive loops. Specifically, we investigate whether and how intransitive stabilisation is affected by: the strength of species competition (inside and outside of the loop), the number of species in the loop directly impacted by outer competitors, and the length of intransitive loops.

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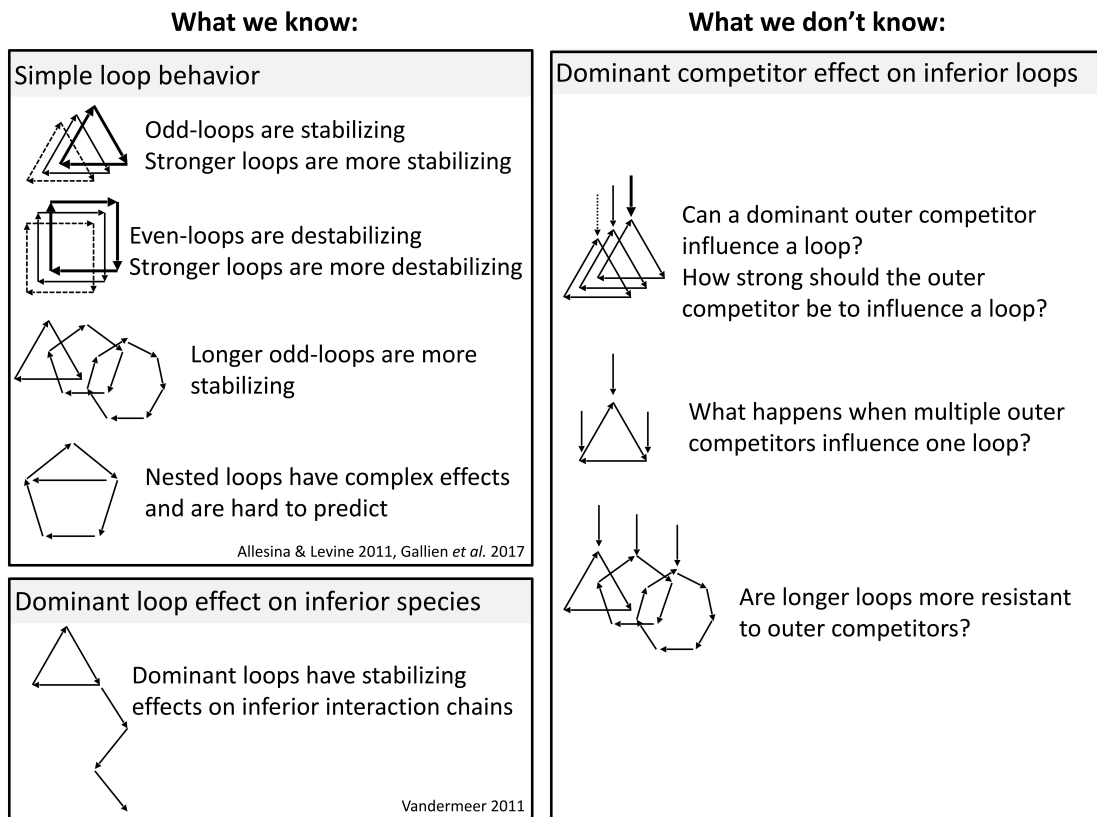


Figure 1. What we know and what we don't know about intransitive loop effects on coexistence.

The expression “stronger loops” here refers to loops in which the fitness difference between species is large (i.e., greater asymmetry in competition relationships). Arrows point to the weaker

90 competitors, and their thickness represents the fitness difference between species.

SIMULATION MODEL, SCENARIOS & STABILITY METRIC

We decomposed and tested the influence of external competitors on the stabilisation provided by intransitive competition loops (i.e., in odd-loops) according to the following questions: (1) How strong should an outer competitor be to influence an intransitive
95 loop? (2) What happens when multiple competitors influence the loop? (3) Are longer loops more resistant to outer competitors than shorter ones? (Fig. 1) To answer these questions, we (i) simulated the dynamics of species abundances (ii) under different scenarios of “outer” competition on intransitive loops, and (iii) evaluated the stability provided by intransitivity in the resulting communities.

100

(i) The simulation model:

We simulated temporal abundance dynamics for given sets of competing species based on Lotka-Volterra (LV) equations. In a LV competition model, the growth rate of species

i can be expressed as: $\frac{d N_i}{dt} = \lambda_i N_i (1 - \alpha_{ii} N_i - \sum_{j \neq i} \alpha_{ij} N_j)$ where λ_i is the intrinsic growth

105 rate of species i , N_i is the abundance of species i , N_j are the abundances of all other species j (with $j \neq i$), α_{ii} is the intraspecific competition coefficient, and α_{ij} are the interspecific competition coefficients representing the per capita effect of species j on species i .

Modern coexistence theory shows that the coexistence of pairs of species is determined by how much resource need they have in common: their *niche overlap* (measured as

110 $NO = \sqrt{\frac{\alpha_{ij} \alpha_{ji}}{\alpha_{ii} \alpha_{jj}}}$; Chesson 2012), relative to whether one is better at acquiring these re-

sources than the other: their *relative fitness difference* (measured as $FD = \sqrt{\frac{\alpha_{jj} \alpha_{ji}}{\alpha_{ii} \alpha_{ij}}}$;

Chesson, 2012). Given this conceptual framework, increasing the competition effect of

species i on the population of species j (α_{ji}) directly translates into an increase in the relative fitness difference of species i over species j ($i > j$, denoting that i has a greater competitive effect on j than j has on i), but it also increases their level of niche overlap (i.e. they have to share more resources, see formulas above). Thus, to explore the effects of increasingly strong competitive interactions without confounding effects linked to changes in resource needs, it is necessary to keep the level of niche overlap constant while varying species fitness differences (as in Gallien et al. 2017; see more details in Supplementary Materials).

For our simulation experiments, interaction coefficients were set to allow both intransitive interactions (to form the intransitive loops), and transitive interactions between loop-species and species outside the loop (see Supp. Mat. and section *ii* for more detail). For simplicity, in the following we identify species by capital letters (from A to I for species within the loop, and from X to Z for species from outside the loop).

(ii) The competition network scenarios:

We parameterized three sets of model scenarios to answer our research questions (see Supp. Mat. for parameter values).

Scenario 1 - How strong should an outer competitor be to influence an intransitive loop?

In scenario 1, we focussed on the response of a 3-species intransitive loop ($A > B > C > A$) to external competition by a single species which impacts only one species in the loop (X with $X > A$). Two main features can influence the outcome of this interaction: the competition between species of the loop (loops with stronger fitness differences are known to be more stabilising; Fig. 1), and the competition between the outer competitor and the species of the loop. In our model, under a given niche overlap between species (and

equal λ_i across species), the competitive superiority of one species over another is determined by their fitness differences (in other words, the level of competition asymmetry). We thus varied independently the fitness differences within the loop, and
140 between the outer competitor and the species of the loop.

We simulated the abundance dynamics of a 3-species loop community until equilibrium, then added the outer competitor and followed all abundance dynamics until the system re-equilibrated. We repeated these simulations along a gradient of increasing fitness difference within the loop. To ensure comparability across simulations, we set all pairwise
145 niche overlaps constant (set to $NO=0.5$), and varied only the average fitness difference between species. Fitness differences were chosen to range from a minimum of 1 (all pairwise interactions in the loop are symmetric) to a maximum of 3 (strong asymmetry of competition), the value of 2 being the threshold separating pairwise coexistence ($FD<2$) from pairwise competitive exclusion ($FD>2$; see Letten et al. 2016 for an in-
150 depths description of the relationship between NO , FD and coexistence). Similarly, the fitness difference between the outer competitor and one species in the loop varied so that it ranged from 1 (symmetric competition, $\alpha_{AX}=\alpha_{XA}$) to 3 (strong competitive exclusion of the loop species, $\alpha_{AX}>\alpha_{XA}$). These values for niche overlap and relative fitness differences were chosen to cover the wide range of values found in empirical studies
155 (e.g., see for example Bimler et al., 2018; Godoy and Levine, 2014; Kraft et al., 2015; Li et al., 2019).

Scenario 2 - What happens when multiple competitors influence intransitive loops?

In scenario 2, we investigated the response of a 3-species intransitive loop to competition from one, two, or three outer competitor(s), each impacting a different species in
160 the loop (which is equivalent to one outer competitor impacting 1, 2, or 3 species of the loop, see Fig. S1). Similarly to Scenario 1, we varied independently the fitness difference

within the loop, and between the outer competitor(s) and the species of the loop. For simplicity, the outer competitors did not interact with each other.

Scenario 3 - Are longer loops more resistant to outer competitors than shorter loops?

165 In scenario 3, we examined the influence of one outer competitor on intransitive loops of increasing lengths. As explained above, we focused here only on stabilising loops (i.e., odd-loops), and thus chose loops of 3, 5, 7, and 9 species (loops with more than 9 species yielding qualitatively similar results to 9-species loops; results not shown). As in Scenarios 1, we varied independently the fitness difference within the loop, and between the
170 outer competitor and the species of the loop. For communities where the intransitive loops contain more than 3 species, species not next to each other in the loop were set to compete symmetrically, following Gallien et al. (2017). Simulations of communities without this symmetric competition can be found in Supp. Mat. (Fig. S2).

175 *(iii) The intransitive stability measure:*

We analysed the simulations by quantifying how coexistence of species within the intransitive loops is promoted or reduced by the intransitive nature of the interaction based on $\overline{\Delta Ri}$, an index tailored for this purpose (Gallien et al., 2017). ΔRi measures the average difference between the invasion growth rate of a focal species i (i.e., the growth
180 rate of i when it is at very low abundance) when all other species are present and at equilibrium abundances, and the invasion growth rate of the same focal species when all but one species of the loop and all competitors are present and equilibrated (i.e., the loop is broken). In the first case (outer competitor(s) + full loop), the focal species can benefit (or be harmed) by the intransitivity, while in the second (outer competitor(s) +
185 broken loop), intransitivity is broken by the removal of a species in the loop. ΔRi is thus the difference between these growth rates averaged over the removal of each individual

loop species, and provides a measure of the importance of the intransitivity for a given focal species. Then averaging over the ΔRi of each loop species, $\overline{\Delta Ri}$ shows the average change in invasion growth rate following the extinction of any species of the loop. $\overline{\Delta Ri}$ >0 indicates that intransitivity contributes to coexistence: removing a loop species from the community actually harms the rare species (even if they compete for resources). Conversely, $\overline{\Delta Ri}$ <0 indicates that any positive effect of intransitivity is smaller than the effects of niche overlap: removing a species helps the rare species. Note that the index is a measure of stability provided by intransitive loops, and should not be computed when outer competitor(s) remove species from the intransitive loop, as intransitivity is then broken and the index loses its meaning (we highlight these cases with grey areas on the figures).

RESULTS

200 *Even a single weak outer competitor can break an intransitive loop*

Our simulations repeat the earlier finding that, in the absence of an outer competitor, intransitive loops have beneficial effects on the stability of species coexistence, even under moderate competition strength (Fig. 2b). However, this stabilising effect is rapidly lost once an outer competitor is added to the system (Fig. 2d). To remain beneficial for species coexistence, fitness differences in the loop must be strong (i.e., pairwise coexistence between the species in the loop is nearly impossible) and fitness difference of the outer competitor must be small (i.e., pairwise coexistence of X and A is possible). In other words, in this system, already moderate fitness differences between the competitor and the loop species A lead to the exclusion of species A (even when X and A alone would co-
205 exist), and thus to the collapse of the loop, unless the stabilising effect of the loop is large
210 (i.e., fitness differences are so large that they would lead to competitive exclusion in

pairwise interactions).

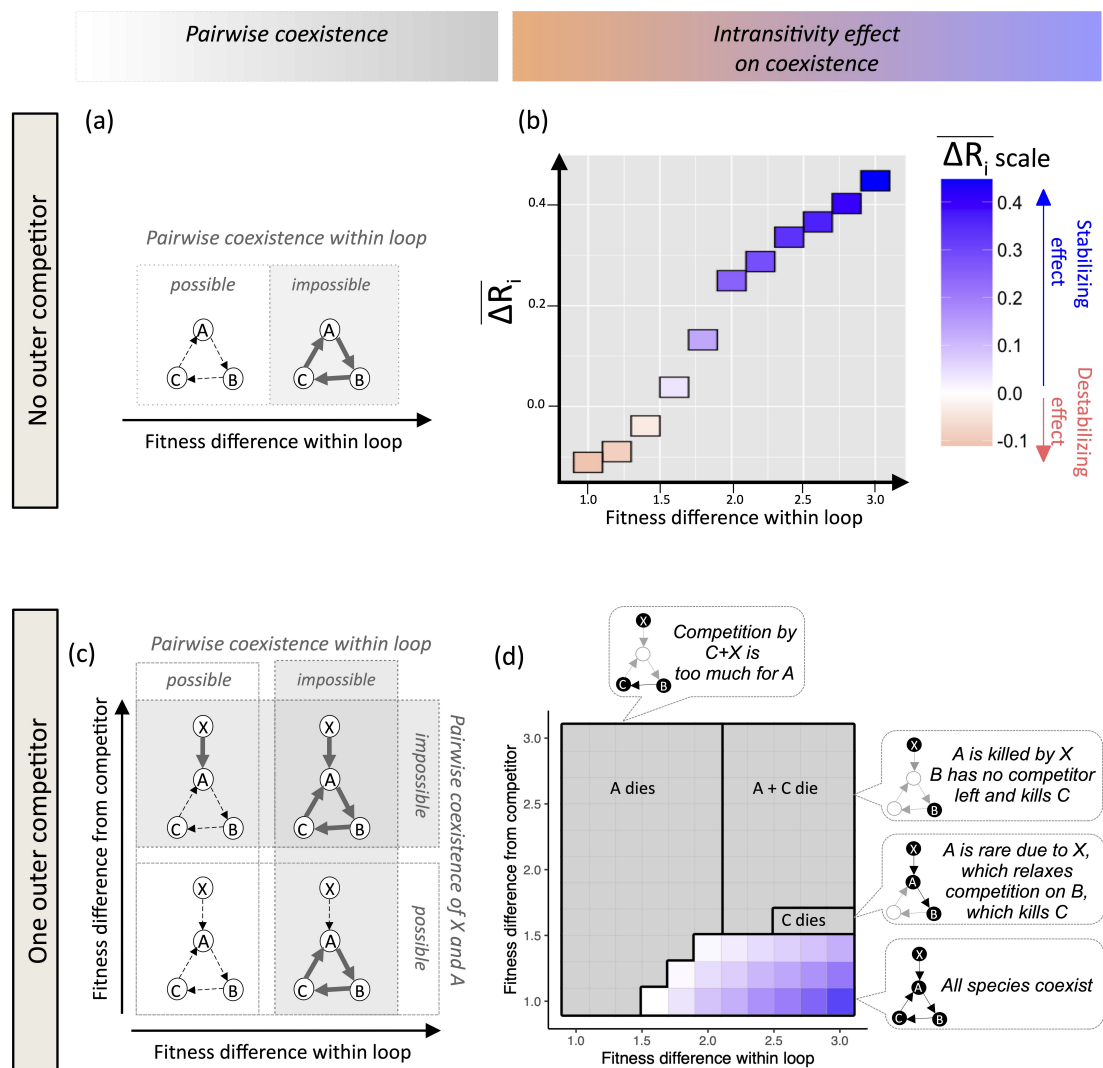


Figure 2. Scenario 1 - The influence of one outer competitor on intransitive loop dynamics. In (a-b) the community contains only an intransitive loop composed of three species ($A > B > C > A$), and in (c-d) an outer competitor (X) is added to the community and it affects only species A ($X > A$). Panels (a) and (c) indicate whether coexistence is possible under pairwise competition only, along a gradient of fitness differences (without (a) or with the outer competitor (c)). Weak fitness difference (FD) allows coexistence of species pairs ($FD < 2$, dashed arrows), whereas strong fitness difference prevents coexistence of species pairs ($FD > 2$, bold arrows), making coexistence at the community level possible only through the intransitive loop. Panels (b) and (d) show results of the simulations. The stabilising effect provided by the intransitive loop for its constituent spe-

cies is measured with the $\overline{\Delta Ri}$ index. Grey areas indicate where at least one species of the loop becomes extinct, and thus where the intransitive stability index cannot be defined. Stability generally increases with fitness differences within the loop (b), but with an outer competitor in the system the final composition of the community depends on fitness differences among all species (d). The small networks illustrate species that coexist at equilibrium (black dots: surviving species, white dots: extinct species), and the direction of pairwise interactions is indicated by arrows pointing toward the weaker competitors.

230 *Multiple outer competitors have non-additive negative effects on intransitive loops*

Introducing outer competitors into the system always reduces the stabilising effects of intransitive loops (Fig. 3), compared to a system without any outer competitors (Fig. 2a). However, increasing the number of outer competitors has non-additive effects on community persistence and stability (Fig. 3). Adding a second competitor has a clear negative effect on the stability of the loop species, because it reduces both the conditions for coexistence of all species in the community and the strength of the stabilising effect of intransitivity. There, only loops with very strong fitness differences together with very weak outer competitors can coexist. The addition of a third competitor has various effects depending on the strength of the competition between the different species. (i) If the outer competitors are strong ($FD > 2$), all species of the loop die. (ii) If the outer competitors are weak ($FD < 2$), the persistence and stability of the loop species decreases less than when a single competitor is present because, by regulating the abundances of all loop species, they also reduce their reciprocal negative influences. However, (iii) even under the relatively favourable effect of three weak competitors, for loops with very strong fitness differences ($FD > 2.6$) the whole system alternates between different stable states (heteroclinic cycles), leading some species to near extinction for longer periods over time, which would make them particularly vulnerable to stochastic extinctions in

the real world. In the end, the persistence of the loop species in the community can drastically and non-intuitively change depending on the number of outer competitors and the strength of pairwise fitness differences: 1 competitor ($X>A$) can lead to the persistence of either $\{A, B, C\}$, $\{B, C\}$, $\{B\}$, or $\{A, B\}$; 2 competitors ($X>A, Y>B$) can lead to $\{A, B, C\}$, $\{B, C\}$, or $\{C\}$, 3 competitors can lead to $\{A, B, C\}$, $\{\emptyset\}$, or $\{heteroclinic\ A, B, C\}$. Note that a further increase of the number of outer competitors always leads to the extinction of at least one species of the intransitive loop (see Fig. S3).

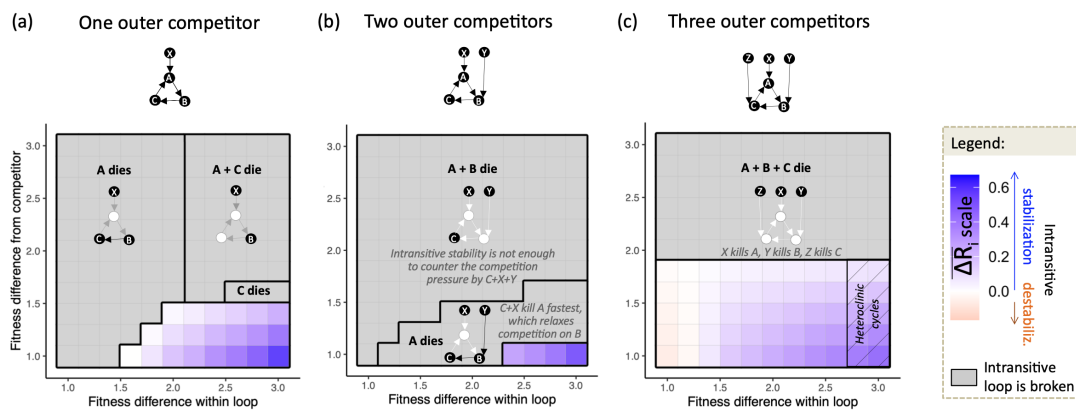


Figure 3: Scenario 2 - The influence of the number of outer competitors on intransitive loop dynamics. The intransitive loop is composed of three species ($A>B>C>A$), and the presence of outer competitors (X, Y, Z) varies between: (a) one outer competitor ($X>A$), (b) two competitors ($X>A, Y>B$), and (c) three competitors ($X>A, Y>B, Z>C$). Similarly to Fig. 2d, we varied independently the strength of fitness differences within the loop, and between the outer competitor(s) and the loop species. Pairwise fitness differences (FD) ranged from 1 (perfect symmetry of competition, i.e., $\alpha_{ij}=\alpha_{ji}$) to 3 (strong asymmetry, i.e., $\alpha_{ij}\neq\alpha_{ji}$), with $FD=2$ being the threshold that separates pairwise coexistence ($FD<2$) from competitive exclusion ($FD>2$). Each panel shows the results of the simulations: either all species coexist and we represent the stabilisation level provided by the intransitive loop for its constituent species (measured with the $\overline{\Delta Ri}$ index); or at least one species of the loop becomes extinct, and thus $\overline{\Delta Ri}$ cannot be defined (grey area). The striped area in (c) highlights conditions when the system oscillates between alternative stable states with species nearing extinction for longer periods over time (heteroclinic cycles). The small networks il-

illustrate which species coexist at equilibrium (black dots: surviving species, white dots: extinct species), and the direction of pairwise interactions is indicated by arrows pointing toward the weaker competitors.

Longer loops are more vulnerable to outer competitors than shorter loops

Long odd loops have been shown to provide a more stabilising effect on species coexistence than short loops (Gallien et al., 2017). However, our simulations show that the longer the loop, the more detrimental the effect of the outer competitor on the stability of the loop (Fig. 4). Already, in the 5-species loops, the persistence of all species is possible only under narrow conditions, with both a very “weak” outer competitor and very “strong” fitness differences in the loop (narrow blue area). In the 7-species loop, the conditions for coexistence of all species are further reduced and rely on oscillations of species abundances that create increasingly longer periods during which at least one species nears extinction and is thus especially prone to demographic stochasticity and extinction (heteroclinic cycles). When species loops reach 9-species, the simple presence of a unique competitor prevents the loop from persisting (regardless of its fitness difference). As intransitive loops get longer, each species has access to fewer resources, making intransitive stabilisation more crucial for coexistence. When only intransitive interactions are at play, the strong fitness differences between neighbouring species in the loop compensate for limited resources (e.g., with fluctuating species abundances over time). However, when an external competitor enters the system and fixes the abundance of a species, it disrupts the regulation of negative frequency dependence (e.g., no rotation of abundances over time). To sum it up, longer intransitive loops mean fewer resources per species, making intransitive loops even more vital for coexistence. Locking species at rare or zero abundances has more harmful effects on longer loops compared to shorter ones.

It is important to note that a single network configuration can lead to many different
295 community richness and compositions depending on the interaction strengths. For in-
stance, depending on the fitness difference between all species, an outer competitor act-
ing on a 5-species loop, can result in 6 outcomes (Fig. 4b): (1) *all species coexist stably*
(light blue area), (2) *all species coexist but with oscillating abundances* (darker blue area
of heteroclinic cycles), (3) *species A dies* because the stability provided by the intransit-
300 ive loop is too weak to counteract the effect of the outer competitor (left hand side), (4)
species E dies because the outer competitor has a “mild” effect on A that propagates until
E via strong within-loop interactions, (5) *species C and E die* because the outer competi-
tor (X) has a “moderate” effect on A, which propagates to C via strong within-loop inter-
actions, which then releases competition on D, which can then kill E, and (6) *species A, C,*
305 *E die* because the additive effects of X and E on species A kill A, which breaks the strong
intransitive loop and thus leads to the extinction of C and E.

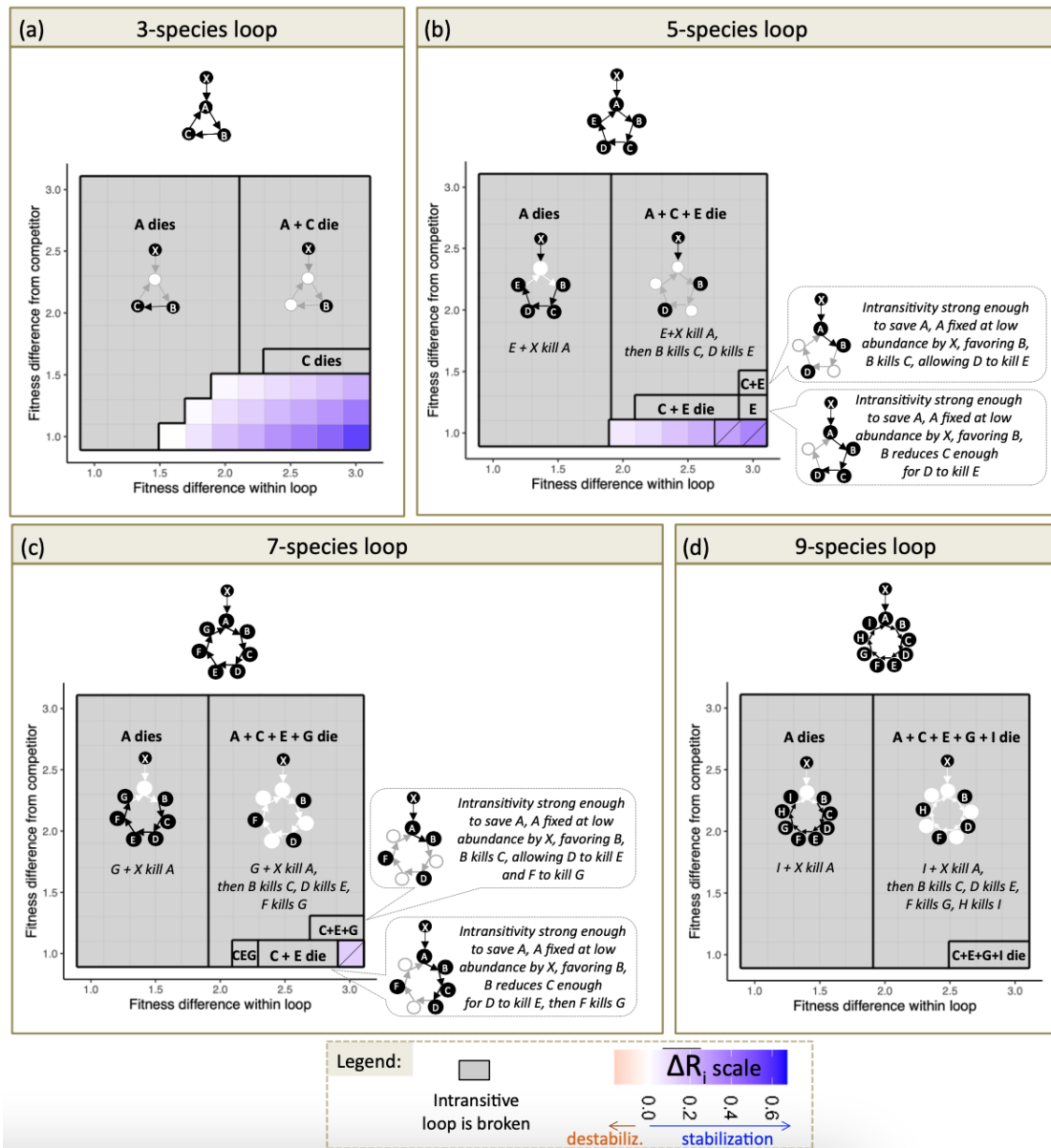


Figure 4. Scenario 3 - The influence of one outer competitor on intransitive loops of increasing length. The intransitive loops are composed of 3, 5, 7, or 9 species, and a single outer competitor (X) influences only one species in the loop ($X > A$). Similarly to Fig. 2-3, we varied independently the strength of fitness differences within the loop, and between the outer competitor and the loop species. Pairwise fitness die differences (FD) ranged from 1 (perfect symmetry of competition, i.e., $\alpha_{ij} = \alpha_{ji}$) to 3 (strong asymmetry, i.e., $\alpha_{ij} \neq \alpha_{ji}$), with $FD=2$ being the threshold that separates pairwise coexistence ($FD < 2$) from competitive exclusion ($FD > 2$). Each panel shows the results of the simulations: either all species coexist and we represent the stabilisation level provided by the intransitive loop for its constituent species (measured with the $\overline{\Delta Ri}$ index); or at least one spe-

cies of the loop becomes extinct, and thus $\overline{\Delta Ri}$ cannot be defined (grey area, the identity of the dead species is indicated with bold letters). The striped area in (b-c) highlights conditions when the system oscillates between alternative stable states with species nearing extinction for longer periods over time (heteroclinic cycles). The small networks illustrate which species coexist at equilibrium (black dots: surviving species, white dots: extinct species), and the direction of pair-wise interactions is indicated by arrows pointing toward the weaker competitors.

DISCUSSION

Past works have introduced intransitive competition as a potentially powerful mechanism of coexistence, especially for large communities. However, we know little about how competitive interactions with species from outside intransitive loops can affect this coexistence mechanism (but see Muyinda et al., 2020). Yet such weaving of intransitive loops into larger biotic networks should be the norm rather than the exception in real communities.

Here, using theoretical simulations, we show that intransitive loops are very sensitive to external competition. Dominant competitors have negative impacts on the dynamics of inferior intransitive loops in all simulations tested, which should reflect the response of natural systems containing similar motifs. A single outer competitor acting on a single species in the loop will result in the extinction of at least one species in the loop, thus breaking the loop, unless the outer competitor is weak (i.e., small FD) and the loop is short and fitness differences within the loop are strong. Increasing the number of outer competitors further reduces species coexistence, unless all species in the loop are similarly affected. Increasing the length of the loops leads to increasing destabilisation by outer competitors. Importantly, a single network configuration can lead to many different community richnesses and compositions, depending on all species fitness differences. To assess whether intransitive loops stabilise species coexistence, one must

therefore not only identify the nature of intransitive loops, but also quantify the complete network of interactions between species in the community.

In this work we have focused on intransitive loops (i) only located at the lowest positions in networks containing (ii) only competitive interactions. Inside complex, species-rich networks of the real world, intransitive loops may also be observed at intermediate positions (i.e., impacted by dominants and impacting inferior species), or even at the top position (i.e., just impacting other species). In fact, intransitive loops at the top-position have been shown to have potential stabilising effects on lower species (Vandermeer, 2011; Vandermeer and Perfecto, 2023; but see Alcántara et al., 2017). But it remains to be shown whether many competitive networks are really dominated by intransitive loops. Additionally, here we focused on the part of the network that contains only competitive interactions, but other types of interactions can impose a comparable abundance decline on intransitive loop species (e.g., predation or parasitism). Thus a top-position inside a competition network may not be a top-position inside the entire multi-trophic network. Although this remains to be formally tested, in a rich multi-trophic system, any species that would have negative effects on the abundance of species in an intransitive loop - such as predators, pathogenes, or parasites - may have similar detrimental effects as our dominant competitors on the dynamics of that intransitive loop.

Practically, our results also show that one cannot infer the effects of intransitive loops on community composition and stability from the architecture of the network alone, while neglecting the strength of fitness differences in both intransitive and transitive interactions (e.g., four possible compositions of the community from Scenario 1; Fig. 2c). Consequently, estimating intransitive effects based on either a mean level of intransitivity at the community scale or the number of loops in the community (e.g., Feng et al., 2020; Laird and Schamp, 2018; Ulrich et al., 2014), but without integrating information

about dominant competitors (and potentially also other types of biotic interactions), may lead to overestimating the contribution of intransitive loops to species coexistence in a system. In the end, all these results call into question the importance of this cyclic
370 network motif for the coexistence and persistence of species in rich communities of the real world.

SYNTHESIS & OUTLOOK

Combining the results of other studies with our own, we conclude that intransitivity does not always contribute to stability: (i) intransitivity stabilises coexistence only in
375 odd-numbered loops (Levine & Allesina 2011), (ii) intransitivity effects are highly variable when multiple loops are intertwined (Gallien et al.2017), and (iii) intransitive loops are highly vulnerable to competition from outer competitors (the present study). It is thus not sufficient to identify the number or proportion of intransitive loops in the system, but we need to know their length, strength, and position in the overall network of
380 biotic interactions, to be able to infer their impacts on species coexistence and biodiversity maintenance.

Together, these findings call for greater caution when inferring the beneficial (or negative) effects of intransitivity on species coexistence in real world communities with a multitude of biotic interactions. Most likely, intransitive loops are a very frequent motif
385 in competition networks, but their positive or negative effects remain extremely difficult to quantify as long as the different types of biotic interactions are studied in isolation. It is probable that more holistic studies of biotic interaction reveal that intransitivity is not as important as previously thought for species coexistence in complex real world settings (see also Losapio et al., 2021).

390 Finally, our findings also raise the broader question of how the outcome of species interactions can change (and sometimes reverted) when neglecting parts of the full network

of biotic interactions (e.g., upper competitors, and eventually other types of interactions such as predation or parasitism). Exciting avenues are opening up for more integrative research on biotic interactions at the scale of the multi-trophic network, and for finding
395 ways to translate and test these theoretical results into natural or experimental systems.

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400 AUTHOR CONTRIBUTION

L.G. conceived the study, L.G. and M.C.C. coded and ran the simulations, all authors analyzed the results, L.G. prepared the figures and wrote the original draft which was reviewed and significantly improved by all authors.

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SUPPLEMENTARY MATERIAL

495 **More details on the simulation model**

We used Lotka-Volterra (LV) model simulations to answer our three research questions: (1) How strong should an outer competitor be to influence an intransitive loop? (2) What happens when multiple competitors influence the loop? (3) Are longer loops more resistant to outer competitors than shorter ones?

500 For each question, we decided to focus on network structures (i.e. the arrangement of transitive and intransitive interactions) that are the simplest in terms of the number of species and interaction links. These three questions and associated scenarios explore minimalist network architectures as follows (also illustrated in Fig. 1 of the Main Text):

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- Scenario 1 evaluates a 3-species loop + 1 outer competitor
 - Scenario 2 evaluates a 3-species loop + 1-2-3 outer competitor(s)
 - Scenario 3 evaluates 3-5-7-9 species loops + 1 outer competitor

We opted for this simplicity for two main reasons. Firstly, species-rich communities often contain several loops of different lengths and degrees of interlocking.

510 By exploring the behavior of basic motifs independently of each other, we can better disentangle the effects of competitive strength, number of competitors, and loop length (i.e., our research questions). Secondly, if the stabilization provided by intransitivity becomes negligible in this minimalist framework, then more complex communities (e.g., with more external competitors) are unlikely to
515 reverse these results.

Within each scenario, the influence of dominant competitors on intransitive loop stability was evaluated across a large range of competition matrices, varying in their strengths of fitness differences between species (121 different matrices per network architecture; 726 matrices over all scenarios). The matrices ranged
520 from symmetric matrices (all interspecific competition coefficients are equal: $\alpha_{ij} = \alpha_{ji}$) to asymmetric matrices with progressively increasing competitive dominance between species (i.e., increasing the difference in pairwise competitive abilities: $\alpha_{ij} > \alpha_{ji}$).

For scenario 1, for instance, the network architecture is composed of one intransitive loop of 3 species ($A > B > C > A$) and one outer competitor X acting on species A ($X > A$). We used the LV model (see equation in the main text) to simulate species abundance dynamics across 11 levels of competitive symmetry within the intransitive loop and 11 levels of competitive symmetry between the outer competitor and the loop species (121 different competition matrices). For simplicity, in all simulations the intrinsic growth rate of all species is identical and set to 1, and the initial abundance are drawn at random in a normal distribution of mean 170 and standard deviation of 20 (for our specific sets of network architecture, preliminary analyses revealed that the choice of starting number of individuals does not influence the equilibrium abundances, only the speed at which it is reached). The only parameters that varied across (not during) simulations are the intra- and interspecific competition coefficients (see below). The simulations are run for 1,000,000 time steps to allow community abundances to reach equilibrium, which was also confirmed visually for each simulation.

Conceptually, the question that we want to explore is: “For each species pair with a given resource niche, i.e., a given niche overlap, does increasing the competitive dominance of one species over the other (i.e., their fitness difference) also changes the stability of their coexistence?” This means that we want to keep the niche overlap between species constant across simulations, and only change the competitive dominance between species. In Lotka-Volterra models, niche over-

lap (NO) between species A and B can be measured as $NO = \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}}$ (Chesson

2012). And prior work has shown that pairwise competitive dominance is determined by species fitness difference, where the fitness difference (FD) of species

A over species B can be measured as $FD = \sqrt{\frac{\alpha_{jj}\alpha_{ji}}{\alpha_{ii}\alpha_{ij}}}$ (Chesson 2012). The formula-

tions of niche overlap (NO) and fitness differences (FD) show that the two indices are not independent from each other: modifying interspecific competition coefficients (e.g., moving from $\alpha_{BA} = \alpha_{AB}$ to $\alpha_{BA} > \alpha_{AB}$) not only impacts species fitness differences, but also their niche overlap. To investigate a gradient of interac-

tions with a fixed niche overlap and increasing competitive dominance (i.e., competitive asymmetry), we used the same parameter ranges as in Gallien et al. (2017), where niche overlap is fixed to 0.5 and fitness differences range from 1 (competition between species is symmetric, and pairs of species can coexist) to 3 (competition is asymmetric and pairs of species cannot coexist). Given that the coexistence of species i and j requires $\alpha_{ij} < \alpha_{ji}$ and $\alpha_{ji} < \alpha_{ii}$, it has been shown that these conditions can be translated into the following inequality: $NO < FD < 1/NO$ (see the nice explanation in Letten et al. 2016). Given our choice of $NO=0.5$, this means that pairwise coexistence is possible for $0.5 < FD < 2$. Since we also do not want to reverse the dominance between i and j (i.e. $\alpha_{ij} \leq \alpha_{ji}$), then FD has a lower bound of 1. This choice of parameters is rather realistic as it encompasses values of niche overlaps and fitness differences that have been found in nature (e.g., Godoy and Levine 2014; Kraft et al. 2015; Bimler et al. 2018; Li et al. 2019).

In practice, first we used the approach of Gallien et al. (2017) to determine the competition coefficients for the species within the intransitive loop (given our choice of niche overlap $NO=0.5$ and fitness differences ranging between 1 and 3, Gallien et al. 2017, Eq. 4). In this set up, the fitness differences (FD) between all pairs of species change to the same value simultaneously (homogeneous fitness differences within the loop), as it has been shown that heterogeneous FD within the loop only decreases the stabilizing effects of intransitive interactions (Gallien et al. 2017). Second, we used these competition coefficients of the species in the intransitive loop to determine the coefficients for the outer competitor(s), e.g., $\alpha_{XX}, \alpha_{AX}, \alpha_{XA}$. The competition coefficient of the outer competitor X on the population of species A is set as $\alpha_{AX}=0.001$, to be coherent with the competition coefficients between the dominant and inferior loop species (as $\alpha_{BA}=\alpha_{CB}=\alpha_{AC}=0.001$; see Gallien et al. 2017 Eq. 4). Then, given the constraints on NO , FD , and α_{AX} , the coefficient of intraspecific competition of the outer competitor (α_{XX}) and its interspecific one with species A (α_{XA}) can be expressed as follows: $\alpha_{XX} = \frac{\alpha_{AX}}{FD \times NO}$ and $\alpha_{XA} = \frac{\alpha_{AA} \times NO}{FD}$. This way we can estimate all coefficients along our FD gradient.

All matrices of competition coefficients and R scripts used for the simulations can be found at <https://doi.org/10.5281/zenodo.8340923>.

585 It can be noted that the fitness differences between species in the intransitive loop have the same value, interactions are thus “homogeneous” between species. Heterogeneous interactions have already been explored in the literature and were shown to generally decrease the stabilizing effects of intransitivity (see supplementary materials in Gallien et al. 2017). We thus did not explore further
590 the influence of outer competitors on heterogeneous loops.

Additionally, in the main text simulations of long intransitive loops, we have assumed that all species of the loop that are not next to each other interact symmetrically (following Gallien et al. 2017). To test the influence of this hypothesis on our results we simulated the same scenarios but with no symmetric interaction
595 between species that are not next to each other in the intransitive loops. The results are qualitatively similar (Figure S2).

All simulations were run on R v.4.1.2 (R Core Team 2021) with the package *deSolve* (Soetaert et al. 2010), and figures are drawn with the help of the packages *ggplot2* (Wickham 2009) and *cowplot* (Wilke 2020).

600 **Supplementary Figures**

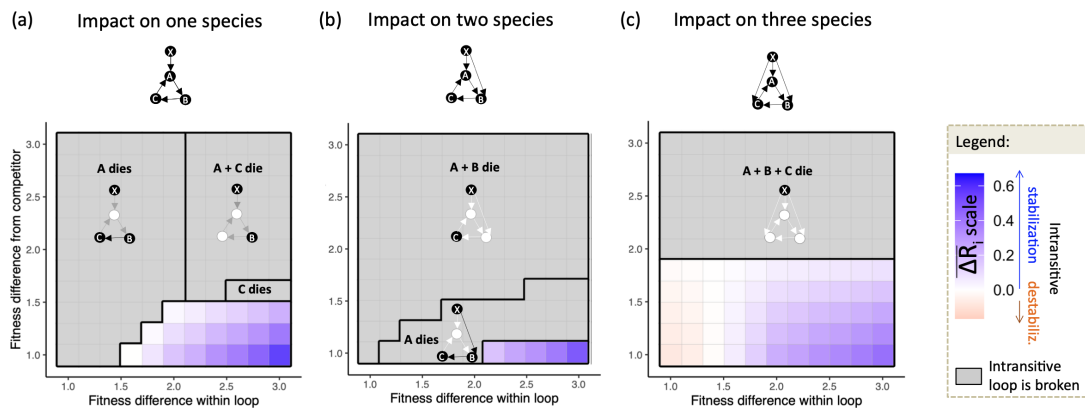
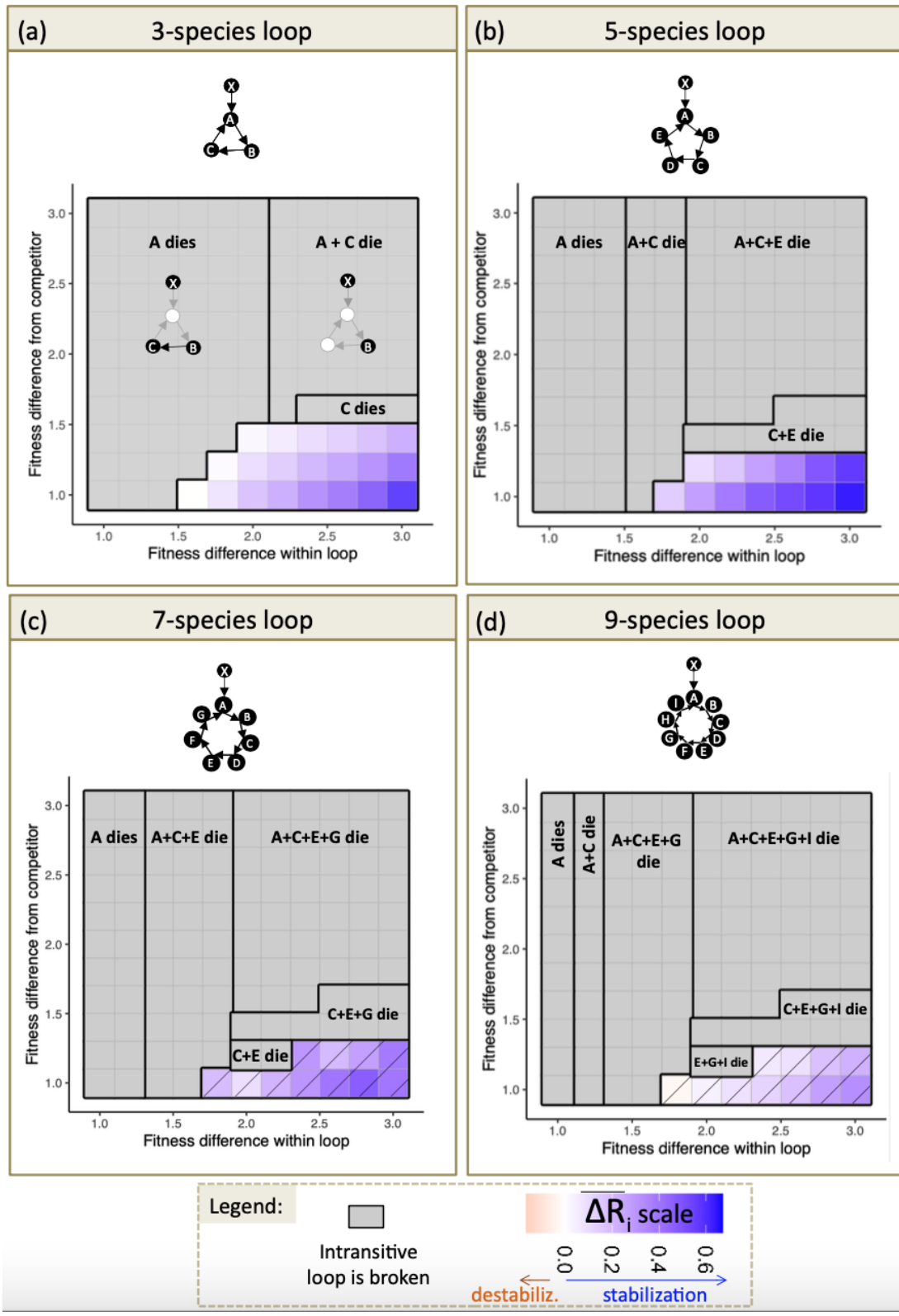


Figure S1. The influence of one outer competitor on multiple species of the intransitive loop and their dynamics (Alternative to Scenario 2). The intransitive loop is composed of three species ($A > B > C > A$), and the outer competitor (X) impacts either: (a) one species of the loop ($X > A$), (b) two species of the loop ($X > A$, $X > B$), and (c) three species of the loop ($X > A$, $X > B$, $X > C$). We varied independently the strength of fitness differences within the loop, and between the outer competitor and the loop species. Pairwise fitness differences (FD) ranged from 1 (perfect symmetry of competition, i.e., $\alpha_{ij} = \alpha_{ji}$) to 3 (strong asymmetry, i.e., $\alpha_{ij} \neq \alpha_{ji}$), with $FD=2$ being the threshold that separates pairwise coexistence ($FD < 2$) from competitive exclusion ($FD > 2$). Each panel shows the results of the simulations: either all species coexist and we represent the stabilisation level provided by the intransitive loop for its constituent species (measured with the $\overline{\Delta R_i}$ index); or at least one species of the loop becomes extinct, and thus $\overline{\Delta R_i}$ cannot be defined (grey area). The small networks illustrate which species coexist at equilibrium (black dots: surviving species, white dots: extinct species), and the direction of pairwise interactions is indicated by arrows pointing toward the weaker competitors.



615 **Figure S2.** Scenario 3bis - The influence of one outer competitor on intransitive loops of increasing length. The intransitive loops are composed of 3, 5, 7, or 9 species, and a single outer competitor (X) influences only one species in the loop (X>A). **All pairs of species of the loop that are not next to each other do not interact.** We varied independently the strength of fit-

ness differences within the loop, and between the outer competitor and the loop species. Pair-
620 wise fitness differences (FD) ranged from 1 (perfect symmetry of competition, i.e., $\alpha_{ij} = \alpha_{ji}$) to 3
(strong asymmetry, i.e., $\alpha_{ij} \neq \alpha_{ji}$), with FD=2 being the threshold that separates pairwise coexis-
tence (FD<2) from competitive exclusion (FD>2). Each panel shows the results of the simula-
tions: either all species coexist and we represent the stabilization level provided by the intransi-
625 tive loop for its constituent species (measured with the $\overline{\Delta Ri}$ index); or at least one species of the
loop becomes extinct, and thus $\overline{\Delta Ri}$ cannot be defined (gray area). The striped area in (b-c) high-
lights conditions when the system oscillates between alternative stable states with species near-
ing extinction for longer periods over time (heteroclinic cycles). The small networks illustrate
which species coexist at equilibrium (black dots: surviving species, white dots: extinct species),
and the direction of pairwise interactions is indicated by arrows pointing toward the weaker
630 competitors.

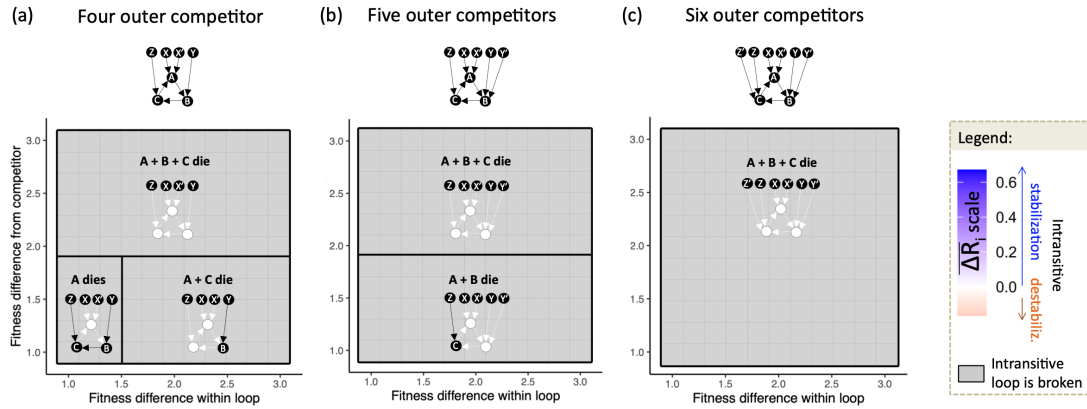


Figure S3. The influence of 4, 5, and 6 outer competitors on intransitive loop dynamics (follow up to Scenario 2). The intransitive loop is composed of three species ($A > B > C > A$), and the presence of outer competitors (X, X', Y, Y', Z, Z') varies
635 between: (a) four outer competitor ($X > A, X' > A, Y > B, Z > C$), (b) five competitors ($X > A, X' > A, Y > B, Y' > B, Z > C$), and (c) six competitors ($X > A, X' > A, Y > B, Y' > B, Z > C, Z' > C$). We varied independently the strength of fitness differences within the loop, and between the outer competitor and the loop species. Pairwise fitness differences (FD) ranged from 1 (perfect symmetry of competition, i.e., $\alpha_{ij} = \alpha_{ji}$) to
640 3 (strong asymmetry, i.e., $\alpha_{ij} \neq \alpha_{ji}$), with $FD=2$ being the threshold that separates pairwise coexistence ($FD < 2$) from competitive exclusion ($FD > 2$). Each panel shows the results of the simulations, here in all simulations at least one species of the loop becomes extinct, and thus $\overline{\Delta R_i}$ cannot be defined (grey area). The small networks illustrate which species coexist at equilibrium (black dots: surviving species, white dots: extinct species), and the direction of pairwise interactions is indicated by arrows pointing toward the weaker competitors.
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