

ARTICLE

Modeling the continua in the outcomes of biotic interactions

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Abstract

The outcome of many ecological interactions lies somewhere along a continuum between pure positive and pure negative effects. Although the popularity of this idea has notoriously risen in the last decades, with the occurrence of continua in interaction outcomes invoked for a wide variety of interactions, the absence of a precise theoretical treatment has led to considerable inaccuracy and ambiguity in its treatment. We develop here a consumer-resource model to explore the occurrence of continua. This model is based on the assumption that the distribution of individual interaction events includes both negative and positive immediate outcomes, with variable frequencies, for at least one of the interacting species. Our study shows that continua in interaction outcomes happen just by varying the sign and impact of individual events. The exact shape of the continua depends on the proportion of positive versus negative events and the relative magnitude of per-capita interaction strengths. Our model shows that continua in interaction outcomes are a key property of most pairwise interactions and are originated from the variable roles played by the interacting partners. It constitutes a step forward in the paradigm change from discrete categorization of ecological interactions to a new perspective over a continuous space.

KEYWORDS

coexistence parameter range, consumer-resource interaction, context-dependency, cusp bifurcation, distributed outcomes, dual interaction, interaction events, interaction norm, interaction outcome, mutualism-antagonism continuum

INTRODUCTION

Biotic interactions are essential components of the biodiversity of all ecological communities (Begon et al., 2006), crucial drivers of the functioning of most ecosystems (Loreau et al., 2001), and one of the most important factors shaping the evolution of species (Thompson, 2005). Biotic interactions can be envisaged as processes where

individuals of different species encounter and interact (*interaction events*). Each of these interaction events entails an immediate effect on at least one of the interacting organisms by providing them with a given resource or service or by damaging, killing, or depriving them from a given resource (the *immediate outcome* of the interaction) (*interaction mechanism* sensu Abrams, 1987). This causes an effect on the fitness of the interacting individuals

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(*individual outcome*). The interaction may subsequently have a long-term effect on the demography, growth rate and dynamics of their populations (*population outcome*) (Abrams, 1987; Jordano, 2016; Schupp et al., 2017). Consequently, biotic interactions can be decomposed in numerous events that have immediate outcomes on any of the interacting individuals and that altogether may affect the fitness of the individuals and the growth rate of the populations (Abrams, 1987; Abrams & Ginzburg, 2000; Araújo et al., 2011; Arditi & Ginzburg, 1989; Bolnick et al., 2003). For example, the immediate outcome for a plant of a pollination interaction is the deposition of pollen onto the stigma by a floral visitor, whereas the individual outcome is the consequence of this deposition for the fecundity of the plant, and the population outcome is the consequence for the growth rate of the population it belongs to. Similarly, the immediate outcome for a predator of a predation interaction is the killing and consumption of another animal, whereas the individual outcome is the consequence of this consumption for the fitness of the predator, and the population outcome is the effects on the dynamics of their populations. Interestingly, the identity of the interaction is usually defined according to their immediate outcomes (pollination, seed dispersal, plant–plant allelopathy, ant-protected plants, intraguild predation, parasitoidism, parasitism, etc.), whereas the type of interaction is defined according to their population outcomes (antagonism, mutualism, competition, commensalism, amensalism) (Abrams, 1987).

Biotic interactions are fluid, dynamic, and labile both at ecological and evolutionary timescales (Abrams, 1987; Bronstein, 2015; Holland & DeAngelis, 2009; Sachs et al., 2011; Thompson, 1982, 1988, 2005). Variation in interaction outcomes can occur at different levels (Figure 1). Although the perception of a variation in the outcome of the interactions has a long history (Ewald, 1987; Haskell, 1949; Leary, 1976; Lidicker, 1979; Yodzis, 1988), its popularity has notoriously risen in the last decades (Bolnick et al., 2011; Bronstein, 2015; Chamberlain et al., 2014; Thompson, 2005, 2013). It is widely assumed nowadays that most interspecific interactions are *context-dependent* (Butterfield & Callaway, 2013; Chamberlain et al., 2014; Frederickson, 2017; Hoeksema et al., 2010; Hoeksema & Bruna, 2015; Maron et al., 2014). Context-dependent variation in interaction outcomes is caused by spatio-temporal changes in abiotic factors (nutrient, climate, temperature, etc.) and community structure and diversity (third party, co-occurring competitors, predators, etc.) (Bronstein, 1994; Chamberlain et al., 2014). Context-dependency causes the occurrence of *interaction norms*, significant spatio-temporal variations in the outcome of interactions (Thompson, 1988, 2005). However, variation in the outcomes of ecological interactions may happen

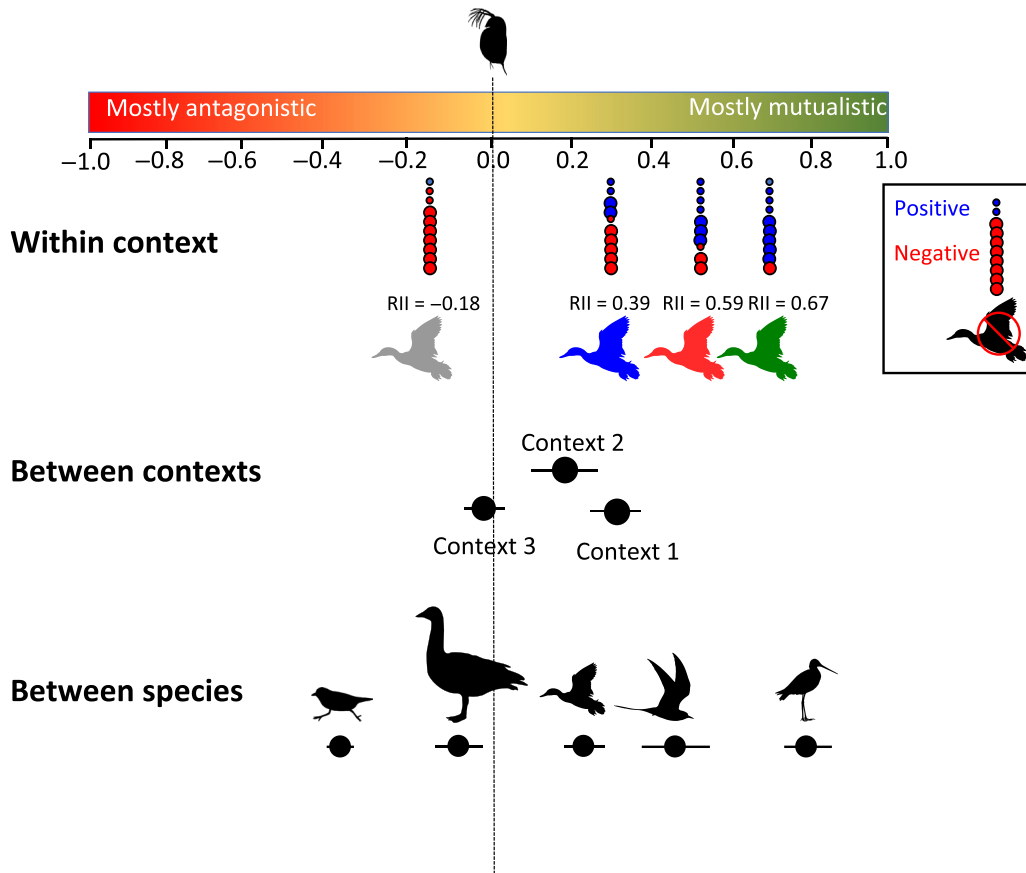
not only between contexts but also within the same ecological context as a result of age, size, phenotype, and genetic differences among the interacting individuals (*distributed outcomes*, Thompson, 1988, 2005, 2013). This variation may sometimes entail radical changes in the effect or service provided by the interacting organisms, causing, for at least one of the interacting species, the coexistence of negative and positive immediate outcomes (*dual outcomes*). For example, a proportion of aquatic invertebrates preyed upon and ingested by waterbirds is effectively killed and digested (negative immediate outcomes for the invertebrates) but another proportion is passively dispersed through endozoochory (positive immediate outcomes for the invertebrates) (Green & Sánchez, 2006; van Leeuwen et al., 2012). Similarly, a proportion of aphids tended by ants are effectively protected (positive immediate outcomes for the aphids) but another proportion is killed and consumed by ants (negative immediate outcomes for the aphids) (Stadler & Dixon, 2005). A proportion of aphid genotypes increase their survival when infected by the symbiont *Regiella insecticola* (positive immediate outcomes) but another proportion decreases (negative immediate outcomes) (Parker et al., 2021). In fact, dual outcomes occur in a wide variety of interactions, whether symbiotic (DiSalvo et al., 2015; Johnson and Graham, 2013; Johnson et al., 1997; Lin & Koskella, 2015; Mandyam & Jumpponen, 2015; Parker et al., 2021; Regus et al., 2015; Sachs & Wilcox, 2006; Saikkonen et al., 1998), or non-symbiotic mutualistic (Brehm & Mortelliti, 2022; Gómez et al., 2019; Navarro, 2000; Quinn & Kokorev, 2002), antagonistic (Belsky et al., 1993; Carper et al., 2016; Delibes et al., 2017; Green & Sánchez, 2006; Maschinski & Whitham, 1989; Paige & Whitham, 1987; Polis et al., 1989), or competitive interactions (Butterfield & Callaway, 2013; Callaway & Walker, 1997). Remarkably, dual outcomes can also occur in traditionally considered fixed interactions. For example, a proportion of predators are damaged or even killed by preys in some predator–prey interactions (Cowlshaw, 1994; Kornilev et al., 2023; Mukherjee & Heithaus, 2013). Similarly, experiments determining the pollinator efficiency using single-visit pollen deposition have frequently found that pollinators transport pollen only in a proportion of the visits, the other visits not providing any service and behaving exclusively as consumers (Herrera, 1987; Spira et al., 1992).

Acknowledging the occurrence of variation in interaction outcomes has led to the proposal of a *mutualism-antagonism continuum* as a useful framework to study the functioning of many disparate interspecific interactions, such as rhizobial symbiosis (Regus et al., 2015), fungal endophytes (Cheplick & Faeth, 2009; Mandyam & Jumpponen, 2015; Saikkonen et al., 1998), myxotrophic algae (Granéli & Turner, 2006), gut endosymbiosis

(Lin & Koskella, 2015), mycorrhizae (Johnson et al., 1997; Johnson & Graham, 2013), seed dispersal (Gómez et al., 2019; Montesinos-Navarro et al., 2017; Perea et al., 2013;

Theimer, 2005), pollination (Rodríguez-Rodríguez et al., 2017), ant-guard interactions (Cushman & Addicott, 1991; Cushman & Whitham, 1989), and brood parasitism

(A) MULTILEVEL NATURE OF CONTINUA



(B) BIDIRECTIONALITY OF CONTINUA

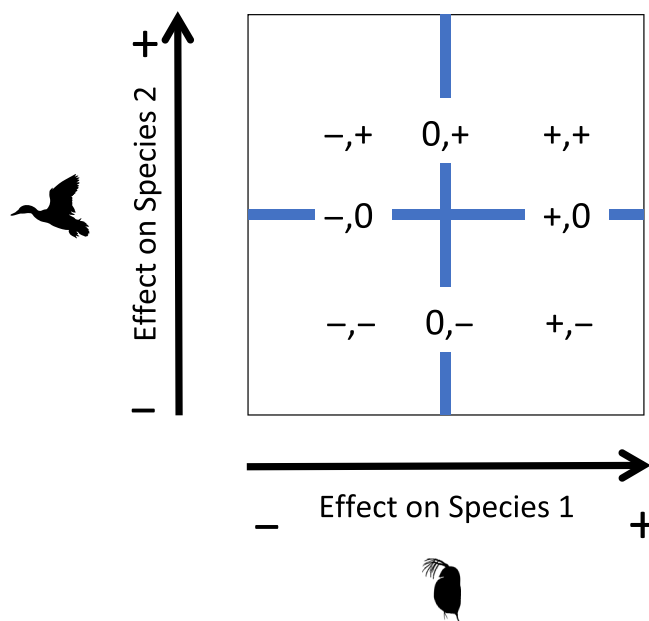


FIGURE 1 Legend on next page.

(Canestrari et al., 2014). According to this idea, the interaction between many species pairs, rather than belonging to a specific type, is located somewhere along a continuum running between pure mutualism and pure antagonism (Johnson et al., 1997; Thompson, 2005). It is important to note that the “mutualism-antagonism continuum” idea has been applied to different organization levels. So, it has been applied to differences in the interaction outcomes among individuals of one pair of interacting organisms in one single context (individuals outcomes; Cheplick & Faeth, 2009), or on one pair of interacting organisms in different contexts (sites, populations, years, etc.) (population outcomes; Canestrari et al., 2014), or between one host species interacting with several partners (Gómez et al., 2019), or even across different pairs of species (Johnson et al., 1997). This means that, as it has been conceived, mutualism-antagonism continuum has a clear multilevel nature (Figure 1A). In addition, in most cases the mutualism-antagonism continuum has been estimated as the variation in the effect of one species on its partner, assuming that the reciprocal effect is always fixed. However, continua may happen for both partners. This bidirectionality in continua result in the possibility of multiple interaction outcomes from competition to antagonism, to amensalism, to commensalism and to mutualism (Figure 1B). To accommodate these two features of the continua (multilevel nature and bidirectionality) to reduce the ambiguity of the idea, we propose the most inclusive term “*continua in interaction outcomes*”. We define *continua in interaction outcomes* as the continuous variation in the outcomes of the biotic interaction at any level (individual, population, species) resulting from the distributed outcomes on one or both partners due to the coexistence of negative and positive immediate outcomes (dual outcomes).

Although variation in the outcomes of ecological interactions is widely accepted (Bronstein, 1994; Chamberlain

et al., 2014; Thompson, 1988), theoretical approaches have defied considering it until recent times (Gibert & Brassil, 2014; Hale & Valdovinos, 2021; Holland & DeAngelis, 2009, 2010; Lichstein et al., 2007; Lloyd-Smith et al., 2005; Okuyama, 2008). In the last decade, several models based on consumer-resource interactions have been developed to explore context-dependency of interactions (Hale & Valdovinos, 2021; Holland & DeAngelis, 2009, 2010; Ke & Nakazawa, 2018; Neuhauser & Fargione, 2004; Revilla & Encinas-Viso, 2015; Wang et al., 2011; Zwolak & Crone, 2012). However, despite the widespread recognition of outcome continua as a frequent feature of many interactions, its existence has not been yet successfully explained. In this study, we develop a consumer-resource model based on the assumption that the population outcomes of the interactions are the end result of numerous interaction events that affect either negatively or positively the individuals of each interacting species. This model shows that continua in interaction outcomes can arise due to the existence of dual immediate outcomes. Our study suggests that continua in interaction outcomes are a fundamental property of most pairwise interactions that origin from the variable roles played by the interacting partners.

METHODS

A direct, consumer-resource model of interactions including dual immediate outcomes

We have used a consumer-resource (C-R) model to study ecological interactions with dual immediate outcomes. C-R models are fundamental to understand interspecific interactions (Lafferty et al., 2015; Martinez, 2020; Pimm, 1980; Turchin, 2003; Williams & Martinez, 2000;

FIGURE 1 (A) The levels at which the outcome of a given interaction may vary, illustrated here with the predation interaction between a hypothetical clonal cladoceran species and a hypothetical dabbling duck species. Four types of ducks differing in genotype or phenotype interact with 10 individuals of a given cladoceran clone within each context (represented by dots). Each time a duck encounters and ingests a cladoceran (*interaction event*), it can either consume it (*negative immediate outcome* in red) or disperse it (*positive immediate outcome* in blue). The size of the dots is proportional to the strength of each interaction event. The effect of ducks on the fitness of each cladoceran clone (*individual outcome*) is expressed as RII values obtained by comparing the outcomes with and without the interaction (see the [Methods](#) section). Negative RII values mean that the interaction is antagonistic, and positive values mean that the interaction is mutualistic. As observed in the figure, the individual outcome varies within each context (*distributed outcomes*) due to differences in the proportion of positive and negative immediate outcomes (*dual outcomes*) and in the magnitude of these effects. This causes the occurrence of *within-context continua in interaction outcomes*, expressed as between-duck differences in RII values. The effect of the ducks on the cladoceran population growth (*population outcome*), pooling together the effects of the four types, changes among contexts due to changes in either abiotic factors or co-occurring interacting organisms (*context dependency*). This causes the occurrence of *between-context continua in interaction outcomes*, expressed as between-context differences in RII values. The effect of the ducks, pooling together across all contexts, differs from the effects caused by other interacting species, such as geese, terns, godwits or plovers, as a consequence of interspecific differences in plant–animal trait matching. This between–species differences in interaction outcomes values have been used to indicate the occurrence of *interspecific continua in interaction outcomes*. (B) The continua in the outcomes of any pairwise interaction may occur for one or both interacting partners. This property makes continua to cause the interactions range across any type of biotic interaction.

Yodzis & Innes, 1992). In these models, resources are those factors that, when exploited at given rates, increase the population growth of consumers. In interspecific interactions resources are entire individuals or part of them that are exploited by the interacting partners. C-R models have proven very useful to describe the behavior of many different types of interactions, such as predator–prey interactions (Turchin, 2003), plant–herbivore interactions (Feng & DeAngelis, 2018), host–parasite interactions (Roberts, 1995), mutualistic interactions (Holland & DeAngelis, 2009, 2010) and facilitation–competition interactions (Dangles, 2019).

Our model was formulated using an extension of the Rosenzweig–MacArthur model. We propose to combine both negative and positive terms of the Rosenzweig–MacArthur model in a single equation to model pairwise interaction with dual outcomes, following some previous approaches (Holland & De Angelis, 2009, 2010; Martinez, 2020; Williams & Martinez, 2000). Our model is as following:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} \right) + N_1 \frac{\varepsilon_1 N_2}{h_2 + N_2} P_1 - N_1 \frac{\alpha_1 N_2}{e_1 + N_1} (1 - P_1). \quad (1)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} \right) + N_2 \frac{\varepsilon_2 N_1}{h_1 + N_1} P_2 - N_2 \frac{\alpha_2 N_1}{e_2 + N_2} (1 - P_2). \quad (2)$$

The first term of the model is the population growth of species *i* independent of the interaction with species *j*, modeled as logistic growth through density-dependence. *r_i* is the maximum per-capita growth rate. *K_i* is the carrying capacity of the logistic growth of the species *i* when there are no interactions with the other study species.

The second term describes the increase in the growth rate of species *i* when interacting with species *j* (by consuming or obtaining a service). This term models the positive individual outcome of the interaction assuming that the positive interaction with *N_j* saturates following a type II functional response. We modeled this response using a Michaelis–Menten equation, mathematically equivalent to Holling’s disc equation (Jeschke et al., 2002; Real, 1977). The parameter *ε_i* is the maximum positive per-capita interaction strength at which the interaction saturates, expressed as the highest positive numerical response of one individual of species *i* to the interaction with species *j* (Berryman, 1992; Feng & DeAngelis, 2018; Holland & DeAngelis, 2009; Real, 1977; Sala & Graham, 2002). The interaction strength saturates with *N_j*, following the structure of the C-R models (Arditi & Ginzburg, 2012; Turchin, 2003). This is probably the simplest assumption that can be made when

modeling positive outcomes (Holland & DeAngelis, 2009, 2010). The parameter *h_j* is, thus, the half-saturation density of species *j* (Arditi & Ginzburg, 2012).

The third term describes the decrease in population growth rate of species *i* when interacting with species *j* (by being killed, consumed, or deprived of growth and reproduction). This term models the negative individual outcome of the interaction assuming that the negative interaction with *N_j* saturates following a type II functional response. Here, *α_i* is the maximum negative per-capita interaction strength at which the interaction saturates, expressed as the highest negative numerical response of one individual of species *i* to the interaction with species *j* (Berryman, 1992; Real, 1977; Sala & Graham, 2002). In this case, the interaction strength saturates with *N_i*, following the classical C-R models for preys (Arditi & Ginzburg, 2012; Murdoch et al., 2003). The parameter *e_i* is then the half-saturation density of species *i* (Arditi & Ginzburg, 2012).

To model the existence of dual immediate outcomes, we multiplied the second and third terms by *P_i* [*0* ≤ *P_i* ≤ *1*], and *1* − *P_i*, respectively. The parameter *P_i* is the proportion of interaction events where the immediate outcomes for the individuals of the species *i* are positive either because the interacting individuals obtained a resource or is provided with a service. On the other hand, *1* − *P_i* is the proportion of interaction events where the immediate outcomes for the individuals of the species *i* are negative, either because it is killed, damaged, or cheated (no service is provided). By making *P₁* = *1* and *P₂* = *0* in our equations, we obtain a standard predator–prey model. However, in many other interactions *P₁* and *P₂* may vary between 0 and 1. We provide in Table 1 some examples suggesting how *P_i* can be recorded in different types of interactions.

Solving the model and testing variation in interaction outcomes

We solved numerically the system of equations by means of standard instructions integrated in the symbolic software Mathematica, following the instruction of NDSolve, which appeals to a classical Runge–Kutta method. We used initial conditions *N₁*(0) = 500 = *N₂*(0) (which is the chosen carrying capacity *K_i* of the habitat if interaction is not allowed), moving *P₁* and *P₂* from 0 to 1 and fixing the rest of parameters as following: (1) Each of the four per-capita interaction parameters (*α₁*, *α₂*, *ε₁*, *ε₂*) was fixed to either 0.1 as an indication of weak interaction or to 0.9 as an indication of strong interaction. This distribution of parameter values produces 16 alternative scenarios resulting from the combination of weak and strong

TABLE 1 Examples illustrating how positive and negative immediate outcomes can be measured in different types of interactions.

Interaction	Species <i>i</i>	Species <i>j</i>	Proportion of positive immediate outcomes for species <i>i</i> (P_i)	Proportion of negative immediate outcomes for species <i>i</i> ($1-P_i$)	Sources
Pollination	Plant	Floral visitor	Proportion of visits to the flowers of a given plant species made by a floral visitor resulting in pollen deposition and transfer.	Proportion of visits without pollen transportation and where the floral visitors behave as consumers rather than as legitimate pollinator.	1
Grazing	Plant	Herbivore	Proportion of seeds of a given plant species accidentally endozoochorously dispersed by grazing ungulates.	Proportion of seeds actually consumed by grazing ungulates.	2
Synzoochory	Plant	Granivore	Proportion of seeds of a plant species cached by a granivorous species.	Proportion of seeds consumed by a species of granivorous species.	3
Ant tending	Aphid	Ant	Proportion of ant-tended aphids that are not preyed upon by ants.	Proportion of ant-tended aphids preyed by ants.	4
Brood parasitism	Cuckoo	Host	Proportion of cuckoos that parasite naïve hosts lacking experience and cognitive abilities to kill their parasites.	Proportion of cuckoos that parasite experienced hosts that kill the parasite eggs or chicks.	5
Predation	Invertebrates	Waterbirds	Proportion of live and viable invertebrates passing through the digestive tract and defecated.	Proportion of ingested invertebrates that are killed and eventually digested.	6
Intraguild predation	Carnivore	Carnivore	Proportion of events where the individual of species <i>i</i> is larger than the individual of species <i>j</i> in systems where predation is size-dependent.	Proportion of events where the individual of species <i>i</i> is smaller than the individual of species <i>j</i> where predation is size-dependent.	7
Facilitation/competition	Plant	Plant	Proportion of seedlings of a plant surviving when associated with another plant species	Proportion of seedlings of a plant dying when associated with another plant species	8
Endoparasitism	Microparasite	Host	Proportion of parasites surviving to the attack of the immune responses	Proportion of parasites killed by the immune system	9

Note: In all cases, the immediate outcomes are measured on species *i* as a consequence of the interaction with species *j*. The column “Sources” includes studies where this metric has been empirically recorded in real systems. (1) Herrera, 1987; Spira et al., 1992; (2) Delibes et al., 2017; (3) Gómez et al., 2019; (4) Stadler & Dixon, 2005; (5) Molina-Morales et al., 2014; (6) Martín-Vélez et al., 2022; van Leeuwen et al., 2012; (7) Polis et al., 1989; (8) Castillo et al., 2010; (9) Ariyaratne & Finney, 2019; Meeusen & Balic, 2000.

interactions (see below). (2) r_i was fixed to 1. (3) h_i and e_i , were fixed to 50. We found that the transient phase was completed, and an equilibrium state was achieved after 100 generations (a numerical integration after 1000 generations provided identical results).

The overall effect, whether positive or negative, of one species on another species needs to be evaluated by comparing population growth with and without the presence of the interacting species (Bogdziewicz et al., 2020; Zwolak & Crone, 2012). To do this, we compared the population sizes of each interacting species resulting from running our

model at all combinations of P_1 and P_2 values with the outcomes obtained from a model solved in the absence of the interaction. To do this, the final population sizes of N_1 and N_2 obtained from the models for each of the 16 resulting scenarios were compared with those obtained from a model solved by fixing all per-capita interaction parameters ($\alpha_1, \alpha_2, \varepsilon_1, \varepsilon_2$) to zero. The comparison between the models with and without interaction was made using an index widely used in ecology to determine experimentally the outcome of the interactions, the Relative Interaction Intensity (RII; Armas et al., 2004). We calculated RII as

$$\frac{N_i^{with\ Interaction} - N_i^{without\ Interaction}}{N_i^{with\ Interaction} + N_i^{without\ Interaction}} \tag{3}$$

Where N_i is the population size at equilibrium after 100 generations. RII varies between -1 (when $N_i^{with\ interaction}$ is zero) and 1 (when $N_i^{without\ interaction}$ is zero) and is symmetrical around zero (Armas et al., 2004). The symmetry property is important since it allows comparing positive and negative outcomes on the same scale (Chamberlain et al., 2014). Negative values indicate that the effect of species j on i is negative, while positive values indicate positive effect of species j on i . We plotted all the RII values in a 2-dimensional space defined by variations in P_1 and P_2 (P -space hereafter) and marked the regions where bifurcations occur. In the resulting P -space, we identified the regions where the outcome of the interactions is positive for both species, for only one species, and for neither species.

All Mathematical codes are available in Zenodo/Github (ptorres-ugr., 2023).

Exploring the continuum in interaction outcomes

The continuum in interaction outcomes was explored by observing how RII values of species 1 vary depending on the gradual change in P_1 for each of the combinations of per-capita interaction strengths. We identified in each case the P_1 critical values where RII changes from negative values to zero or positive values (P_1^* hereafter). Because RII is calculated at equilibrium, P_1^* is the value of P_1 at which interaction changes sign for species 1. This analysis was made for several values of P_2 to check for possible interactions between P_1 and P_2 . Because the model is symmetrical, the results are identical for the species 2 and, therefore, are not shown here.

RESULTS

Variation in interaction outcomes

The comparison of the population sizes at equilibrium with and without interactions by means of RIIs indicates that the whole range of outcomes can be found occupying different regions of the P -space (Figure 2). In addition, this analysis also shows the existence of transitions between positive and negative outcomes (Figure 2). Interestingly, the patterns followed by these transitions varied depending on the values of the per-capita interaction parameters (Figure 2).

When all per-capita interactions are weak (Figure 2a), the P -space is divided in four almost identical regions

identifying the combination of positive and negative outcomes for each of the two species. The interaction is negative for the two species when their P_i values are low, changing to positive as P_i values increase. Consequently, the interaction is $-$, $-$ in the bottom left corner of the P -space, $+$, $+$ in the upper right corner and $+$, $-$ in the other two corners (Figure 2a). When increasing the strength of the positive per-capita interaction (ϵ_1 and/or $\epsilon_2 = 0.9$), the pattern of transition is qualitatively similar, differing only in the relative extension of the region associated with positive and negative outcomes and the P_i values where the negative–positive transitions occur (Figure 2b–d).

A qualitatively different situation is observed when the per-capita negative interaction of species 1 onto species 2 is strong ($\alpha_2 = 0.9$). In this case, species 2 becomes extinct below a given threshold of P_2 , the exact position of this threshold depending on the value of the other three per-capita interaction parameters (Figure 2e–h). This creates a large region of the P -space where the interaction is absent. In the region where both species coexist, the behavior of the system is similar to the previous four scenarios, with a steady change from antagonism to mutualism as the proportion of positive interactions increases. The symmetrical situation, when the per-capita negative interaction of species 2 onto species 1 is strong ($\alpha_1 = 0.9$), causes opposite scenarios (Figure 2i–l). In this case species 1 becomes extinct at low values of P_1 , that is, a high proportion of positive interactions are necessary for species 1 to survive, and the region of P -space where both species coexist is again small. The change from negative to positive effects occurs for species 1 at large values of P_1 (Figure 2i–l).

Another qualitatively different situation is observed when both per-capita negative interactions are strong ($\alpha_1 = \alpha_2 = 0.9$) (Figure 2m–p). When this occurs, one or both species become extinct in a large region of the P -space, causing the interaction to collapse. The small region of the P -space where the two species can coexist is divided in four subregions where the interaction is negative for both species, negative for one species, and positive for the other, or positive for both species (Figure 2m–p). In the language of the classical theory of catastrophes (Kuznesov, 1998; Poston and Stuart, 1979), what we found in this scenario is a subcritical cusp bifurcation. Outside the cusp, one of the species becomes extinct (Figure 3). Inside the cusp (white areas), there are three nontrivial equilibria and only one of them is stable (Figure 3). The stable manifold of the two unstable equilibria determines the frontier of the coexistence area.

To check the robustness of our results, we changed the values of α_1 , α_2 , ϵ_1 , ϵ_2 in a continuous way from 0.1 to 0.9 and recorded the resulting changes in the P -space

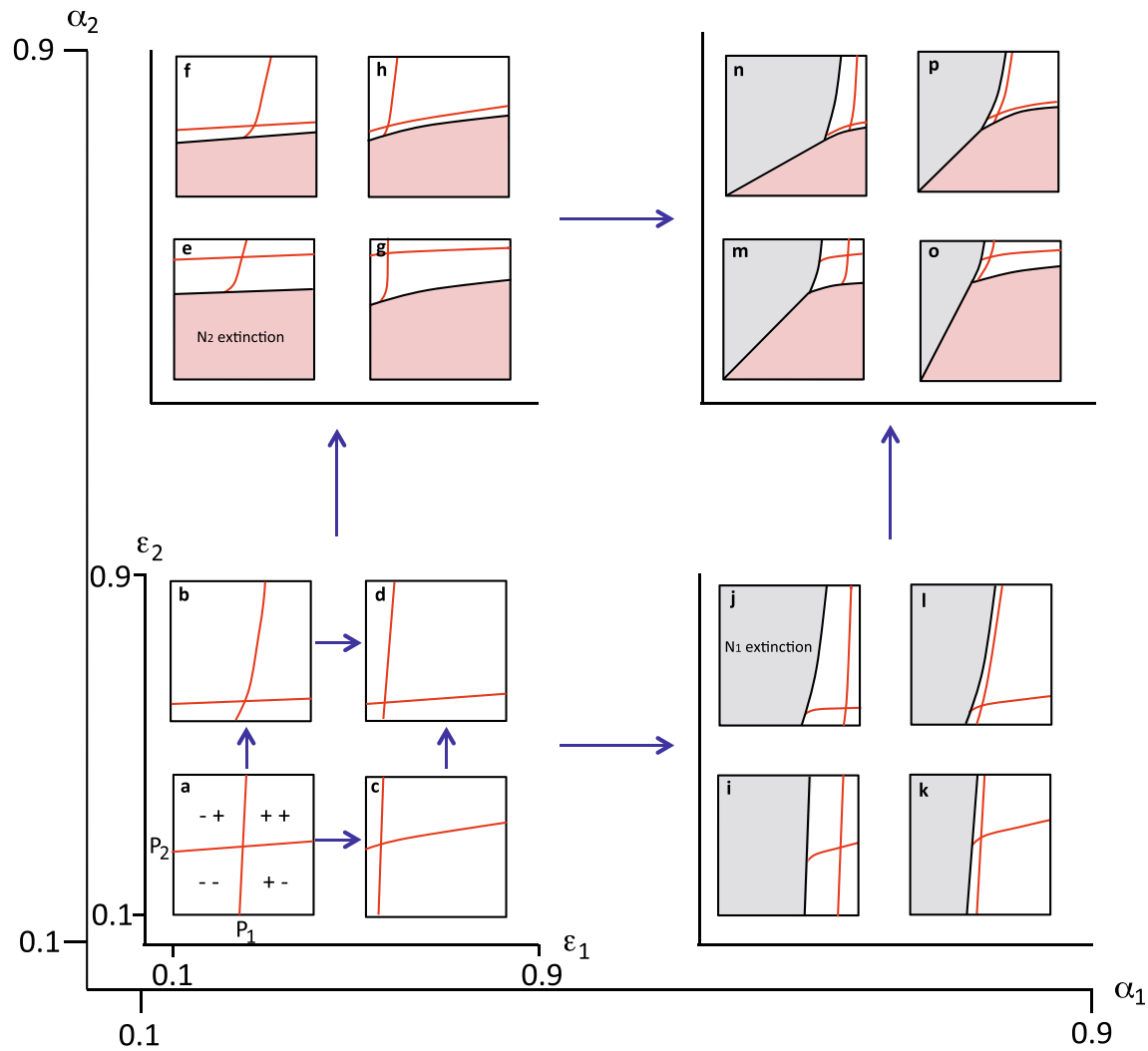


FIGURE 2 Transitions between interaction outcomes, quantified as changes in the sign of RII values, across the P -space for two contrasting values (0.1 and 0.9) of the negative (α_i) and positive (ϵ_i) per-capita interaction strengths. The x and y axes of each panel depict the continuous variation of P_1 and P_2 from 0 to 1, respectively. Red thin lines delimit the regions of the P -space with different interaction outcomes. As depicted in the (a) panel at the lower-left corner, the upper-right region delivers mutualistic outcomes (+, +), the upper-left and the lower-right deliver antagonistic outcomes (-, +) and (+, -), and the lower-left region competitive interactions (-, -). Thick black lines delimit the region of the P -space where interaction collapses because one or both species become extinct. Gray areas are the regions where N_1 becomes extinct, red areas are the regions where N_2 becomes extinct, and white areas are the regions where both species coexist. The blue arrows indicate the transition between scenarios as we change the parameters of the model (alphas and epsilons) from 0.1 to 0.9.

patterns. We observed the existence of a smooth transition between any pair of scenarios, represented by blue arrows in Figure 2. The region of extinction for any of the two species appeared when the corresponding $\alpha_i > 0.32$. We additionally checked the robustness of our results by changing two orders of magnitude the values of both r_1 and r_2 , from 0.1 to 1 to 10 for each of the 16 scenarios. The patterns appearing when changing the per-capita growth rates reflect what we have found when changing the other saturation parameters (Appendix S1). This includes the existence of regions in the P -spaces where one of the species becomes extinct and the appearance of cusp bifurcations when r 's values are low and

symmetrical (Appendix S1). All these analyses suggest that the patterns that we found and are provided in Figure 2 are robust.

Continua in interaction outcomes

Our analysis shows that the value of P_1^* varies depending on the relative strengths of positive and negative per-capita interactions and the proportion of positive immediate effects of species 1 on 2 (P_2) (Figure 4).

When the negative per-capita interaction is weak for species 1 and both positive per-capita interactions are

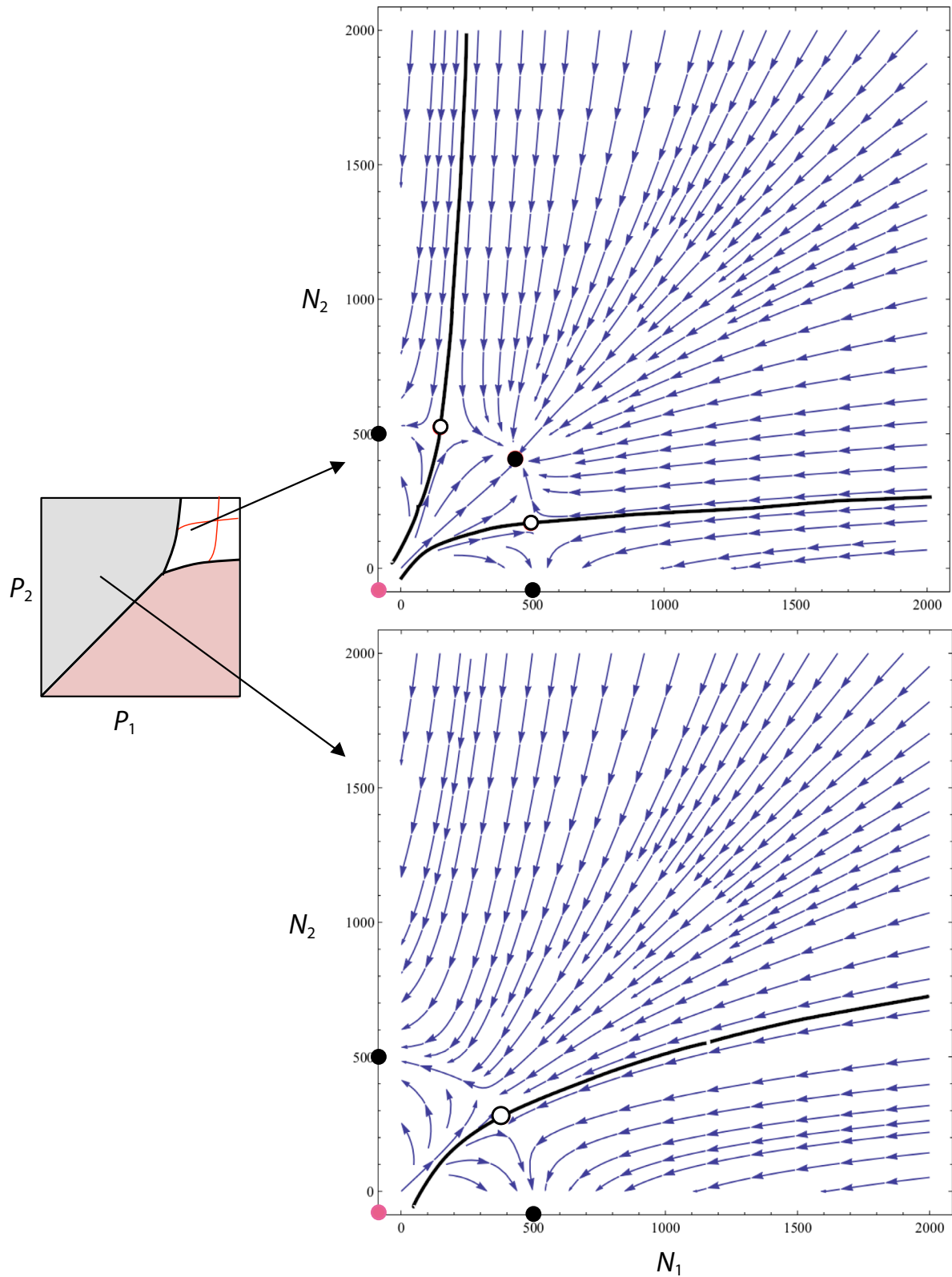


FIGURE 3 Phase-plane diagrams for the population dynamics of the two interacting species when positive interactions ($\epsilon_1 = \epsilon_2 = 0.1$) are weak and negative interactions ($\alpha_1 = \alpha_2 = 0.9$) are strong (scenario m in Figure 2). Upper diagram illustrates a situation where both species coexist but the interaction is negative for both of them (the region marked in the bifurcation diagram with the arrow). Bottom diagram illustrates a situation where species 1 has gone extinct and species 2 stays (the region marked in the bifurcation diagram with the arrow). Thick lines are separatrices (frontiers between extinction and coexistence regions), stable equilibria are notated with black filled nodes, unstable equilibria with red nodes, and saddle points with hollow nodes.

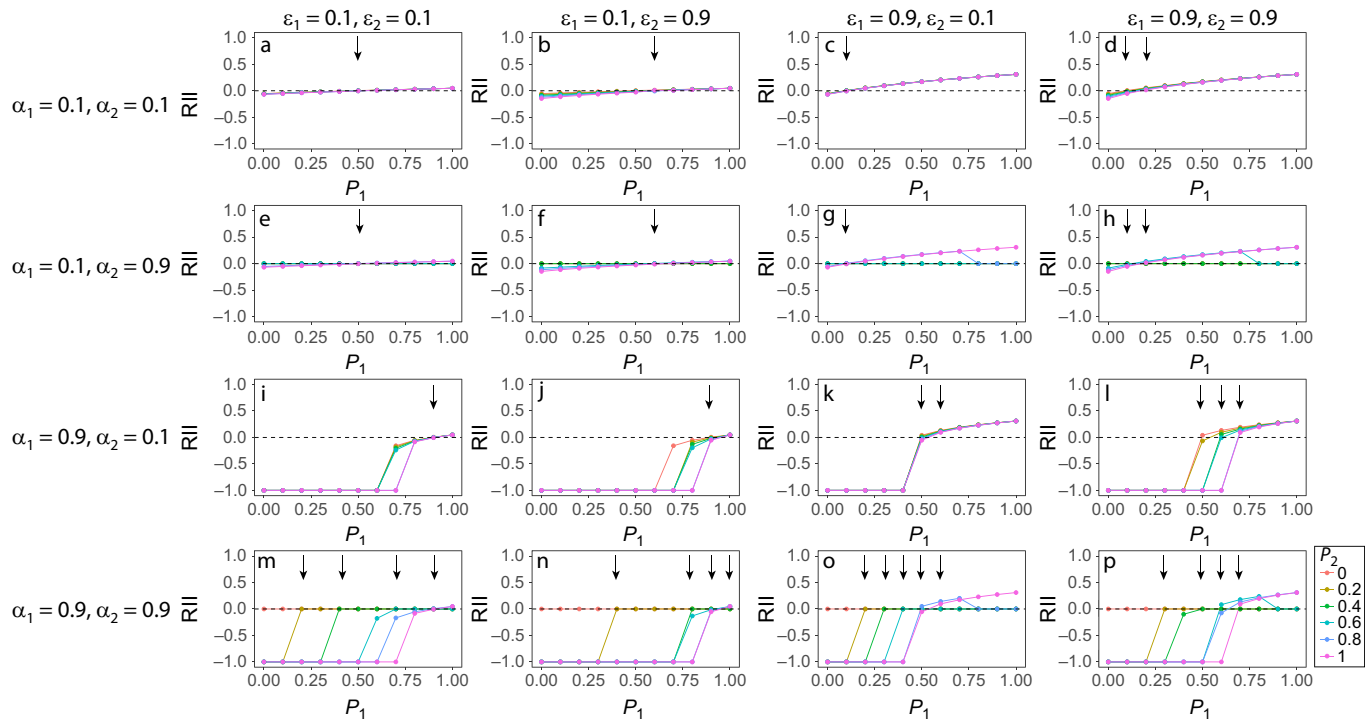


FIGURE 4 Continua in interaction outcomes for species 1 depicting the change in the sign of the RII values as a function of changes in the proportion of positive individual interactions (P_1), for strong (0.9) and weak (0.1) values of positive (ϵ_1, ϵ_2) and negative (α_1, α_2) per-capita interaction strengths, and proportion of positive individual interactions for the other interacting species (P_2). The critical values of P_1 at which the changes in the sign of the RII values take place (P_1^*) are shown by arrows. The a–p letters inside each panel show the different combinations of alphas and epsilons that correspond with the scenarios shown in Figure 2.

also weak ($\alpha_1 = \epsilon_1 = \epsilon_2 = 0.1$, Figure 4a,e), a gradual increase in the values of RII is observed, with P_1^* equal to 0.5 for all P_2 values (Figure 4a,e). When negative per-capita interaction is weak for species 1 ($\alpha_1 = 0.1$) but positive per-capita interaction is strong for species 2 ($\epsilon_2 = 0.9$), P_1^* is 0.6 (Figure 4b,f). When negative per-capita interaction is weak ($\alpha_1 = 0.1$) but positive per-capita interaction is strong ($\epsilon_1 = 0.9$) for species 1, there is also an steady increase in the RII, but P_1^* occurs this time at much lower values, the exact point depending on the value of P_2 , the smaller the P_2 value the sooner the change from negative to positive (Figure 4c,d,g,h). That is, the interaction is positive for a given species not only due to the proportion of positive immediate outcomes receiving from the other species but also depending on the proportion of negative immediate outcomes giving to the other species.

When negative per-capita interaction is strong only for species 1 ($\alpha_1 = 0.9$) but positive per-capita interaction is weak ($\epsilon_1 = 0.1$), RII of species 1 is -1 during most of the range of P_1 values, indicating that N_1 is zero and species 1 is extinct (Figure 4i,j). At intermediate values of P_1 , the abundance of species 1 suddenly increases and RII becomes larger than zero, the interaction changing from negative to positive (Figure 4i). P_1^* is thus reached

at large values of P_1 (Figure 4i,j). When the positive per-capita interaction for species 1 becomes strong ($\epsilon_1 = 0.9$), P_1^* is reached at intermediate values (Figure 4k). When the two positive per-capita interaction parameters become strong, the behavior of the continua becomes more complex (Figure 4l). So, RII is still -1 for a large range of P_1 values. However, and contrasting with the previous situation, the increase in abundance of species 1 occurs at different values of P_1 for different values of P_2 , and P_1^* values are more evenly distributed. Again, P_1^* occurs later at larger values of P_2 (Figure 4l).

The most complex behavior occurs when all per-capita negative interactions are strong (Figure 4m–p). In this situation, RII is zero along all P_1 values if P_2 is zero. This is a surprising result, because it means that when species 1 has not any positive effect on species 2, it does not benefit from the interaction. When P_2 is low ($P_2 = 0.2$ & 0.4), RII is -1 during a short range of P_1 values, rising then to zero for the rest of the P_1 values. This means that when species 1 has scarce positive effects on species 2, it goes extinct unless it receives a certain amount of positive interactions from its partner. In any case, RII values do not rise above zero, meaning that the interaction is not beneficial for species 1. At intermediate values of P_2 ($P_2 = 0.6$), RII is -1 during a considerable

range of P_1 values, rising then to positive values but dropping again to zero at large values of P_1 (Figure 4m–p). Only when P_2 is large ($P_2 = 0.8$ & 1.0) RII remains positive, although P_1^* is over 0.50. That is, species 1 must have frequent positive effects on species 2 to obtain a benefit from the interaction.

DISCUSSION

Novelty and generality of our model

Biotic interactions have been intensely examined, both theoretically and empirically, during the last century, and because of the vast body of knowledge accumulated during this period, some general principles have been developed. However, there are still significant gaps that need to be addressed to build a comprehensive and definitive theory on the evolutionary and ecological consequences of biotic interactions. One of the most relevant gaps in the theory of biotic interactions is related to the fact that they are ecologically and evolutionarily labile. This implies that many interactions do not have precise signs, blurring the boundaries between the different types of interactions (Holland & DeAngelis, 2009). Sometimes, the interacting organisms play dual roles (Gómez et al., 2019; Thompson, 1982, 1988, 2005). Consequently, most of the time, the outcomes of biotic interactions move along a continuum (Johnson et al., 1997). The models developed up to date have successfully described the context dependency of biotic interactions (Holland & DeAngelis, 2009, 2010; Ke & Nakazawa, 2018; McGill, 2005; Neuhauser & Fargione, 2004; Revilla & Encinas-Viso, 2015; Wang et al., 2011; Zwolak & Crone, 2012). We provide here a model that goes one step further and shows that the outcome of the interactions may vary in such a way that continua in interaction outcomes may occur even without any change in the context. This occurs because our model approaches the interaction between any pair of species from their fundamental components, the interaction events. In comparison to previous models, the presence in our model of the parameter P_i , a parameter that indicates the proportion of interaction events that are positive or negative for the interacting organism, allows modeling the occurrence of variation in the immediate outcomes of the interactions. By including the idea of distributed and dual outcomes, the model is more realistic and interaction events vary in their immediate outcomes (positive vs. negative) even under the same environmental conditions.

An important distinctiveness of our theoretical approach is that it teases apart the direct negative effect of an organism on the fitness of its partner from the

decrease in fitness resulting from the investment in the production and maintenance of interaction traits, because the negative term in our model is not the cost caused by investing in an interaction trait but the negative numeric response of one species to the interaction with the other species. This opens the possibility of evaluating separately the effect resulting from establishing an interaction from that of displaying a trait that it is useful only when the interaction occurs. In the current assessment of the model, we have not considered any cost of the interaction traits, to focus on the consequences of changing the magnitude of the parameters of the dual immediate effects. In addition, because we have not explored the systematic variation in other parameters, we cannot predict the behavior of the system across these dimensions of the parameter space. We will explore in future studies the consequences of modifying the magnitude of these parameters for the transition patterns found here. Nevertheless, we are confident that the pattern shown in this study is robust, since it remained similar after the perturbation of saturation parameters and the maximum per-capita growth rate.

Our model also describes those situations where both partners are negatively affected, as shown by the $-$, $-$ region appearing in most P -space scenarios of Figure 2. This type of mutually negative interactions is traditionally associated with competitive interactions. Because our model focuses on direct interactions, it cannot be applied to classic exploitative indirect competitions. Nevertheless, when competition occurs by interference, the interaction is direct. In many of these competitive interactions, one partner may even provide a service to the other partner. For example, many competing plants may facilitate the growth, reproduction, and survival of their partners by ameliorating the stressful environmental conditions (Bertness & Callaway, 1994). In this type of interactions, outcomes can range from $-$, $-$ to $-$, 0 to $-$, $+$ and even $+$, $+$ (Yang et al., 2022). Mutually negative interactions may occur in non-competitive interactions. They may occur in, for example, interactions where the preys consume some life-history stages of their parasitoids (Obregón et al. 2012) or kill their predators (Cowlshaw, 1994; Mukherjee & Heithaus, 2013), or when predators are engaged in mutual predation and intraguild predation (Polis et al., 1989). Mutually negative outcomes may even happen within the context of mutualistic interactions. For example, some ant-tended *Lycaenid* butterflies could compete with their mutualistic tending ants when they are adults because they visit the same plant species for floral nectar (Atsatt, 1981). Likewise, many bird and mammal species that forage together forming mutualistic heterospecific groups can sometimes compete and interfere agonistically (Cimprich & Grubb, 1994; Pomara et al., 2003; Stensland et al., 2003; Zamora et al., 1992).

As a consequence of our theoretical approach, our model uses the same equation to model those direct interactions that are always negative (i.e., many predator–prey interactions or interference competitions), always positive (i.e., many mutualisms and commensalisms), and those interactions where positive and negative immediate outcomes coexist (Butterfield & Callaway, 2013; Callaway & Walker, 1997; DiSalvo et al., 2015; Gómez et al., 2019; Johnson et al., 1997; Johnson & Graham, 2013; Lin & Koskella, 2015; Mandyam & Jumpponen, 2015; Paige & Whitham, 1987; Regus et al., 2015; Saikkonen et al., 1998). Therefore, a main strength of this model is its generality, because it can be applied to any classical type of interspecific interaction.

Main predictions of our model

Our model contains several testable predictions about how the continua in the outcomes of biotic interactions behave. First, our model predicts that the critical value of P_1 where the transition between positive and negative outcomes occurs is not fixed but varies depending on the per-capita interaction strengths. Specifically, we found that mutualistic interactions are more likely not only when positive immediate outcomes are more frequent but also when per-capita positive interactions are strong because mutualistic partners are more effective (e.g., $\varepsilon_1 = 0.9$, Figure 4). This finding is congruent with the results obtained from many previous models examining mutualistic interactions (Hale & Valdovinos, 2021). Interestingly, our model has found that strong per-capita positive interactions facilitate the occurrence of mutualisms even when the proportion of interaction events with negative immediate outcomes is high (i.e., low values of P_1 and P_2), an indication of the frequent occurrence of cheating interactions. Presence of cheaters is common in most mutualisms (Jones et al. 2015; Sachs, 2015), where they seem to improve their stability (Ferriere, 2002; Foster & Kokko, 2006), diversity, and complexity (Wechsler & Bascompte, 2022). Our model is in concordance with these theoretical results, and it also predicts that mutualisms can be stable even under the presence of a considerable frequency of cheaters as long as the beneficial effect of the mutualistic partners is high.

It is widely admitted the existence of a trade-off between interaction strength and stability of consumer-resource models (Murdoch et al., 2003; Ushio et al., 2018; Vasseur & McCann, 2005). Whereas an increase in the per-capita interaction strength has been frequently associated with the destabilization of consumer-resource interactions (McCann, 2012; Vasseur & McCann, 2005), many theoretical and empirical studies have shown that

weak interactions often lead to greater stability (Barabas et al., 2016; Gellner & McCann, 2016; Karakoç et al., 2020; May, 1974; McCann et al., 1998; Ushio et al., 2018). Our model is again in concordance with these theoretical predictions and found that an increase in per-capita strength of the antagonistic interaction may result in a crash in the populations of the interacting organism that may lead to its extinction. In those scenarios where per-capita negative interactions are strong there is an ample region of the parameter space where one species goes to extinction. However, this effect vanishes when increasing the frequency of interacting events with positive immediate outcomes for the resource. That is, our model predicts that increasing the proportion of positive interaction events counteracts the detrimental effect of strong negative interactions and confers stability to the system.

However, the shapes of the continua in interaction outcomes (P_i^*) are molded not only by the P_i values but also by the relative proportion of P_i and P_j values. In fact, as shown in Figure 4, the interaction is positive for a given species not only due to the proportion of positive immediate outcomes receiving from the other species (P_i) but also depending on the proportion of positive immediate outcomes providing to the other species (P_j). When the per-capita interaction strengths are high, our model predicts that the relevance of P_j is more important, and that the more beneficial a given species is for the other species the more detrimental it is for itself (i.e., a larger value of P_i is needed to reach the threshold from negative to positive outcome). This is an interesting prediction that merits further testing with the establishment of empirical experiments. Altogether, these results suggest that the continua in interaction outcomes are not just a linear function of the proportion of positive versus negative interaction events affecting the target species but are also influenced by retroactive effects mediated by the population dynamics of the partner species.

Properties of the continua in interaction outcomes

Any continuum in interaction outcomes can be envisaged as a gradient resulting from the combination of per-event effects of one interacting species on its partner. Our theoretical approach may help to identify some general properties of continua in interaction outcomes.

First, continua in interaction outcomes can occur just for one member or for both members of the interacting pair. This is because, although ecological interactions are defined by the occurrence of reciprocal, bidirectional effects, they are actually the combination of two unidirectional effects (Vázquez et al., 2015; Yodzis, 1988). This

property, the fact that continua can be unidirectional or bidirectional, is crucial because it is the main reason why the continua does not range along one single mutualism-antagonism axis but can also take place along the two axes defined by the two effects occurring in any pairwise interaction (Figure 1B). This bidimensionality of the continuum is what causes the range not only between mutualism and antagonism but also commensalism, ammensalism, and competition (Figure 1B).

Second, continua in interaction outcomes have been proposed mostly when comparing the between-context variation in interaction outcomes (Canestrari et al., 2014; Lin & Koskella, 2015; Maschinski & Whitham, 1989; Saikkonen et al., 1998). In this case, continua in interaction outcomes are the consequence of the occurrence of interaction norms (Figure 1A). However, our theoretical approach shows that continua in interaction outcomes is multilevel and can also occur within context as a consequence of within-population variation in dual immediate outcomes (Lin & Koskella, 2015; Mandyam & Jumpponen, 2015; Regus et al., 2015). That is, our model indicates that the existence of context-dependency is not necessary for the occurrence of continua in interaction outcomes. In fact, we propose that dual outcomes at within-context level may scale up and cause the appearance of context dependency. Under this idea, continua expressed at higher levels of interaction (individuals, populations, and species) are the consequence of dual outcomes occurring at the lowest level of interactions (interaction events).

Third, continua in interaction outcomes have often been presented as patterns resulting from combining information of multiple and disparate pairwise interactions (Gómez et al., 2019; Johnson et al., 1997; Johnson & Graham, 2013; Perea et al., 2013; Saikkonen et al., 1998; Stadler & Dixon, 2005). However, because the continuum in interaction outcomes is a pattern that informs us about how fuzzy is the outcome of particular biotic interactions, we consider that it has theoretical and empirical significance mostly when explored for pairs of interacting species separately or for one species interacting with a set of species (Figure 1A). In this sense, our proposal is analogous to the approach used to study context dependency, a phenomenon considered to be a property of each single pairwise interaction (Chamberlain et al., 2014).

Applicability of the model to real-world ecological interactions

A fundamental consideration is to assess how applicable is our theoretical approach. The only extra information that our model requires with respect to previous models is the distribution of immediate outcomes of interaction

events. Although gathering this information could be considered a difficult task, this approach is already taken by field ecologists working on interaction effectiveness, interaction intensity, coevolution, eco-evolutionary dynamics, individual specialization, or individual-based networks (e.g., Bolnick et al., 2003; Brehm & Mortelliti, 2022; Gómez et al., 2019; Thompson, 1988, 2005). To show the applicability of our model, we briefly describe here some aspects of the natural history of a few interactions to show how the distribution of immediate outcomes of interaction events is routinely assessed. For example, when assessing the trophic interaction between waterbirds and their invertebrate preys, many studies have counted the proportion of live and viable invertebrates appearing in feces and pellets (P_i), in some cases after having been fed a known number of invertebrates, versus the proportion that were killed and consumed during the digestion process ($1-P_i$) (Martín-Vélez et al., 2022; van Leeuwen et al., 2012). Likewise, when studying the interactions between plants and synzoochorous seed dispersers, studies usually quantify the proportion of encounter seeds that are dispersed (P_i) to be eventually cached in different microsites differing in suitability for seed germination, seedling emergence and survival, versus the proportion of those killed and consumed in situ ($1-P_i$) (e.g., Forget, 1992; Gómez, 2003; Gómez et al., 2008; Muñoz & Bonal, 2007; Pesendorfer et al., 2016). When studying the effectiveness of floral visitors as pollinators, many studies quantify the proportion of visited flowers receiving some pollen on the stigma or donating some pollen to the visitors (P_i) versus those where the visitors did not touch the stigma or anthers and consumed pollen and/or nectar without transporting and transferring pollen and behavior ($1-P_i$) (Herrera, 1987; Spira et al., 1992). When studying the interaction between vertebrates and their endoparasites, many studies record the proportion of parasites surviving to the attack of the immune responses and thereby infecting and living on the host tissues (P_i) versus those killed by some immune system components such as eosinophils and macrophages ($1-P_i$) (Ariyaratne & Finney, 2019; Meeusen & Balic, 2000). These few examples, selected from a wider diversity of other interactions with similar information, indicate that our model can be easily applied to real-world ecological interactions.

Scaling up from pairwise interactions to food webs and interaction networks has been done by extending consumer-resource models to a multi-species level (Hale, Valdovinos & Martinez, 2020; Lockwood et al., 1997; Montoya & Solé, 2003; Pimm, 1980; Schneider et al., 2016; Valdovinos et al., 2010; Williams & Martinez, 2000, 2004, Yan & Zhang, 2019). Under this idea, two-species models are used as building blocks of more complex systems

involving many interacting species (Martinez, 2020; Yodzis & Innes, 1992). The model described in this study can be also scaled up to generate a multi-species model. We presume, however, that the resulting model would be more complex than most previous ones because the pairwise interactions include both positive and negative effects. Nevertheless, it is worthy to explore how the extension and intensity of dual immediate outcomes and the presence of continua in interaction outcomes may influence the dynamics of ecological communities (Martinez, 2020; Yodzis & Innes, 1992), the appearance of higher-order interactions (Kleinhesselink et al., 2022), and the functioning of ecosystems (Schneider et al., 2016).

CONCLUSIONS

Considering the interaction event as the fundamental unit that generates the properties of a given pairwise interaction, we have developed a new model that allows assigning the position of a given pairwise interaction along a continuum between competition, antagonism, amensalism, commensalism, and mutualism within the same environmental context. This means that the changes in sign are not just derived from changes in the environmental context, but essentially originate from the variable roles played by the interacting partners. Any pairwise interaction could in principle change from mutualistic to commensalistic to antagonistic to competitive within the same context. The general model described here provides a useful tool for assessing the net impact of interacting organisms on their partner for any type of interspecific interaction, irrespective of the type of relationship establishing between them. Thus, our model facilitates the transition from a classical categorical standpoint of biotic interactions to a more realistic perspective providing a treatment of the interactions over a continuous space. This allows the identification of subtle changes in the distribution of interaction outcomes and affords new insight, fostering the development of new theoretical and empirical advances in the study of biotic interactions.

AUTHOR CONTRIBUTIONS

The study was conceived, performed, and written by all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No data were collected for this study. Codes (ptorres-ugr, 2023) are available Zenodo at <https://doi.org/10.5281/zenodo.7551807>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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