

The big ifs in the outcomes of species interactions: review and insights from the *Interaction Function (IF)* model

Desenlaces condicionales en interacciones entre especies: revisión y perspectiva del modelo *Función de Interacción (FI)*

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Abstract— The conceptual framework for species interactions calls for a new perspective: conditional outcomes are not rare; but, rather, closer to the norm. Interactions may shift or switch between beneficial and detrimental following variations in the (context-dependent) balance of costs and benefits involved for each species. A classic (simple) model such as a Lotka-Volterra can be adjusted to represent these (complex) dynamics by introducing the appropriate nonlinearities in the interspecific terms. The Interaction Function (IF) model introduces a density-dependent function that takes values along the negative to positive continuum; a change in sign denotes a shift in the effect of one species on the other. In this paper I discuss the foundations and development of the IF model, along with other models and conceptual bodies that have emerged on the topic. A brief advance on the central results: (i) the systems present multiple stable equilibria where species may coexist at any combination of interaction outcomes (+, −, 0), or one be excluded, (ii) transitions between outcomes occur either gradually (environmental conditions vary) or abruptly (drastic change in population abundances leads to another domain of attraction); catastrophic jumps are also possibilities, (iii) fragmentation of space and dispersal trigger source-sink dynamics that cause further variation in the outcomes at local and regional levels, and, remarkably, dynamic variations in the sink or source roles of localities and populations also occur. The fundamental conclusion is that the beneficial or detrimental role of a species in an association is a spatiotemporal dynamic quality, determined by the balance of many concurrent density-dependent effects, some reinforcing, some counteracting, one another.

Keywords—context-dependent, alternative stable states, conditional outcomes, spatiotemporal dynamics, density-dependence, cost-benefit, theoretical ecology, mutualism, antagonism, exploiter

Resumen— El marco conceptual de interacciones entre especies requiere una nueva perspectiva: los desenlaces variables (condicionados) no son raros; están más bien cerca de ser la norma. Las interacciones pueden cambiar entre beneficiosas y perjudiciales debido a variaciones en el balance (contexto-dependiente) de los costos y beneficios involucrados para cada especie. Un modelo clásico (simple), como Lotka-Volterra, se puede ajustar para representar estas dinámicas (complejas) introduciendo las no linealidades apropiadas en los términos interespecíficos. El modelo de Función de Interacción (FI) para desenlaces condicionales introduce una función denso-dependiente que toma valores a lo largo del continuo negativo a positivo; un cambio de signo denota un cambio en el efecto (denso-dependiente) de una especie sobre la otra. En este artículo analizo los fundamentos y desarrollo del modelo FI, junto con otros modelos y marcos conceptuales que han surgido en el tema. Un breve avance de los resultados centrales: (i) los sistemas presentan múltiples equilibrios estables donde las especies pueden coexistir, en cualquier combinación de desenlaces de interacción (+, −, 0), o una especie puede ser excluida, (ii) ocurren transiciones entre desenlaces, ya sea gradualmente (condiciones ambientales varían) o abruptamente (cambio drástico en abundancias poblacionales conduce a otro dominio de atracción); saltos catastróficos también son posibilidades, (iii) la fragmentación del espacio y la dispersión, desencadenan dinámicas fuente-sumidero que causan mayor variación en los desenlaces a nivel local y regional y, notablemente, también ocurren variaciones dinámicas en los roles de fuente y sumidero de las localidades y regiones. La conclusión fundamental es que el papel beneficioso o perjudicial de una especie en una asociación es una cualidad espacio-temporal dinámica, determinada por el balance de múltiples efectos denso-dependientes concurrentes, algunos que se refuerzan, otros se contrarrestan, entre sí.

Palabras clave—contexto-dependiente, estados estables alternativos, transiciones en desenlaces variables, dinámica espacio-temporal, denso-dependencia, costo-beneficio, ecología teórica, mutualismo, antagonismo, explotador

Two monks were arguing about a flag. One said: 'The flag is moving'. The other said: 'The wind is moving'. The sixth patriarch happened to be passing by. He told them: 'Not the wind, not the flag; mind is moving'.

- Mumon Ekai (1228) *The Gateless Gate*

PRELUDE

Interactions with conditional outcomes, or context-dependent interactions, have received extensive attention over the past years. One foot in front of the other, a vast body of empirical and theoretical knowledge (observations, field and lab experiments, conceptualization, mathematical models) has been built on the dynamic nature of the outcomes in population associations. This has come hand in hand with the trending interest in promoting mutualism as a relevant interaction in the structuring of natural communities, as are competition and predation. And this is because mutualism happens to be one of the strongest representative of a conditional interaction.

The beginnings. In 1988, J. N. Thompson wrote, 'Just as variation in traits in populations is the raw material for the evolution of species, variation in outcome is the raw material for the evolution of interactions'; he was introducing his exhaustive review on the evolution of interspecific interactions. In 1994, J. L. Bronstein published an insightful review on conditional outcomes in mutualistic interactions based on empirical data and observations. It stated clearly the importance of considering a different perspective: 'any interaction might be considered to occupy a potentially dynamic position along a continuum of possible outcomes, ranging from beneficial to progressively more antagonistic' as a result of the balance of costs and benefits involved for each partner species. She referred mainly to those interactions that involve both mutualistic and antagonistic effects from one species to the other and vice versa. This is the case, for instance, of the association between plants and insect pollinators: plants receive the benefit of pollination from the insects, but these eat their fruits, or may demand high production of flowers and nectar; in turn, pollinators get food and nests, but plants may abort the fruits carrying their eggs and larvae. Thus, this interaction may shift between mutualism and parasitism (either way) depending on the net balance of costs and benefits for each species, which in turn depends on the relative abundances of the two species and on general environmental conditions (this is a widely reported case in the literature, see e.g., Herre and West, 1997; Addicott and Bao, 1999; Van Der Kooi et al., 2021).

A lot has happened since. The new perspective of conditionality in the outcomes has triggered the revision of many other (or all) species associations (e.g., Agrawal et al. 2007; Chamberlain et al. 2014; Hoeksema and Bruna 2015; Messan-Rodriguez et al. 2018; Song et al. 2020), and has demanded a solid new conceptual framework beyond just conditional mutualism; one that defines the outcome of any population interaction as a dynamical entity, subject to variations conditioned by demographic or environmental conditions, not only in intensity, but more importantly, in its

beneficial or detrimental nature.

In this article I explore, first, the empirical and natural framework, some representative cases of pairwise interactions with conditional outcomes, with the aim of finding common (or distinct) features and mechanisms that allows some categorization. Second, I present and discuss analyses and insights drawn from theoretical models. I do this by following the trail of a model I have developed over some years, the *Interaction Function (IF)* model (Hernandez, 1998, 2008, 2009, 2015, 2021; Hernandez and Barradas, 2003), discussing, comparing and complementing relevant results and contributions, along with other models and conceptual bodies that have emerged on the issue of conditional or context-dependent interactions.

On the whole, this paper aims to present a fluid narrative on the subject of the conditional nature of some species interactions, supported by theoretical models and concepts, but avoiding the most formal (mathematical) details, which can be found in the original articles and references.

ON BEING CONDITIONAL IN NATURE

Interactions between populations have been categorized from many angles, both empirically and theoretically. There are the definite (static) labels of parasitism, predator-prey, competition, mutualism, commensalism, etc., where a victim is always a victim, a competitor is always a competitor, and so on. And there are those cases where the beneficial presence of one species may become detrimental, or vice versa; that is, when a victim becomes an exploiter, or a mutualist becomes a parasite or a predator, and so forth. Nature provides examples to fit all the possibilities we could think of. The point is that after years of trying to build robust categorizations we end up with more exceptions than rules. That is the nature of nature.

In this section I look at the empirical or natural angle, those features that we observe in nature, in interactions between two populations in which the outcome is conditional. By *outcome* I mean the beneficial or detrimental effect of one species on the other (formalities on this issue will come later), by *conditional* I mean that it may change according to some circumstances related, or not, to the interacting species.

I present now brief recounts of some typical cases of conditional interactions, highlighting: benefits and costs for each species, their causes of variation, possible outcomes for the interaction, conditions that trigger changes in the outcomes (for one or both species), and provide some references for more detailed information.

1. *Plant, insect and pollination.* Adult insects oviposit on the plant and its larvae feed on the seeds and fruits; this is the benefit for the insect, but it also represents a cost for the plant. The plant can abort some of the fruits selectively: those that contain more insect eggs and larvae; this is a cost to the pollinator. The benefit for the plant is clearly pollination, but there is a cost involved in the production of flowers and nectar, also, if there are few

- pollinators this benefit is low, and if there are many, the cost of feeding the larvae is high. Then, this interaction can result in a mutualism or a parasitism, where the parasitized species can be either the insect or the plant. The outcome depends on the net balance of benefits and costs, which in turn depend on the relative abundances of the species and on general environmental conditions (e.g., Herre and West 1997; Addicott and Bao 1999; Holland et al. 2002).
2. *Epibiont and host.* Epibionts (anemones, sponges, algae) live and grow on the surface of hosts (crabs, insects, algae, etc.). Hosts benefit from the protection from predators by the epibionts (camouflage, active defence), however, it may involve costs due to surface harm or mobility impairment. Both, the degree of protection and of harm caused, largely depend on the proportion of host surface covered by the epibiont. Epibionts benefit from substrate and mobility (greater access to nutrients) provided by the host; however, hosts can lead them to unfavourable environments. Predators may reject or attack the epibiont-host symbiont depending on the epibionts being unpalatable or a preferred prey, thus, the predator species present in the environment also affect the outcome of the association. The interaction can be mutualism or parasitism, where the parasitized species can be either the epibiont or the host (Vance, 1978; Duffy, 1990; Threlkeld et al., 1993; Wahl and Hay, 1995).
 3. *Mycorrhizae: plant and fungus.* Mycorrhizae are fungus-plant associations that involve transfer of nutrients from the soil. The fungus, attached to the roots, provides the plant with the phosphorus it needs. This is beneficial for plants in soils with low nutrient availability, however, in fertile soils the action of the fungus may be unnecessary. The plant provides the fungus with carbon compounds that it withdraws from its own organism, thus the net balance of costs and benefits may be negative for the plant, particularly if the densities of fungi are high. Thus, in this interaction the role of the fungus can vary between mutualistic and parasitic, depending on environmental conditions and abundances (Johnson et al., 1997; Gange and Ayres, 1999).
 4. *Mullerian mimics.* At low densities, interactions between Mullerian mimics are mutualistic as they facilitate the training of predators in recognizing unpalatable prey. At higher densities they become competitors because they share resources (Gilbert, 1983).
 5. *Whelks and lobsters.* In South Africa, at Malgas Island whelks are the favourite prey of an abundant population of rock lobsters; at Marcus Island, 4 Kms apart, same environmental conditions, rock lobsters are completely absent, whereas very high densities of whelks are present. According to local reports, the situation in Marcus Island occurred after a temporary environmental disturbance that caused the extinction of lobsters, allowing the considerable increase in the whelk population. When a thousand lobsters were introduced in an attempt to recolonize the region, they were overwhelmed and consumed until complete extinction by whelks within a week.
- The interchange of roles between prey and predators prevents the reinvasion of lobsters on this island (Barkai and McQuaid, 1988).
6. *Ants and aphids.* Ants benefit from their association with aphids because they provide excretions or secretions (honeydew) rich in sugars and amino acids. Aphids are tended by ants (cleaning, transport, shelter) and get protection against natural predators, however, benefits for aphids may be low or even negative if aphid densities are high, or if predator densities are low. Thus, the mutualistic ant may become a parasite (exploiter). On the other hand, the higher the quality of the host plant fluids, the higher the quality of the honeydew produced by the aphids, thus, more ants are attracted, which is beneficial for the aphids; however, when the quality of the honeydew produced is low, and/or the ants have another source of food (e.g. flowers), the ants may predate on the aphids, given there is a high density of aphids per ant. Thus, the mutualistic ant becomes a predator. Ants need protein food (insect prey) for larvae growth and egg production by the queen, and sugary food as energy source for workers; then, the different ant roles respond to different nutritional demands of the ant colony (Addicott, 1979, 1981; Cushman, 1991; Cushman and Addicott, 1991; Sakata, 1994, 1995; Stadler and Dixon, 1998; Del-Claro and Oliveira, 2000; Offenberg, 2001; Stadler et al., 2002; Revilla and Encinas-Viso, 2015).
 7. *Seeds and rodent seed dispersers.* Rodents consume seeds, but also provide seed dispersal (scatter, hoarding, caching) which has a beneficial effect on the growth rate of plant populations, however, this effect can be low at low rodent densities. Each rodent may: eat the seed in situ, or remove it (e.g. bury it, scatter), in which case the seed may: germinate, or be eaten by the rodent later. The seed-rodent interaction switches from mutualism to predation with the increase of rodent abundance per seed (Zeng et al., 2021; Zhang et al., 2021).
- From the cases described above some features emerge on how the variations in the outcomes occur, or what are the conditions that trigger, or allow, a variation in the outcome. First, note that, in all cases, for a variation in outcome to occur, there has to be an appropriate relative abundance of the two species; and secondly, some other general environmental conditions, particular to each case, favour one outcome or the other. Additionally, we observe that variations in the outcomes may be gradual or sudden, reversible or irreversible, part of a life cycle or phenology of the species, and they may occur in both species or only in one. From this, I recognize two general trends in the variation in the outcome of the interactions:
- (i) Those that shift – from mutualism to parasitism or competition – and may swing back**
- Cases 1 to 5: plant-pollinator, epibiont-host, plant-fungus (mycorrhiza), mimic-mimetized, whelks-lobsters.*

These cases show how the outcome of the interaction depends on the net balance of benefits and costs for each species, which in turn depend on species densities and some environmental conditions. Then, depending on the particular form of these relationships the balance for each species may vary, not only in intensity, but may go through negative (detrimental), neutral and positive (beneficial) values. Therefore, the pairwise interaction may go, as in a sort of swing process, through the different possibilities: from mutualism to parasitism (either way), or to competition, or amensalism, etc., following the variation of conditions.

(ii) Those that switch – be a mutualist or be a predator – choose every time

Cases 6 and 7: ants-aphids, rodents-seeds.

In these cases the outcome of the interaction depends not only on the net balance of costs and benefits for each species, but also on the different demands of the species life cycle or population structure. The key feature in this category is that each individual can play the two roles (e.g. predator and mutualist) and will act as one or the other depending on relative densities and environmental conditions at that moment. Therefore, the two possible interactions are occurring simultaneously in the system.

About (i) and (ii) – to shift and swing or to switch

Note that in the cases of ant-aphid and seed dispersers, both *shift* and *switch* situations occur: there is a *shift* situation between mutualism and parasitism, and it is from either of these that the *switch* to predation occurs. That is, every ant, at every moment, when facing an aphid makes the decision (there are chemical and environmental cues to help) of either tending or eating it, depending on the nutritional demand of the ant colony. Ants only choose to predate if there are enough aphids to provide honeydew, and/or there are other sources of nectar, otherwise, the ant will not eat the aphid and will look for proteins (if needed) in other insect species. Then, it will tend the aphid, under a mutualistic or exploitative role, context-dependending. Similarly, seed dispersers will choose between eating or not a seed; if not eaten, the seed may be taken somewhere else (scattered, buried, etc.), where it can germinate.

In the (only) *shift* situation there is no decision making, nor simultaneous roles of the species, rather, the whole two-species system would be in one type of interaction at a time, be it a mutualism, parasitism, or competition, etc., depending on the beneficial or detrimental outcome of the benefits and costs balance for each species at that moment and circumstance.

ON MODELLING THE DYNAMICS OF CONDITIONAL OUTCOMES

The classical Lotka-Volterra (*LV*) model expresses the dynamics of interacting species in terms of the sum of the effects that each species has on the per capita growth rate of every other; these effects are linear functions of densities. For two interacting populations with densities N_1, N_2 , the model

can be written as,

$$\frac{dN_i}{dt} = r_i N_i \left(1 + \alpha_{ii} \frac{N_i}{K_i} + \alpha_{ij} \frac{N_j}{K_i} \right) \quad i, j = 1, 2 \quad (1)$$

where r_i is the intrinsic rate of increase of species i , K_i is the carrying capacity, and α_{ii} and α_{ij} are the intraspecific and interspecific interaction coefficients, respectively. Note that the positive or negative effect of one population on the growth rate of the other is determined by the signs of the α_{12} and α_{21} coefficients: both positive for mutualism, both negative for competition, one positive and one negative for a victim–exploiter (consumer–resource) interaction, null and positive for commensalism, and null and negative for amensalism. Also note that this form of the model corresponds to facultative interactions (the species reach their carrying capacities when the other species is not present), for obligate interactions some adjustments can be made; will not be considered here, though. See Appendix A for more details on the Lotka–Volterra model.

The Interaction Function (*IF*) model (Hernandez, 1998, 2008, 2009; Hernandez and Barradas, 2003) follows the general reasoning of the *LV* model but introduces a notion that allows the study of the dynamics of interactions with conditional outcomes: interaction coefficients α_{ij} , are not constant but density-dependent functions $\alpha_{ij} \equiv \alpha_{ij}(N_i, N_j)$ that can take both positive and negative values at certain density ranges. That is, the effect of species j on species i can be either beneficial ($\alpha_{ij} > 0$) or detrimental ($\alpha_{ij} < 0$) depending on population densities (and some parameters included in its formulation to represent environmental conditions). Then, for a two-species system the model can be written as,

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \left[1 - \frac{N_1}{K_1} + \alpha_{12}(N_1, N_2) \frac{N_2}{K_1} \right] \\ \frac{dN_2}{dt} &= r_2 N_2 \left[1 - \frac{N_2}{K_2} + \alpha_{21}(N_1, N_2) \frac{N_1}{K_2} \right] \end{aligned} \quad (2)$$

where $\alpha_{ij}(N_i, N_j)$ measures the per capita effect of species j on the population growth rate of species i at given N_1, N_2 densities, and $\alpha_{ii} = -1$, which is a common assumption for this kind of model, meaning that the intraspecific interaction remains linear.

What's in the shape of the interaction functions $\alpha_{ij}(N_i, N_j)$

The concept behind the density-dependent interaction function $\alpha_{ij} \equiv \alpha_{ij}(N_i, N_j)$ is that it represents the net balance of the benefits and costs involved for species i due to the presence of species j , which, as exposed in the natural cases above, are in turn density-dependent. Then, the actual form of the function comes from $\alpha_{ij}(N_i, N_j) = \text{Benefits}(N_i, N_j) - \text{Costs}(N_i, N_j)$, and depending on the particular shapes of these, at given density ranges, the interaction can be beneficial ($\alpha_{ij} > 0$) or detrimental ($\alpha_{ij} < 0$). Figure 1 depicts two basic examples, in both benefits are greater than costs at lower N_j , but costs grow faster, thus, at higher N_j costs are higher than benefits; hence the shift in sign in the net balance.

To explore the general features (mechanisms, processes, patterns) of the *IF* model, there is no need to express the

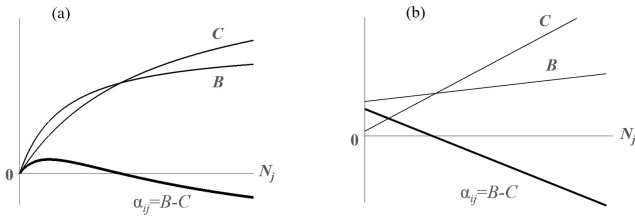


Figure 1: $\alpha_{ij}(N_i, N_j)$ functions resulting from density-dependent (Benefits-Costs) functions, with specific formulations (a) $B = bN/(d + N)$ and $C = cN/(f + N)$, (b) $B = b + dN$ and $C = c + fN$. In both cases curves cross at an intermediate density, thus the sum is positive at low densities, negative at higher densities. The general shapes of the resulting $\alpha_{ij}(N_i, N_j)$ functions can be expressed directly as a (a) quadratic ratio $\alpha = (bN - N^2)/(1 + cN^2)$ and (b) linear $\alpha = b - cN$.

costs and benefits formulations explicitly, only generic forms of the α_{ij} 's are needed, as long as these comply with the condition that it shifts in sign with density. To make the point clearer, we could assemble a hypothetical model as follows,

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \left[1 - \frac{N_1}{K_1} + \left(\frac{b_1 N_2 - N_2^2}{1 + c_1 N_2^2} \right) \frac{N_2}{K_1} \right] \\ \frac{dN_2}{dt} &= r_2 N_2 \left[1 - \frac{N_2}{K_2} + (b_2 - c_2 N_1) \frac{N_1}{K_2} \right] \end{aligned} \quad (3)$$

Equations (3) depict the *IF* model with the two general functional forms of $\alpha_{ij}(N_i, N_j)$ presented in Figures 1(a,b), i.e., a quadratic ratio in $\alpha_{12}(N_2)$ and a linear form in $\alpha_{21}(N_1)$. Parameters b_i, c_i , give the actual shape to the curves, they represent the way in which general (biotic or abiotic) conditions are reflected on the interactions intrinsic features, e.g., saturation values, sensitivity of the interaction to changes in the partner's density, thresholds between positive and negative interactions, etc. Note that in model (3) both $\alpha_{12}(N_2)$ and $\alpha_{21}(N_1)$ functions take positive values at low partner's density and become negative at higher densities; thus, this model could correspond to the situations of the *shift* case (i) defined in the section above.

A quick look at model (3) allows a first outline of the stability properties; it shows that at non-trivial equilibrium ($dN_1/dt = dN_2/dt = 0$) populations may coexist, (say at N_1^*, N_2^*), or one species may be excluded, the other at its carrying capacity, ($N_i^* = K_i, N_j^* = 0$). However, the specific nonlinearity introduced by the $\alpha_{ij}(N_i, N_j)$ interaction functions will provide a remarkable spectrum of possibilities.

Spoiler alert: the model presents multiple stable equilibria – at different interaction outcomes

Now I look into the graphical stability analysis of the *IF* model, that is, the nullclines (or zero-growth isoclines) for N_1 and N_2 , and equilibria solutions, for different sets of parameters in phase-plane. This kind of analysis has the virtue of conveying all needed (global) information about the system. To perform it we use explicit formulations for the $\alpha_{ij} \equiv \alpha_{ij}(N_i, N_j)$ interaction functions; figure 2 shows some of the patterns obtained when two linear $\alpha_{ij}(N_i, N_j)$ interaction functions, $\alpha_{ij} = (b_j - c_j N_i)$, $i, j = 1, 2$, are used

in model (2). In this figure we can observe graphically the results that the quick look at the model above already told us: that the system may present a single stable solution (figures 2a and 2b), or multiple solutions at stable equilibria (alternative stable states), where species may coexist (figure 2c), or one species may be excluded, the other is at its carrying capacity (figure 2d).

I must add a comment here. The shape of the nullclines: humped closed crossing both axes, which ultimately is responsible for the appearance of multiple equilibria, occur for any interaction function α_{ij} chosen, as long as it complies with the condition that it takes values along the positive to negative continuum as density increases; the hump occurs at the change in sign of the α_{ij} function (details in Hernandez, 1998; Hernandez and Barradas, 2003).

The next pertinent step is to determine whether these solutions correspond to different outcomes in the nature of the interaction. The proper (formal) characterization of the outcomes in the interactions is not a trivial issue, and there is hardly a consensus among authors. I discuss this fully in Hernandez (2009), and present here the main ideas in Appendix B. For now, suffice it to say that I regard the outcome of an interaction in terms of its beneficial or detrimental nature towards the other species, and this is defined by comparing the performances of the species alone and when the other species is present. In more formal terms, an interaction is *beneficial, neutral or detrimental* for a *species i*, if when associated with a *species j* it reaches an equilibrium density N_i^* that is *greater, equal or smaller* than its carrying capacity K_i , respectively.

Note that the graphs in figure 2 allow for a representation of these ranges as quadrants in phase space where equilibria solutions lie. I use the classic symbols (+ +), (– –), (+ –), (– +), to denote types of interaction: mutualism, competition, and victim-exploiter (either way), respectively. Neutral interactions: commensalism and amensalism, are obviously also present, sort of midway between the others, however, I will not mention them explicitly, just to keep things simple. Note that the order in the signs in this nomenclature corresponds to the signs in $(\alpha_{21} \alpha_{12})$, at a given point in the plane. A comment aside: sometimes the signs of the jacobians are used to categorize types of interactions, however, this is misleading, their signs refer to stability properties only (see Appendix B).

Thus, we definitely show that the outcome in the interactions may be different for different sets of parameters. That is to say, the concept introduced in the *IF* model allows the representation of variable outcomes in the interaction for the same two species, depending on relative densities and general environmental conditions. Now, what about the dynamics of these variations?

The outcomes of interactions are dynamic – they transit in gradual, abrupt or catastrophic manner

From the patterns shown in figure 2 we see that as parameters change, the relative positions of the nullclines change,

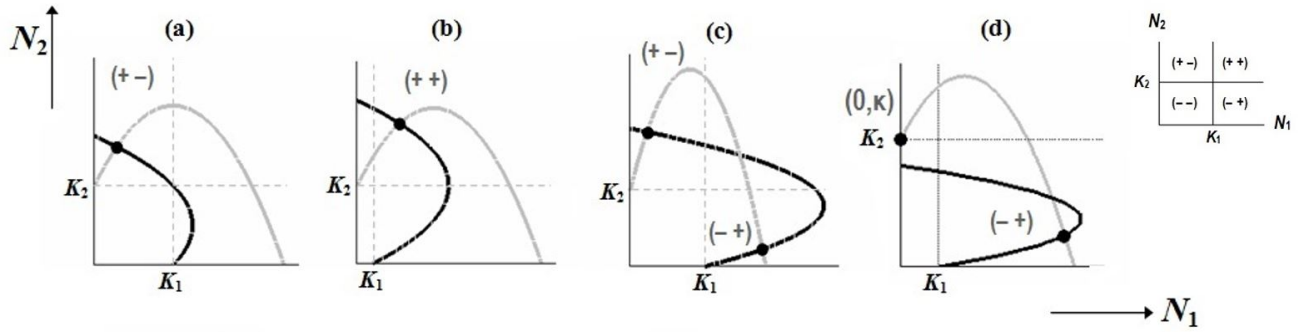


Figure 2: Nullcline graphics in phase plane for *Interaction Function* model (2) with linear $\alpha_{ij} = b_j - c_j N_i$, for $i, j = 1, 2$, for four sets of parameters. N_1 nullcline (light curve), N_2 nullcline (dark curve), stable equilibria (N_1^*, N_2^*) (dark dots), dashed lines at K_1 and K_2 define quadrants for outcomes of interaction (legend upper corner). Formal stability analyses in Hernandez (1998, 2008); Hernandez and Barradas (2003).

causing equilibrium solutions to appear and disappear by processes of bifurcations and annihilations of the stationary states. In so doing, there are also changes in their stability properties. The appropriate way to present and analyse these is in a bifurcation diagram, which displays equilibrium solutions with respect to parameter values. Figure 3 shows the bifurcation diagram for N_1^* vs K_1 for the *IF* model, that is, the equilibrium density that species 1 would reach at different carrying capacity values (all other parameters are kept constant and equilibrium densities N_2^* vary along with N_1^* according to the model dynamics, but are not shown in the figure). The *S* shape of the diagram is typical of the hysteresis phenomenon (Thom, 1972; Zeeman, 1977). The solid upper and lower branches contain the stable equilibrium values and the dark dashed line that joins them contain the unstable equilibria. Observe that for low K_1 values there is only one corresponding N_1^* (e.g., dots at A), at higher K_1 there are two (one on each branch, e.g., dots at B, C and D), and at very high K_1 the system reaches a unique fixed stable equilibrium at $N_1^* = K_1$ (i.e., species 2 is excluded; off the graph borders). Note that these situations correspond to cases (a) to (d) in figure 2. Bifurcation diagrams can be (and were) constructed for any of the two equilibrium densities, N_1^* or N_2^* , with respect to any of the model parameters: K_i and those in the α_{ij} functions (parameter r_i was kept constant along all studies). For the *IF* model all combinations yielded hysteresis behaviour.

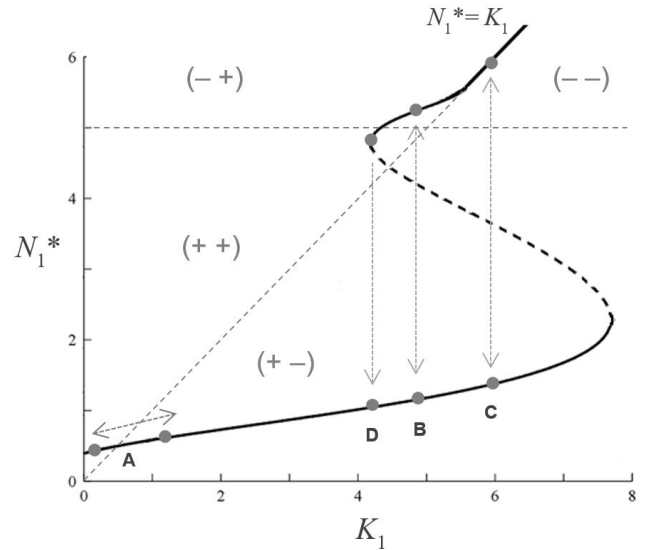


Figure 3: A typical bifurcation diagram for the *IF* model. Equilibrium density for species 1, N_1^* , vs. its carrying capacity, K_1 ; other parameters constant. Equilibrium densities for species 2, N_2^* , vary according to the model dynamics (not shown). Solid dark (upper and lower branches) contain stable N_1^* , intermediate dark dashed line contain unstable N_1^* . Straight light dashed lines define sections for the type of interaction (see text and figure 2).

The diagram in figure 3 also allows the delimitation of sections for the different outcomes of the interaction: (+ +), (- -), (+ -), (- +); these correspond to the quadrants defined in figure 2. Therefore, it shows remarkably clear the ways in which the system may transit along the different outcomes as the parameter varies. This is illustrated at some locations in the diagram. At (A) a transition between (+ +) and (+ -) happens by gradually increasing parameter K_1 , and vice versa. At (B) the system might be either on the upper branch, at a (- +), or the lower, at a (+ -), transitions between the two situations may occur if the population densities change, so that they move between domains of attraction; note that this happens at a constant K_1 value, i.e., same environment. An equivalent situation occurs at point (C) between an exclusion of species 2, species 1 at carrying capacity, i.e., $(K_1, 0)$, and

a (+ -). The transition at (D) shows a catastrophic event, a typical hysteresis performance that occurs at a turning point: say that the system is at the upper branch in the (- +) region, then K_1 starts decreasing gradually and so follows N_1^* ; when the border of the branch ends (the turning point) the system drops to the stable equilibrium in the lower branch. Thus, the system undergoes an abrupt decrease in the N_1^* equilibrium density due to a minute variation of the K_1 parameter. This is called a cusp catastrophe (Thom, 1972; Zeeman, 1977).

We gather then, according to the model, that there are two basic modes of transitions in the outcomes of interactions: (i) gradual, smooth, driven by monotonic variation of parameters, that is, by changes in the environment that induce changes on intrinsic properties of the interactions (sensitivity

ties in the effect of one species on the other, saturation values, etc.); and (ii) abrupt, driven by drastic changes in (relative) densities, between alternative stable states, that is, they occur under the same environmental conditions. The catastrophic jumps are threshold situations, sort of midway between the two modes because they are abrupt, between alternative stable states, however, they are triggered by a (minute) change in a parameter. So, voila! a mechanism for the variation in the outcomes of conditional interactions has been described.

An appealing speculation on lobsters and whelks

As a speculative reflection, note that the diagram in figure 3 suggests a possible explanation for the lobsters and whelks case in South Africa (mentioned above). Say the situation in Malgas Island corresponds to coexistence at point C, where the interaction is (+ -), that is, whelks (N_1) are the prey of lobsters (N_2); and, as reported, this was also the original situation for Marcus Island. Then, a huge (but temporary) perturbation extinguished all lobsters at Marcus, taking the system to the upper branch, at $(K_1, 0)$, i.e., whelks reach their carrying capacity after the removal of their main predators. The attempted reintroduction of lobsters failed because the relative densities were not enough to bring the system to the lower branch again. This could also be visualized as a catastrophic jump at the turning point at the right end of the lower branch.

Are there bifurcations and catastrophes everywhere?

The phenomenon of hysteresis is receiving particular attention in recent years in the field of ecological studies, in particular, as very small variations in the environment can cause drastic changes in the systems, is a matter of great interest in subjects related to climatic changes. One of the most relevant (worrying) issues in a hysteretic regime is that once a catastrophic jump has occurred, reversing the conditions that caused it does not ensure going back to the same place, it has to go all the way along the curve and jump again at next turning point. Therefore, it is crucial to determine if the occurrence of a drastic change in a system is due to the presence of a hysteresis phenomenon, or is just a response to some drastic environmental change; it is also fundamental to have the possibility of interpreting early signals to anticipate critical situations (Scheffer and Carpenter, 2003; Schröder et al., 2005; Dakos et al., 2015).

AN IF MODEL FOR MYCORRHIZAE – A FORE-TASTE

One of the population associations that has shed more light into the understanding of conditional interactions is mutualism (cooperation, facilitation). This is because the more one looks into the mutualistic natural situations the more one gets the idea that the balance of costs and benefits involved for the mutualistic species is not always positive, rather, it very easily shifts towards the antagonistic sides, for either species.

As mentioned above, mycorrhizae are associations of fungal species attached to the roots of plants. Traditionally, this interaction has been classified as mutualistic due to the mu-

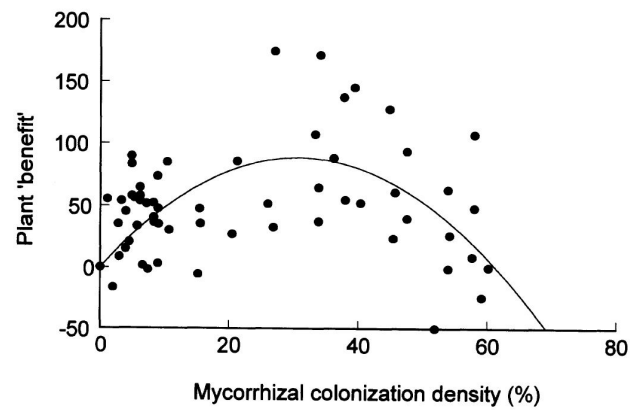


Figure 4: Experimental results and fitted curve, of the net benefit received by plants with mycorrhizae as a function of their density (modified from Gange and Ayres, 1999).

tual exchange of nutrients between species; however, the net balance of benefits and costs can be negative for the plant in fertile soils and/or at high fungi densities, in which case the fungus becomes a parasite (exploiter) of the plant.

I want to introduce here a succinct preview of an Interaction Function model for mycorrhizas (not out yet, coming soon, with an appealing evolutionary twist) mainly to raise two particular issues: experimental data used as an input for the costs-benefits interaction function, and the case where no alternative stable states are possible.

Gange and Ayres (1999), with experimental data from Gange and Nice (1997), estimated the net ‘benefits’ (their marks, meaning that it is the net balance after taking out costs) that the plant receives at different densities of fungal colonization; they fit a second-order polynomial curve (see figure 4). Their results indicate that at high fungus densities the net effect to the plant becomes negative; that is, the costs outweigh the gross benefits.

The function fitted to the data is a parabola and represents the density-dependent effect of the fungus on the plant, i.e., it provides an explicit formulation for the fungus interaction function, α_{21} , for a model in equation (2),

$$\alpha_{21}(N_1) = b_2N_1 - c_2N_1^2 \tag{4}$$

where N_1 and N_2 represent the fungus and plant abundances, respectively, b_2 and c_2 are parameters that shape the curve. On the other hand, I can assume that the net effect of the plant on the fungus is always positive, with saturation, thus, we can use the hyperbolic benefits curve shown in figure 1(a) for the plant interaction function, α_{12} ,

$$\alpha_{12}(N_2) = \frac{b_1N_2}{1 + c_1N_2} \tag{5}$$

where b_1 and c_1 are the shape parameters. Introducing these formulations in model (2) we get,

$$\begin{aligned} \frac{dN_1}{dt} &= r_1N_1 \left[1 - \frac{N_1}{K_1} + \left(\frac{b_1N_2}{1 + c_1N_2} \right) \frac{N_2}{K_1} \right] \\ \frac{dN_2}{dt} &= r_2N_2 \left[1 - \frac{N_2}{K_2} + (b_2N_1 - c_2N_1^2) \frac{N_1}{K_2} \right] \end{aligned} \tag{6}$$

Figure 5 shows some representative patterns of the graphical stability analysis obtained for model (6). In figure 5(a) the parameters are such that the outcome of the interaction, at stable coexistence (crossing of nullclines), is mutualistic, i.e. both equilibrium densities N_1^* and N_2^* , are greater than their corresponding carrying capacities, K_1 and K_2 , meaning that each species causes a positive effect on the population growth on the other. Figure 5(b) shows a transit to a parasitism (fungus as exploiter) when parameters of the interaction functions, α_{12} or α_{21} , are varied; this may be caused by intrinsic changes in the way each species has effects on the other, e.g. sensitivity, or saturation values, caused, in turn, by variations in some biotic or abiotic environmental conditions. Figure 5(c) shows a transition to parasitism when the carrying capacity of the plant, K_2 , is higher. This may illustrate the situation of a fertile soil for the plant, that is, the plant on its own would reach a higher equilibrium density than in association; the help of the fungus is not needed, on the contrary, depletes the plant's performance.

The fungus nullcline has no hump

It is important to comment here significant differences between the nullclines in figure 2 and those in figure 5. Specifically, observe that the nullcline for the fungus in figure 5 is not closed, it has no hump shape. This is because the fungus always receives benefits from the plant, that is, the interaction function α_{12} (equation 5), although non-linear, is always positive. Also note that, looking at the patterns in figure 5, the fungus nullcline will never go to the (+ -) quadrant (which would mean that the plant is the exploiter), it just moves along the quadrants on the right hand side (fungus always wins). And a relevant consequence in this case is that there are no multiple stable equilibria situations. That is, there are no abrupt or catastrophic transitions between outcomes, only gradual.

FRAGMENTATION OF SPACE TRIGGERS SOURCE-SINK DYNAMICS – AND FURTHER VARIATION IN THE OUTCOMES

Now I want to introduce the effects of spatial heterogeneity, that is, the dynamics of conditional outcomes when the interacting species are allowed to disperse along patches. This is done in a two-patch model of explicit local dynamics, using the general Interaction Function model (2), with linear $\alpha_{ij}(N_i, N_j)$ in both equations, performing within each patch. Dispersal between patches is included in the model through parameters γ_i and δ_i , which are fractions of the respective population densities. The model for two species $i, j = 1, 2$ becomes,

$$\begin{aligned} \frac{dN_i}{dt} &= r_i N_i \left[1 - \frac{N_i}{K_i} + (b_i - c_i N_j) \frac{N_j}{K_i} \right] - \gamma_i N_i + \delta_i M_i \\ \frac{dM_i}{dt} &= s_i M_i \left[1 - \frac{M_i}{L_i} + (g_i - h_i M_j) \frac{M_j}{L_i} \right] - \delta_i M_i + \gamma_i N_i \quad (7) \end{aligned}$$

The first equation in (7) represents the local dynamics in patch 1, with population densities N_1 and N_2 ; the second equation represents the local dynamics in patch 2, with the same two species, densities M_1 and M_2 . Parameter γ_i , $i = 1, 2$, represents the (constant) fraction of species 1 or

species 2 that migrates from patch 1 to patch 2; parameter δ_i , $i = 1, 2$, the fraction from patch 2 to patch 1, accordingly. The rest of the parameters denote the pairwise interaction performances and general environmental conditions, for each patch (as defined in sections above).

A variety of different situations can be explored: patches with same or different environments, single or multiple solutions before migration starts, in different outcome regimes, in coexistence or exclusion, and all combinations of these. Figures 6 and 7 display two particular cases on phase plane graphs.

The main result gathered from the spatial *IF* model (7) is that the fragmentation of space (spatial heterogeneity) with migrations between patches, do promote further variations in, first, the outcome of interactions, both at the regional and local scales; and second, in the number of stable solutions (produced by bifurcations or annihilations of equilibria). Significant trends in these dynamics can be summarized after exploring several different situations (Hernandez, 2008):

(i) The variation in the outcome for a given species is favourable when migrations (emigration, immigration, or both) imply a proportional increase in individuals of that species within the patch. Thus, a victim can become a mutualist or an exploiter, an excluded species can invade, and a good competitor can exceed its own carrying capacity. And of course, vice versa, dispersal is detrimental for a species when it involves a proportional decrease in its local density. This I labelled as the '*enhancement effect of dispersal*'.

(ii) Regardless of which species migrates, bifurcations of equilibrium points occur in the patches that receive the migrations, and annihilations occur in the patches that provide the migrations. Thus, the number of equilibrium solutions, at each patch, increase or decrease correspondingly, when dispersal of individuals is allowed. In addition, the bifurcations and annihilations of equilibria only occur within a range of intermediate migration rates, that is, they do not occur if the rates are very low or very high. Similar results of this phenomenon are in Gyllenberg and Hanski, 1992; Hanski and Zhang, 1993; Hanski et al., 1995; Shurin et al., 2004.

Sources or sinks? – whatever, they also shift and swing

The results of the *IF* models acknowledge that both positive and negative density dependence processes drive the dynamics of interactions with variable outcomes, depending on density ranges; and these occur at both local and regional dynamics, adding up with reinforcing or contrasting effects. Source-sink dynamics is the appropriate framework for discussion of these issues, and provides fascinating inferences and insights. Some hints: Although in the model migration is considered density-independent (i.e., migration rates are constant) there are density-dependent effects associated with dispersion *per se* (Amarasekare and Nisbet, 2001; Amarasekare, 2004). For sink populations with low local abundance, it is beneficial to receive individuals because it increases their growth rates (*rescue effect*); however, this represents costs for the source populations, due to the loss

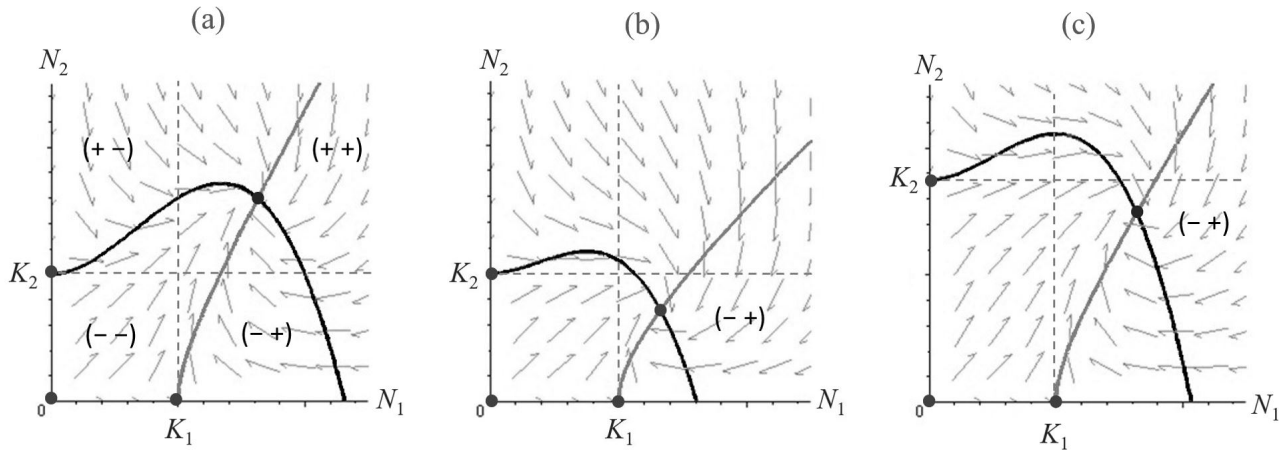


Figure 5: Graphical stability analysis of the *IF* model for a mycorrhiza association: fungus (species 1), plant (species 2), nullclines for fungus (light line) and plants (dark line), for given sets of parameters, stable equilibria at crossing nullclines (dark dot), outcomes of the interactions shown in quadrants defined by carrying capacities, K_1 and K_2 , (a) mutualism, (b) transit to parasitism (lower b_1 or b_2 , or higher c_1 or c_2), (c) transit to parasitism (higher K_2).

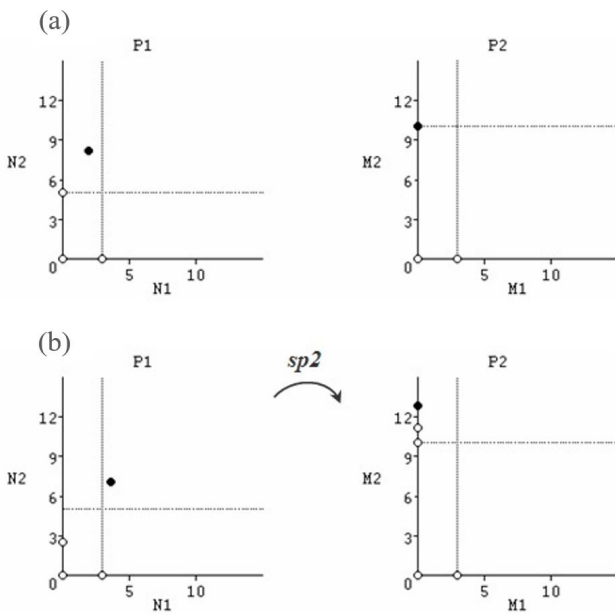


Figure 6: Effect of migration on outcome of interaction between species 1 (*sp1*) and species 2 (*sp2*) from patch 1 (P1) to patch 2 (P2); quadrants at carrying capacities define outcome of interaction (see figure 2); stable equilibria (black dots), unstable equilibria (white dots), (a) In isolated patches: single stable solutions; in P1: victim-exploiter; in P2: *sp1* excluded, *sp2* at carrying capacity, (b) Migration of *sp2* from P1 to P2 causes variations in outcomes; in P1: to mutualism; in P2: still exclusion of *sp1*, but *sp2* reaches equilibrium density higher than carrying capacity (modified from Hernandez, 2008).

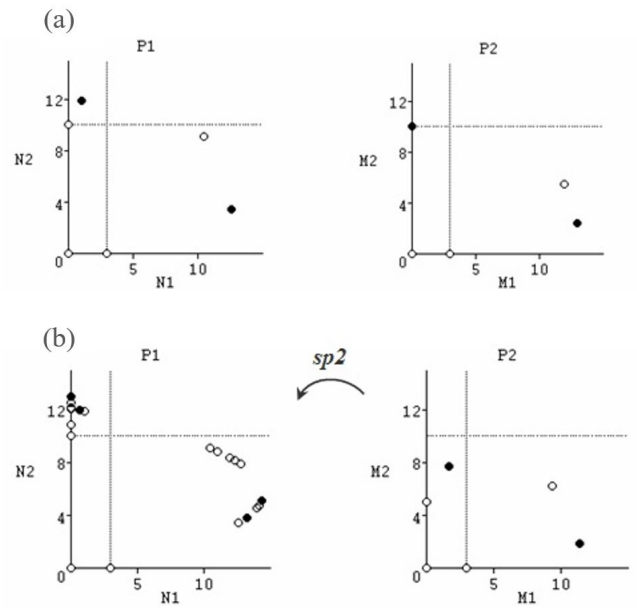


Figure 7: As in figure 6, but effect on multiple stable states situation (a) In isolated patches: alternative stable states; in P1: both victim-exploiter situations, but with role reversal; in P2: one exclusion-carrying capacity situation, and one victim-exploiter, (b) Migration of *sp2* from P2 to P1 causes variation; in P1: number of equilibria increase (clouds of points), each original stable solution bifurcates, top: into one exclusion, one victim-exploiter, lower: into two victim-exploiter; in P2: *sp1* invades where it was excluded, in competition with *sp2*, lower: still victim-exploiter (modified from Hernandez, 2008).

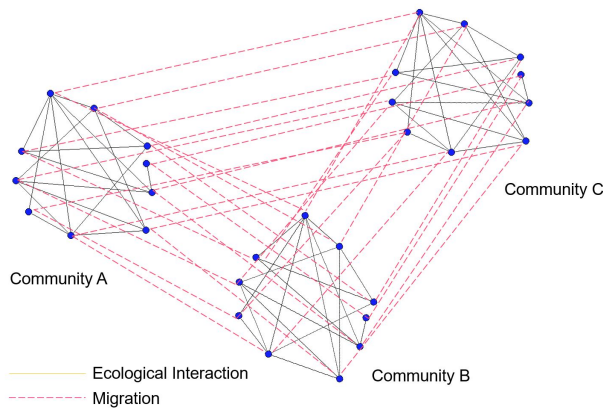


Figure 8: Metacommunitarian setting of the experiments; example of three communities with ten species per community (from Griffon and Hernandez, 2019).

of reproductive individuals. Then, at the regional level, dispersion incorporates cost-benefit relationships on growth rates, which can reinforce or counteract the cost-benefit balance that occurs at the local level. Therefore, the model shows not only the dynamics of variation of outcomes in the interactions (in the roles of victim, exploiter, mutualist, etc.), but also, that the roles of source or sink of the populations are dynamic and may vary at the regional level. Finally, just as environmental parameters at the local level can cause catastrophic jumps between outcomes in the interaction, the spatial model predicts that migrations promote jumps between outcomes at the regional level, which may or may not act in accordance with the local effects. More discussion on this in Hernandez (2008) and at a wider revision on density-dependence and spatial heterogeneity in Hernandez (2015).

A round-up finale, so far. In the context of variable or conditional population interactions, the concept of the *role of a species* does not make sense on its own; rather, it becomes a *spatiotemporal dynamic quality*.

THE SPATIAL *IF* MODEL, THE ECOLOGICAL NETWORK AND THE AGROECOSYSTEM

The spatial *IF* model (7) has been used as a framework to explore the dynamics of networks of ecological interactions. I briefly present here two particular cases: randomly constructed networks and real networks associated to specific agroecosystems (complete studies in Griffon and Hernandez, 2014, 2019; Griffon and Rodríguez, 2017).

The *random ecological networks* include all possible types of interactions (+, -, 0, and conditional outcomes); the proportions of each are defined by a random process. The systems were evaluated at community and metacommunity levels (3 to 80 nodes, 1 to 3 networks); see figure 8.

The model used for the community dynamics (Lotka-Volterra) included interaction functions $\alpha_{ij}(N_i, N_j)$ in the equations, *sensu IF* models. The dynamics were numerically explored, until extinction or persistence of the networks. The experiments show a vast number of extinctions (after just

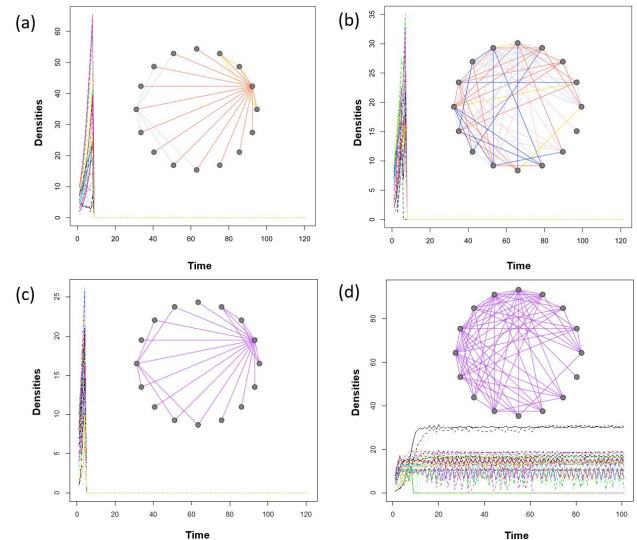


Figure 9: Ecological networks and population dynamics in (a) Monoculture and (b) Conuco, with fixed interactions; (c) Monoculture and (d) Conuco, with conditional interactions. Colours in network links represent different types of interaction: victim-exploiter (red), competition (yellow), mutualism (dark blue), amensalism (pink), commensalism (light blue), conditional interaction (purple). Colours in the dynamics represent densities of different species (from Griffon and Hernandez, 2014; Griffon and Rodríguez, 2017).

a few iterations), and the persistent communities present low percentages of surviving species. The most notable results are that spatial heterogeneity significantly reduces species loss; that persistent communities show an increase in the proportion of positive and nonreciprocal interactions (commensalism and amensalism) with respect to the initial network, and that the systems are locally stable (Griffon and Hernandez, 2019).

The *real ecological networks associated to agroecosystems* were constructed to study relevant properties that may lead in the decision making of agricultural practices, and obtain practical clues for farmers. Two particular agroecosystems were studied: a corn monoculture and a multi-species ancestral crop system (*Conuco*); the latter presents a greater number of interactions and interaction types. The *LV* equations included either fixed α_{ij} values, or interaction functions $\alpha_{ij}(N_i, N_j)$, so that systems without and with conditional interactions were explored. The numerical simulations were performed with parameters taken from field data and (experienced) knowledge of local farmers (Griffon and Hernandez, 2014; Griffon and Rodríguez, 2017). The typical long-term dynamics obtained for each topology are displayed in Figure 9. The fix interactions situations (figures 9a and 9b) show non-persistent dynamics, and so does the monoculture network topology with conditional interactions (figure 9c); whereas the Conuco system shows persistent dynamics in all cases (figure 9d).

One crucial result is that the presence of conditional interactions generates persistence (in the Conuco system). However, it was also found that spatial heterogeneity and dispersal (the metacommunity) increases the probability of persistence (rescue effect). As a matter of fact, in some cases the persis-

tence is only ensured if there are several ecosystems connected; this situation points to the necessity of the coordinated participation of more than one farm in the implementation of ecological management programs (e.g., pest control), which involves additional social human issues to consider.

Metaphorically speaking

The ecological network model with conditional outcomes was also used to investigate the dynamics of the transitions between the monoculture and the agroecological (Conuco) systems (Griffon et al., 2021). This was performed by modifying the architecture of the networks (increase / decrease the number of interactions) along the transitions. One interesting result is that the topological features that confer persistence to the agroecological (multi-species) system, prevail even when the number of interactions are considerably reduced; not so in the networks generated from the monoculture. In general, the resulting paths to transit from one system to the other, or the reverse, bring to mind the graphic representation of a cusp catastrophe surface (similar in shape to figure 3), in which divergent trajectories can lead to alternative states (the monoculture and the agroecological systems) and can shift from one to the other abruptly (catastrophe) or smoothly (along the surface). This *metaphorical* representation reduces the complexity of the system and facilitates its interpretation, i.e., we can study the action of the Lotka-Volterra dynamics on the system (which is the ultimate responsible for any outcome, but has too many parameters to look at) by exploring the general patterns that emerge from large-scale properties that can be grasped more easily.

When looking at the results of the long-term persistent dynamics, with interactions that end up sometimes with stationary values, some other times oscillatory, but that were all generated from conditional interaction functions $\alpha_{ij}(N_i, N_j)$, one cannot avoid thinking that all interactions in nature, no matter how rigid they seem, are intrinsically variable.

WRAPPING UP - MODELS FROM AND FOR EVERYONE – TAKE YOUR PICK

There are extensive reviews in the literature on a variety of topics on population interactions: about categorizations; about the classic pillars competition and predation, and lately, mutualism, being promoted to a third pillar; and about many other related issues, you name it. In this paper I deal with the particular topic of population interactions with conditional outcomes, or context-dependent interactions, but I do not intend to provide a full revision on the subject. Rather I aim to address very specific issues using the framework of the Interaction Function (*IF*) model; and with this set a ground to comment on other related works and insights, and hopefully induce some debate of ideas in the minds of those reading this.

It is undeniable the impact of the Lotka-Volterra model in setting the basic principles for the study of the dynamics of population interactions. I find that one of the most relevant features is that it sets a link between scales and levels, that

is, the quantification of the effects of individual features that may or may not have impact at the population level, all the *per capita*s. From this, models have expanded in many directions: to the community level, where they meet the ecological networks approach; to evolutionary issues, where fitness finds a proxy in terms of population growth rates; to spatial issues and the metacommunity level, where migrations make all the difference; and all these go from the in-depth mathematical studies, with all the dancing of variables, corollaries and parameter thresholds, to the down-to-earth application of results to very specific ecological problems.

Along the narrative of this paper I have dropped references, here and there, when writing about specific issues; now I want to comment on some other references to complement on knowledge and viewpoints. I must add here a very personal worry (which has been addressed lately by other authors, though). Sometimes the access to the scientific production of papers is biased to only some regions of the world and some languages; I am aware that there is a huge production going on in the other regions and the other languages, but (for reasons I will not debate here) there is very limited access to that and, therefore, no cross-references from other papers. I honestly would have loved to find and discuss here those papers with top scientific standard contents and original ideas, but which have received no citations due to limited access to them. Thus, I already apologize if this bias is also present in the set of works discussed here.

The fundamental results occur because the nonlinear term can shift in sign - maths talking

I want to single out the central results drawn from the Interaction Function (*IF*) model on the dynamics of conditional interactions, explored along the previous sections, and proceed from there,

1. The model presents either unique or multiple stable equilibria (alternative stable states) where species may coexist at any combination of interaction outcomes: (+ +), (– –), (+ –), (– +), and corresponding neutrals, or one species may be excluded, the other at its carrying capacity, or both may be excluded; for given sets of densities and parameters.

2. Transitions between interaction outcomes can occur in two modes: (i) by variation of the parameters, which reflect intrinsic features of the interaction itself and/or extrinsic general environmental conditions; (ii) by the variation of population densities, which brings the system to a different domain of attraction (in the multiple stable equilibria situation). The transitions may occur gradually or abruptly (including cusp catastrophes).

3. When spatial heterogeneity and migrations are included, negative and positive density-dependent processes, at local and regional levels, act in reinforcing or contrasting manner, causing further variation in the outcomes of the interactions and, more importantly, inducing the populations

to perform as sources or sinks, and this occurs in a dynamical fashion, that is, the source and sink roles also shift in a conditional, context dependent, manner.

A crucial statement comes out from results 1 and 2 – and 3 follows

The key factor responsible for the performance described in the results is the specific nonlinearity introduced in the interspecific term of the model, that is, the effect of one species on the *per capita* growth of the other is a density-dependent function that can take values along the negative-positive continuum. This is the attribute that produces the humped, closed crossing both axes, shapes of the nullclines (the hump occurs at the change in sign of the function), which in turn produce the equilibria patterns observed, and hence, the results mentioned above.

As commented previously, the *IF* model produces these same patterns and results for any formulation of the interaction function $\alpha_{ij}(N_i, N_j)$, as long as it takes positive and negative values as density varies (details in Hernandez, 1998; Hernandez and Barradas, 2003). In contrast, but reinforcing the argument, the always positive α_{ij} interaction function in the model for mycorrhizas depicted above produces an open nullcline, with no humps, crossing only N_1 -axis, which excludes the possibility of multiple stable equilibria (gradual transitions between outcomes can occur, though).

Hence, these results are of a mathematical (almost geometrical) nature. And this is a precious value of the theoretical work, it can lead to features not easily observed otherwise. However, it is imperative now to look into the way the functional forms were originally conceived, the biological facts that prompt them, and then, we get ecological relevant information. Maths is not alone.

Maths talks but ecology matters

In the case of the *IF* model the reason behind the formulation of the interaction function is related to the forms of the costs and benefits involved in the association. For instance, it is biologically sound to consider that both benefits and costs for each species grow with the partner's density up to a saturation level; or other forms can be explored, also sound. Thus, one way or the other this provides the mechanism that promotes the behaviours observed.

Therefore, it is interesting to look into other models that ended up with the same results as the *IF* model but starting from different ecological principles. This is the case, for instance, of the consumer-resource model, which was also developed to study the dynamics of transitions between outcomes of conditional interactions, and arrived at the same results, 1 and 2, stated above (Holland and DeAngelis, 2009, 2010). The model (also based on Lotka-Volterra dynamics) considers that each species in a bi-directional interaction acts as both a consumer and resource of the other. This is included in the interspecific term of the population growth equations, for each species, as the sum of two

density-dependent, saturating, functional responses (inspired by classical predator-prey models). For some parameters this sum takes values in the positive to negative continuum, hence, the model reaches the same central results (1 and 2) as the *IF* model. No surprise at all there; however, the valuable fact is that the model provides a different ecological route or mechanism to understand the dynamics of conditional interactions. And no doubt, there will be more to come.

General revisions on population interactions with conditional outcomes are abundant, some with an empirical approach, some that include models (e.g., Bronstein, 1994; Chamberlain et al., 2014; Messan-Rodriguez et al., 2018; Song et al., 2020); many are focused on the mutualism-antagonism situation, which also sheds light on the broader topic (e.g., Herre et al., 1999; Hale and Valdovinos, 2021; Zhang et al., 2020), or on particular biological systems that present variable outcomes (e.g. Agrawal et al., 2007; Baraza et al., 2006; Norkko et al., 2006; Lee et al., 2009; Hoeksema and Bruna, 2015).

A large body of work on the dynamics of interactions with conditional outcome focus on further rigorous theoretical analyses of these strongly nonlinear systems. In-depth mathematical analyses provides additional knowledge into mechanisms, patterns, predictions, etc., see e.g. González-Guzmán (2006); Graves et al. (2006); Lara and Rebaza (2012). Messan-Rodriguez et al. (2018) develop a model to investigate the dynamics of bi-directional resource exchange between two local ecosystems in a metaecosystem framework; they show that the outcomes of the interactions and the persistence of the ecosystems depend on the relative cost and benefit of resource exchange. They perform a thorough mathematically oriented analysis (bifurcation analysis), but always keeping in mind the biological meaning of their results and conclusions. This article provides an excellent vast and explanatory account of models on the dynamics of pairwise conditional interactions in the literature.

In the mutualism-antagonism spectrum there are abundant models, especially in the past years. Hale and Valdovinos (2021) provide a constructive review on many of these models, with a historical approach, and categorize them according to specific features (e.g., mechanisms, assumptions, predictions); Hale et al. (2020) developed a general model for mutualism under the assumption that costs associated with rewards are negligible at the population level (or can otherwise be accounted for in parameter values). This provides a proper framework to study mutualism in cases where these conditions apply. Thompson et al. (2006) find that immigration and emigration of mutualistic partners have different effects on the interaction outcomes if the effects of the mutualism acts differently on the demographic rates (reproduction and mortality) of the populations.

Revilla and Encinas-Viso (2015) study transitions between mutualism and antagonism in the herbivory-pollination situation with a phenological approach; different stages of the insect life cycle have effect on different parts of the plant, that is, adult insects interact with flowers in a mutualistic way (pollination), but larvae consume the leaves, acting as

exploiters (herbivory). Thus, the balance of costs and benefits come from consumer-resource dynamics. They build a model of ordinary differential equations for the growth rates of plants, flowers, adult insects, and larvae, which include intra- and inter-specific terms, the latter as saturating functional responses. The synchrony of events and the rates of development along the insect life cycle are determinant on the outcome of the interaction, e.g. time spent as antagonist (larva) with respect as mutualist (adult). They discuss the external drives that may cause changes in the insect life cycle (temperature, plant nutrients, pesticides) hence acting on the balance between mutualism and antagonism. Models on evolutionary issues in Revilla and Křivan (2018); Křivan and Revilla (2019), complement these ideas. This approach to modelling might be appropriate to study the *switch* situations described in the case (ii) in the second section above.

Zhang (2003) develops a model to study interactions that go from competition to mutualism between low and high population densities, which promotes coexistence; Zhang et al. (2007), following the *IF* model and Zhang (2003), study stability properties of transitions between outcomes, very mathematically oriented. Zhang et al. (2020), study the role of mutualism between antagonists in regulating ecological and evolutionary processes, density-dependent transition between mutualism and antagonism which should be favoured by natural selection (in a coevolutionary process), includes also an extensive review of other models and empirical work on rodents.

Some models study particular biological systems with variable interaction outcomes, using the *LV* model, or *IF* model approach. Neuhauser and Fargione (2004) model the mycorrhiza-plant interaction; the outcome between mutualism and parasitism is defined by population densities and environmental conditions. Sánchez-Garduño et al. (2014) build a mathematical model, based on a *LV* model, to study the main phenomenological features of the case of role reversal in the predator-prey interaction between whelks and lobsters in South Africa (mentioned above); they present results for both the temporal and spatiotemporal cases. Momo et al. (2006) modelled the dynamics of a marine plankton community to study the effect of UVB radiation on the community. They used four coupled ODE's of population growth rates and experimental data. Among other results, they found that if UVBR decreases predation all population abundances change and the community is driven to a new equilibrium. If nutrients supply is very large an indirect interaction of apparent competition emerges in the community, if there is an increase in the common predator population, whereas in conditions of nutrient depletion an apparent mutualistic interaction is expected. This provides an interesting situation of conditional apparent interactions.

I already commented, in section 5 above, on the series of papers by Griffon and Hernandez (2014, 2019); Griffon and Rodríguez (2017); Griffon et al. (2021), in which the spatial *IF* model is used to build ecological networks aiming to find results that can be applied in the agroecological field. I want to comment on two works that share two separate lines with the Griffon et al., papers: one theoretical, related to the

model development; the other applied, in the agroecological field.

Regarding the development of ecological networks, Yan and Zhang (2014) developed a model which share the structure and approach of Griffon and Hernandez (2014), that is, based on *LV* equations for many species, build ecological networks that include all types of interactions, with the possibility of changing sign, i.e., variable outcomes (the difference in the formulations is that Griffon and Hernandez use difference equations whereas Yan and Zhang use differential equations, also they do not do spatial analysis). The relevant issue is that Yan and Zhang (2014) also found that the persistence of complex networks is highly influenced by interactions that can shift sign; according to their results, the persistence increases or decreases depending on shifts occurring from positive, or to negative, or neutral, and at given density ranges.

With respect to applications on the agroecological field, the work of Bageta et al. (2018) studies the interaction between vine (*Vitis vinifera* L.) and cover crop, using a model also based on the *IF* model. They first explore the interactions with field experiments, and use these data to feed the model. They conclude that the interactions between the vine plant and the cover crop can shift between commensalism and amensalism, which means that the cover crop does not have a detrimental effect on vine growth.

What if theoretical interpretations do not feel natural

When, from a theoretical stand, we are trying to interpret and represent an observation of nature, we should aim for consistency. In the topic of the characterisation of interaction outcomes there are theoretical discrepancies (among them, and with natural observations), and as usually happens, all sides pose their arguments and proofs. In particular, I want to comment on the use of the jacobians of the community matrix to characterise population interactions (see Appendices A and B for some details, and Hernandez, 2009, for thorough elaboration and discussion). The rationale behind the use of the jacobians comes in terms of the responses of interacting populations to small perturbations at equilibrium, e.g., if a small increment in the equilibrium density of one species causes an increase in the other's, then the outcome is considered as beneficial (from the former to the latter), and so on for all combinations (increases and decreases, actions and responses). These are interpreted as representing the general effects of one species on the other, hence, pairs of responses end up categorising the interactions as mutualism, competition, victim-exploiter, etc. However, when applied to some models (see e.g., Zhang, 2003; Neuhauser and Fargione, 2004; Zhang et al., 2007, 2020; Lara and Rebaza, 2012), sometimes the results show, for instance, a victim-exploiter outcome assigned to a situation in which both populations reach higher densities than their corresponding carrying capacities. According to the rationale used along this article, this situation should correspond to a mutualism because both populations show a better performance in association than they would alone. As discussed in Appendix B and Hernandez (2009), the jacobians evaluate shifts between

stability modes (nodes and focus) in the dynamics near equilibrium, not shifts in the outcomes of interactions (sometimes they coincide, mathematically).

Having said this, the question is, is it ecologically appropriate to consider an interaction as victim-exploiter when it is observed that the two populations reach higher densities in association than alone? I say no, they should be characterised as mutualists. The debate, however, has more angles and edges. I personally consider that theoretical frameworks should be consistent and formally correct because they are meant to provide the guidelines to explore and understand the natural world. However, I also acknowledge that sometimes the empirical realities are far from the theoretical conditions. For instance, not always (to say the least) we can tell if a real system is at, or even close to, a stable equilibrium, or we do not know, neither have the means to measure, the carrying capacities, or maybe to know about those small effects after perturbations is what we need for a management program; and so on. All these considerations have a proper place in the discussion. Nonetheless, my stand is that theoretical research must be pristine, although some rough corners and dirty shoes will have to be agreed for the field setting.

After maths and after thoughts

What have we learned? . . . have we?

Nature is ambiguous, variation is the rule, diversity is the rule. The ineffable nature of nature.

Scientists do not make the rules, they just try to understand; some for the sake of curiosity, the nature of humans, others to take control, the nature of humans. The human condition.

Labels and structures are deeply embedded in the minds. That's what we think we need to do to understand. Maybe, as understanding makes its way through, we will learn to perceive the lines more than the dots; hopefully in our way to transcending the lines too.

A monk asked Fuketsu: 'Without speaking, without silence, how can you express the truth?'

Fuketsu observed: 'I always remember springtime in southern China. The birds sing among innumerable kinds of fragrant flowers'.

- Mumon Ekai (1228) The Gateless Gate

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APPENDIX A. THE LOTKA–VOLTERRA MODEL AND LEVIN'S COMMUNITY MATRIX

(Excerpts from Hernandez, 2009)

The dynamics of two interacting populations with densities N_1 and N_2 can be modelled by the system

$$\frac{dN_i}{dt} = F_i(N_i, N_j) \equiv N_i f_i(N_i, N_j) \quad i, j = 1, 2 \quad (\text{A.1})$$

F_i is the total population growth rate of species i , and f_i the *per capita* growth rate, as a function of population abundances. When $dN_1/dt = dN_2/dt = 0$, the system is at equilibrium $N^* = (N_1^*, N_2^*)$.

The generalised Lotka–Volterra model expresses the *per capita* growth rates of each interacting species as linear functions of the densities of other species (see e.g., Case, 2000). For a community of n interacting species the model can be written as

$$\frac{dN_i}{dt} = N_i \left(r_i + \sum_{j=1}^n a_{ij} N_j \right) \quad i, j = 1, 2 \quad (\text{A.2})$$

where r_i and a_{ij} are constant parameters; r_i is the intrinsic growth rate of species i and the a_{ij} are interaction coefficients that express the effect of a species j on a species i . For an equivalent model, Levins (1968) defined the *community matrix* A as the square matrix containing all a_{ij} coefficients. The signs of a_{ij} and a_{ji} pairs denote the type of interaction between species i and j : both signs equal for competitors, opposite signs for predator–prey (Levins, 1968).

For a two-species system the *per capita* expression of model (A.2), in matrix form, is

$$\begin{pmatrix} \frac{1}{N_1} \frac{dN_1}{dt} \\ \frac{1}{N_2} \frac{dN_2}{dt} \end{pmatrix} = \begin{pmatrix} r_1 \\ r_2 \end{pmatrix} + \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \end{pmatrix} \quad (\text{A.3})$$

which shows clearly the 2-by-2 *community matrix* A of elements a_{ij} .

A generic Lotka–Volterra (*LV*) model for two interacting populations, with explicit carrying capacities K_i , is commonly written as

$$\frac{dN_i}{dt} = N_i r_i \left(1 + \alpha_{ii} \frac{N_i}{K_i} + \alpha_{ij} \frac{N_j}{K_j} \right) \quad i, j = 1, 2 \quad (\text{A.4})$$

where α_{ii} is the intraspecific interaction coefficient (usually considered $= -1$, for linear intraspecific competition), and α_{ij} is the interaction coefficient between the two populations; the interactions are facultative for both populations, they reach carrying capacity K_i in the absence of species j .

Interaction coefficients α_{ij} play a crucial role in the representation and categorization of the types of interactions involved in the system. In plain terms it expresses how an individual of one species experiences the presence of the other species, both in strength (magnitude) and regarding its beneficial or detrimental nature (positive or negative); it accounts for how much one individual is worth in terms of an individual of the other species. Thus, it is a parameter related to the individual level that has an effect on the population level, that is, on the *per capita* (and hence, on the total) population growth of the other species.

If interaction coefficients α_{ij} are constant, model (A.4) allows for linear representations of the dynamics of all basic population interactions. The positive or negative effect of one population on the growth rate of the other is defined by the signs of α_{12} and α_{21} coefficients: both positive, or both negative, for mutualism and competition, respectively; one positive and one negative for a victim-exploiter (consumer-resource) interaction; for commensalism and amensalism, one coefficient is null and the other positive or negative, respectively.

In matrix notation, model (A.4) can be written as

$$\begin{pmatrix} \frac{1}{N_1} \frac{dN_1}{dt} \\ \frac{1}{N_2} \frac{dN_2}{dt} \end{pmatrix} = \begin{pmatrix} r_1 \\ r_2 \end{pmatrix} + \begin{pmatrix} \alpha_{11} \frac{r_1}{K_1} & \alpha_{12} \frac{r_1}{K_1} \\ \alpha_{21} \frac{r_2}{K_2} & \alpha_{22} \frac{r_2}{K_2} \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \end{pmatrix} \quad (\text{A.5})$$

which shows clearly that elements $\alpha_{ij}r_i/K_i$ correspond to the interaction coefficients a_{ij} in (A.3); thus, Levins' *community matrix* A (A.3) for the generic *LV* model (A.4) is

$$A = \begin{pmatrix} \alpha_{11} \frac{r_1}{K_1} & \alpha_{12} \frac{r_1}{K_1} \\ \alpha_{21} \frac{r_2}{K_2} & \alpha_{22} \frac{r_2}{K_2} \end{pmatrix} \quad (\text{A.6})$$

Therefore, according to the Levins' *community matrix* approach, the signs of the α_{ij} coefficients in model (A.4) uniquely determine the nature of the interactions, as expected. That is, the sign patterns of pairs $(\alpha_{21} \alpha_{12})$, written as $(+ +)$, $(- -)$, $(+ -)$, $(- +)$, $(0 0)$, correspond to mutualism, competition, victim-exploiter, commensalism, amensalism and neutral, respectively.

APPENDIX B. ON THE (DEBATED) APPROACH TO DEFINE THE NATURE OF POPULATION INTERACTIONS

(Abridged from Hernandez, 2009)

In the literature we find a variety of criteria on the appropriate way to categorize the *types* of interactions between populations (see e.g. Berlow et al., 1999, 2004); the term *type* may refer to the *strength* (magnitude), to the *nature* (beneficial or detrimental), or both. In this Appendix I discuss some

formalities on the appropriate characterisation of the *nature* of population interactions, with emphasis on the appropriateness of different approaches. I will be referring to some expressions of Appendix A above.

The relative performance approach

A widely common approach to characterise types of interaction is by comparing its performance alone with that in association (e.g. May, 1981; Berlow et al., 1999, 2004; Thompson et al., 2006; Holland and DeAngelis, 2009; Revilla and Encinas-Viso, 2015; Messan-Rodriguez et al., 2018). An interaction is *beneficial* if the population reaches a higher equilibrium density in the presence of the other species than in its absence; if it is lower, the association is considered *detrimental*.

We can quantify this statement using a Lotka-Volterra model as in (A.4) above. If N_i^* is the equilibrium density of species i when it grows in association with species j , and K_i is the carrying capacity K_i , then the difference $(N_i^* - K_i)$ measures the beneficial or detrimental effect of species j on species i . This expression divided by the carrying capacity K_i provides an appropriate *per capita* measurement of the intensity and sign of the interaction as experienced by each species. This can be formally expressed as

$$\Delta K_i^* = \frac{N_i^* - K_i}{K_i} \quad (\text{B.1})$$

Hence, the *nature* of the interaction from a comparative or *relative performance approach* is characterised by the signs of

$$\Delta_K^* = (\Delta K_2^* \quad \Delta K_1^*) \quad (\text{B.2})$$

so that, mutualism $(+ +)$ corresponds to $N_2^* > K_2$ and $N_1^* > K_1$, victim-exploiter or consumer-resource $(+ -)$ to $N_2^* > K_2$ and $N_1^* < K_1$, and competition $(- -)$ to $N_2^* < K_2$ and $N_1^* < K_1$. When $N_i^* = K_i$, then $\Delta K_i^* = 0$, thus the interaction is neutral. For obligate interactions it is assumed that $K_i = 0$.

When K_i is not an explicit parameter in the model, the corresponding value can be calculated; it is the magnitude of N_i^* evaluated at $N_j = 0$; that is, the value of N_i that satisfies $F_i(N_i, 0) = 0$ in equation (A.1) above.

For the Lotka-Volterra model (A.4), with linear intraspecific coefficients $\alpha_{ii} = -1$ and $\alpha_{ij}\alpha_{ji} < 1$, the stable equilibrium solutions can be expressed as

$$N_i^* = K_i + \alpha_{ij}N_j^* \quad (\text{B.3})$$

from which is easy to show that (B.1) becomes

$$\Delta K_i^* = \frac{\alpha_{ij}N_j^*}{K_i} \quad (\text{B.4})$$

Thus, the signs of $\Delta_K^* = (\Delta K_2^* \quad \Delta K_1^*)$ in (B.2) are given by the signs of $(\alpha_{21} \alpha_{12})$: $(+ +)$ mutualism, $(- -)$ competition, $(+ -)$ or $(- +)$ victim-exploiter, $(+ 0)$ commensalism, $(- 0)$ amensalism, $(0 0)$ neutral. Therefore, the resulting types of interaction for model (A.4) from the *relative performance approach*, Δ_K^* are consistent with the Levins' *community*

matrix A (A.6) above.

The *Interaction Function (IF)* model for the dynamics of interactions with variable outcomes is expressed as (equation 2, in main text)

$$\frac{dN_i}{dt} = N_i r_i \left[1 + \alpha_{ii} \frac{N_i}{K_i} + \alpha_{ij}(N_i, N_j) \frac{N_j}{K_i} \right] \quad (\text{B.5})$$

where $\alpha_{ij}(N_i, N_j)$ is the interaction function that accounts for the balance of density-dependent costs and benefits involved in the association for species i ; this function can take values in the negative and positive continuum.

By symmetry with (A.6) we can compute the *community matrix A* for the *IF* model as

$$A = \begin{pmatrix} \alpha_{11} \frac{r_1}{K_1} & \alpha_{12}(N_1, N_2) \frac{r_1}{K_1} \\ \alpha_{21}(N_1, N_2) \frac{r_2}{K_2} & \alpha_{22} \frac{r_2}{K_2} \end{pmatrix} \quad (\text{B.6})$$

That is, as the interaction functions, $\alpha_{ij}(N_i, N_j)$, are density dependent, so is the *community matrix*, $A \equiv A(N_i, N_j)$, and it is clear that the signs of the elements of A evaluated at any (N_i, N_j) are again the signs of the corresponding $\alpha_{ij}(N_i, N_j)$; hence, at equilibrium these correspond to the signs of $(\alpha_{12}^* \alpha_{21}^*)$.

By symmetry with (B.3), the equilibrium solution for the *Interaction Function* model (B.5) is

$$N_i^* = K_i + \alpha_{ij}^*(N_i^*, N_j^*) N_j^* \quad (\text{B.7})$$

thus, as in (B.4), we get

$$\Delta K_i^* = \frac{\alpha_{ij}^*(N_i^*, N_j^*) N_j^*}{K_i} \quad (\text{B.8})$$

Therefore, the signs of ΔK_i^* and of α_{ij}^* are always the same, hence, the outcomes from the *relative performance* approach and Levins' (1968) *community matrix* are consistent.

Note that these characterisations also correspond to the graphical representation within quadrants in the N_i, N_j phase plane defined by straight lines drawn at K_i and K_j (see e.g., figure 2, in main text).

The misleading use of the jacobian

The jacobian matrix is the essential tool for stability analysis in the systems examined here. However, sometimes it is also used to categorize types of interactions. This ambivalence in the usage of the jacobians has led to confusion and misconceptions in the characterisation of population interactions. Let's elaborate.

The jacobian matrix J for the dynamical system defined in (A.1) is obtained by taking partial derivatives with respect to population densities, that is, a matrix with elements $J_{ij} = \frac{\partial}{\partial N_j} \left(\frac{dN_i}{dt} \right)$, for $i, j = 1, 2$. This means linearizing the system, thus, if it is evaluated at a given point we can study

the dynamics of small perturbations in the neighbourhood of that point. The off-diagonal elements of J^* evaluated at equilibrium, say $(J_{21} \ J_{12})^*$ or $(J_{21}^* \ J_{12}^*)$, assess the response of the growth rate of species i to small changes in the density of species j at equilibrium. For instance, a positive J_{21}^* means that a small increment in N_1 at equilibrium causes an increase in the growth rate of species 2, hence N_2 increases, whereas if negative, a small increment in N_1 at equilibrium causes N_2 to decrease. These responses were interpreted as representing the effects of one species on the other, that is, the signs of the $(J_{21} \ J_{12})^*$ pairs were matched to the types of population interactions: (+ +) for mutualism, (− −) for competition, (+ −) for predator-prey, etc. In other words, the jacobian matrix was considered as an extension of Levins' community matrix (May, 1973).

On the other hand, the stability properties of these dynamical systems can also be inferred from the jacobian matrix evaluated at equilibrium, in particular, from its eigenvalues. The equilibrium is stable, if and only if the real parts of all the eigenvalues are negative, otherwise it is unstable (or a saddle point). If the eigenvalues have no imaginary parts, the perturbed system moves monotonically to, or away from, equilibria (a node), if the imaginary parts are non-zero, the movement is oscillatory (a focus); also May (1973).

And, this is where metrics collide and disentangling is required. Some evaluations and comparisons can be performed on different systems and get some answers; this was done in Hernandez (2009), I present here a succinct recount.

The jacobians were analytically and numerically evaluated in well-known classical linear and nonlinear models of population interactions (e.g. Lotka–Volterra competition, Rosenzweig–MacArthur predator-prey, etc.). The results show that in all these cases the signs of $(J_{21} \ J_{12})^*$ are uniquely determined, either positive or negative, and they correspond exactly to the signs of elements $(\alpha_{21}, \alpha_{12})^*$ of the community matrix A (A.6); it is also shown that they correspond to the signs in ΔK_i^* (equation B.2), i.e., to the relative performance approach. Therefore, all types: (+ +), (− −), (+ −), etc., obtained from the three approaches are coincident in these systems.

The inconsistencies arise when interactions with variable outcome are evaluated. In these models (e.g. IF models in Hernandez 1998, 2008, competition-cooperation model in Zhang, 2003, mutualism-parasitism model in Neuhauser and Fargione, 2004) the signs of $(J_{21} \ J_{12})^*$ are not univocally determined, they are defined as a subtraction of terms, thus they can take negative or positive values (depending on densities and parameters). The same models were evaluated with the relative performance approach; the results show that the signs of $(\Delta K_2^* \ \Delta K_1^*)$ also vary for different sets of parameters. The assessment of both sets reveals that in some cases the results from the two approaches agree, in some others they do not. On the other hand, as expected from statements made above, the outcomes from the relative performance approach and those from the community matrix A , do agree, in all cases, that is, signs of $(\Delta K_2^* \ \Delta K_1^*)$ are always the same as signs of

$(\alpha_{21}, \alpha_{12})$.

The disentangling

When the elements of the jacobian, $(J_{21} J_{12})^*$, are evaluated in models for interactions with variable outcomes, and these present the possibility of different signs for different sets of parameters (as described above), one might be tempted to interpret this as representing the shifts in the outcomes of interactions. It is not so; it is nothing more than shifts between stability modes: from node to focus, or vice versa. This can be analytically proven from the formal expression of the eigenvalues of a 2-by-2 matrix, from which the thresholds between focus and nodes can be easily computed and seen to correspond to the shifts (details in Hernandez, 2009). This can also be easily observed graphically in a phase plane representation (e.g. figure 2 and 5, in main text). The jacobians are the slopes on the nullclines at equilibrium (linearization at equilibria), the shifts in sign correspond to the changes of slopes, hence, changes in the eigenvalue conditions between focus and node.

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