When cheating turns into a stabilizing mechanism of mutualistic networks

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FD designed the study and performed all analyses. EB, MAM, TS and EG collected the data and performed trait measurement. FD, SA, TS and EB curated the data. FD wrote the first draft and all authors contributed to final writing and editing.

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Abstract

Mutualistic interactions, such as plant-mycorrhizal or plant-pollinator interactions, are widespread in ecological communities and frequently exploited by cheaters, species that benefit from interactions without providing commodities in return. Cheating is often thought to negatively affect the fitness of the cheated individuals, but its effect at community level remains poorly studied. Here, we describe two different kinds of cheating in mutualistic networks and show that they have very different consequences for the ecological stability of the community. Conservative cheating is when a species cheat on their mutualistic partners to escape the cost of mutualistic interactions. In contrast, innovative cheating occurs when a species cheats with partners that it would otherwise not have access to. Using a theoretical model, we found that network persistence is negatively affected by conservative cheating but can be enhanced by innovative cheating. Innovative cheating becomes a stabilizing mechanism when cheaters have few mutualistic partners, cheat at low or intermediate frequency and when the cost associated with mutualism is not too high. In this case, the negative effects of cheating on partner persistence are overcompensated at the community level by the positive feedback loops arising in mutualistic networks. Using an empirical dataset of plant-bird interactions, we found that observed cheating patterns are highly consistent with theoretical cheating patterns that increase network persistence. This result suggests that eco-evolutionary dynamics tend to produce cheating patterns that increase the ecological stability of communities. Thus, cheating observed in nature could contribute to stabilize mutualistic communities instead of destabilizing them.

Significance Statement

Cooperative interactions among species (mutualism) are widespread in nature. In those systems cheaters benefit from resources while escaping the cost of cooperation, which can lead to community collapse. While cheating is often considered to occur in existing mutualistic interactions (conservative cheating), species can also cheat on species that have never been mutualistic partners (innovative cheating). Using a theoretical model, we show that innovative cheating can increase the number of species coexisting at ecological equilibrium, in contrast to conservative cheating, which decreases the number of species persisting at equilibrium. Empirical data show that innovative cheating in plant-bird interaction networks is common, suggesting that cheating could contribute to the stability of natural mutualistic communities.

Main text

Introduction

Mutualism, an interaction that benefits all species involved, is widespread in the web of life (1, 2). In natural systems involving mutualism, it is common to find cheaters, species reaping benefits from interactions without providing benefits to their partners (3, 4). Cheating has been descried in mycorrhizal (5), plant-pollinator (6), cleaning fish (3) and seed-dispersal (7) interactions. Evolutionary theory has shown that a stable coexistence of mutualists and cheaters is possible (8–10), explaining their persistence in nature. Using pollination as a study model, few ecological studies has shown that illegitimate interactions between plants and pollinators (cheating, *i.e.* nectar robbing) affect the structure of the interaction networks (6, 11), but the consequences of cheating for the ecological stability of these communities has been largely overlooked.

From an evolutionary perspective, widely based on game theory, cheating is only viewed as a way to escape the cost associated with mutualism (8, 12–14), for example, energy expenditure due to nectar production in plants or foraging in animals. In this case, while the species could interact legitimately, they cheat because the cost of cheating is lower than the cost of legitimate interactions. However, species can also cheat to profit from partners that are otherwise unavailable, when a legitimate interaction is not possible because of a physiological or morphological barrier (15, 16). In the first case, cheating is directly detrimental for the mutualism because it replaces mutualistic interactions with antagonistic or commensalistic ones (Fig. 1a). We termed this type of cheating, where the interaction niche of the species remains constant (Fig. 1b), conservative cheating. In the second case, cheaters use a partner that is otherwise unavailable, thus resulting in new interactions that would not exist in a purely mutualistic framework (Fig. 1a). We termed this second type of cheating, where the interaction niche of the cheater expands (Fig. 1b), innovative cheating.

The consequences of cheating for community stability likely depend on whether cheating is conservative or innovative, as they re-organize the structure of interactions in different ways. For conservative cheating, we always expect that it decreases network persistence, because mutualistic interactions, which tend to increase persistence (17), are replaced by antagonistic or commensalistic ones. This is especially the case when guilds strongly depend on each other. For innovative cheating, the outcome on network persistence becomes uncertain because it will increase the persistence of the cheaters, as they can rely on more partners, but the resulting niche expansion could promote competitive exclusion of other species from the same guild. If cheaters are specialists (*i.e.* with few partners), we expect that innovative cheating increases the overall network persistence, because it will increase persistence of specialists species. Specialists are often the most vulnerable species to extinction (18, 19), thus increasing their persistence could increase the overall network persistence through positive feedback loops arising in mutualistic networks. If cheaters are generalist species, we expect that their persistence will be only slightly enhanced by innovative cheating, as they already have many partners. In this case, innovative cheating is more likely to promote competitive exclusion, leading to a decrease in network persistence.

Empirical data show that innovative cheating is common in pollination networks, because birds or insects often rob nectar in flowers with long corolla in which nectar is difficult to access through mutualistic interactions (15, 20, 21), stressing the need to understand the consequences of this specific kind of cheating at the community level. To test hypotheses developed above, we first used a theoretical ecological model, without evolutionary dynamics, to assess the consequences of conservative and innovative cheating for the ecological stability of bipartite mutualistic networks, measured as network persistence. Using these results, we formulated conditions in which cheating increases ecological stability of communities. To see if these conditions are met or not in nature, we explored cheating patterns in empirical mutualistic networks of plant-bird interactions, which have both legitimate and illegitimate interactions between birds and open flowers. Finally, to close the loop between theory and data, we used these empirical data to parametrize our model and assess how observed patterns of cheating affect network persistence.

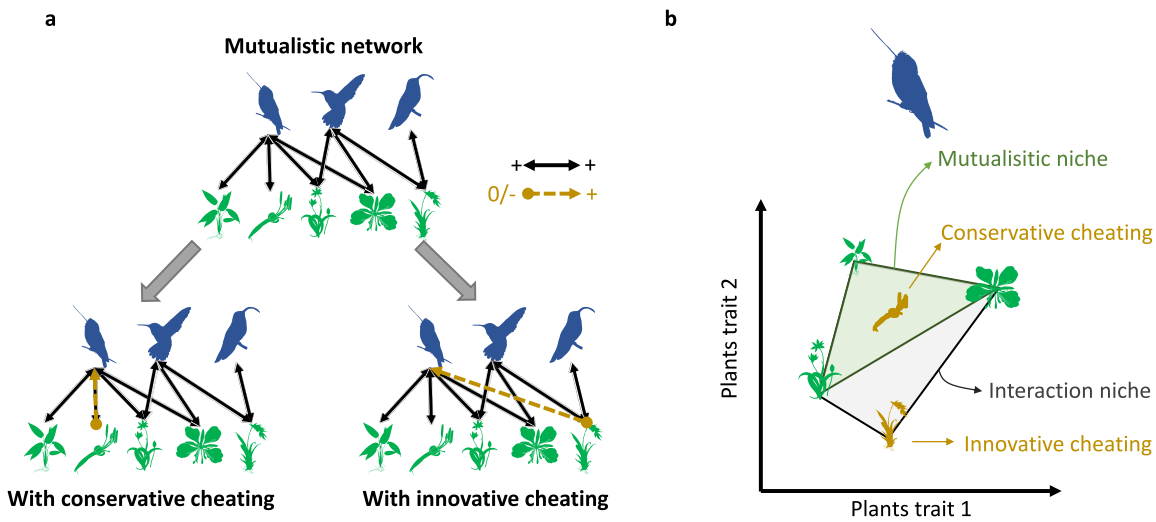

Figure 1: Cheating can be conservative or innovative. *(a) Above, mutualistic network built using only +/+ (legitimate) interactions and below, mutualistic networks including one illegitimate interaction. Cheating is conservative if it happens between partners that were already linked by a mutualistic interaction, or innovative if it happens between partners that were not linked by a mutualistic interaction. (b) Cheating characterized in a niche concept. Symbols represent the position of the legitimate (green) and illegitimate (yellow) partners of a given species of pollinator in their trait space. Conservative cheating occurs within the mutualistic niche, which is the convex hull determined by trait combination of legitimate partners. Innovative cheating occurs with plants that are outside of the mutualistic niche and lead to an expansion of the interaction niche, defined as the convex hull determined by trait combination of legitimate and illegitimate partners.*

Results

We used a generalized Lotka-Volterra model with two guilds, 20 plant and 20 pollinator species, embedded in an obligatory mutualistic relationship. We incorporated three parameters to model cheating: the proportion of pollinator species cheating ($\bar{\Delta}$), the cheating frequency of these cheaters (Ω), the proportion of innovative cheating *vs* conservative cheating (Ψ); and a fourth parameter to model the cost associated with mutualism (Λ), that is likely to mediate the effect of cheating. For simplicity we assumed that only pollinators cheat, so only they were able to interact illegitimately with plants, *i.e.* piercing the flower corolla and robbing the nectar without pollinating. Cheaters escape the cost associated with mutualism while robbed plants do not benefit from these interactions and still pay the cost associated with mutualism. We also assumed no additional cost due for plants to cheating than the one associated with mutualism. To test how the degree of generalism of the cheaters affected the consequences for community persistence we performed simulations for two scenarios: when the cheaters were the most generalist species or when they were the most specialist species in the community (*cf.* Methods).

Our simulations showed that the output of cheating on network persistence, measured as the percentage of persisting species at equilibrium, could be negative or slightly positive (Fig. 2a & S1) and strongly depended on its conservative *vs.* innovative character.

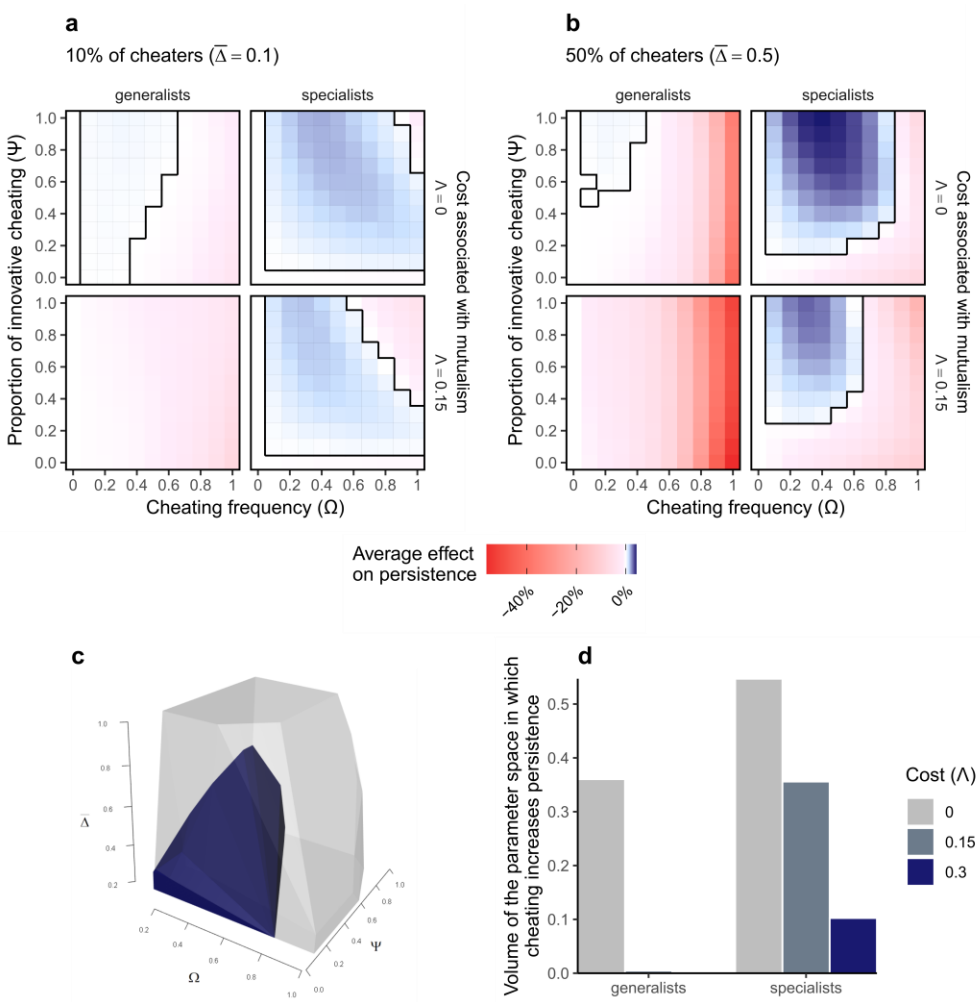

Figure 2: Innovative cheating can increase network persistence. *Network persistence (percentage of persisting species at equilibrium) as a function of cheating frequency (Ω), proportion of innovative cheating (Ψ), cost associated with mutualism (Λ) and scenario (cheaters are generalist or specialist species) for (a) a case with 10% and (b) a case with 50% of animal species cheating. The colours represent the average effect of cheating on network persistence relative to the corresponding case with no cheating (Ω = 0). Positive values (blue) indicate higher persistence with than without cheating, while negative values (red) indicate the opposite, a negative effect of cheating on persistence. Results are presented for initial values of connectance φ=0.4 and averaged over the 500 initial conditions. The black boxes represent the space in which cheating has a positive effect on network persistence, which is represented in 3D for the specialist scenario in (c) for Λ=0 (grey) and Λ=0.3 (dark blue). (d) represents the volume of this 3D space as a function of the scenario and the cost associated with mutualism. A cost of Λ=0.15 or Λ=0.3 corresponds to 10% or 20% of benefits associated with mutualism, respectively (Λ/α = 0.1 or 0.2).*

As expected, when cheating was conservative it almost always negatively affected network persistence, because cheating decreases benefits of plant-animal interactions for plants, thus decreasing their persistence. In an obligatory mutualism, interacting guilds depend on each other, therefore a decrease in plant persistence is likely to negatively affect overall network persistence. Regardless of its conservative/innovative character, cheating had a more negative (or less positive) effect on persistence when there was a cost associated with mutualism (Λ>0, Fig. 2a), *i.e.* when illegitimate interactions are antagonistic. Similarly, in average, cheating had a less negative (or more positive) effect on network persistence when cheaters were specialist species than when they were generalists (Fig. 2a). This difference is because cheating makes specialists better able to persist and thus can buffers the negative effects of cheating on their partners through positive feedback loops arising in mutualistic networks (Fig. S2). In contrast, cheating had few positive effects on persistence of generalist species (Fig. S2), so when they cheat, cheating is likely to negatively affect network persistence.

The window of parameters in which cheating increases network persistence, relative to cases with no cheating, mostly correspond to the cases when: cheaters were specialists, cheating was innovative with intermediate frequencies and the cost associated with mutualism was low (Fig. 2 & S1). This parameter space can be represented in 3 dimensions (Fig. 2c), using the three parameters controlling for cheating distribution, the proportion species cheating ($\bar{\Delta}$), the cheating frequency of these cheaters (Ω) and the proportion of innovative cheating (Ψ). The scenario of simulation, generalists *vs.* specialists, and the cost associated with mutualism strongly affected the volume of the parameter window in which cheating had a positive effect on persistence (Fig. 2c-d). Cheating increased network persistence by 4.7% maximum, suggesting that if cheating could have a positive effect on persistence, it however remained a weak effect. This positive effect on network persistence tended to disappear when cheaters were generalists and with the increasing cost associated with mutualism (Fig. 2b) but remained even when the proportion of cheaters was high (Fig. 2d), if the overall level of cheating, measured as $\bar{\Delta} \times \Omega$, was not too high (Fig. S3).

In extreme cases, when cheating frequency increased above a given value, innovative cheating could have a more negative effects on network stability than conservative cheating (Fig. 2a & S1). This result is likely because when the frequency of innovative cheating increases, specialists switch from facilitators to competitors (Fig. S4). This is because innovative cheating expands the interaction niche of specialists, thus increasing competition with other species, while it does the opposite for generalists (Fig. S4). Thus, the drop in persistence observed for high frequencies of innovative cheating was likely due to competitive exclusion promoted by cheaters that were initially specialists.

Taken together, these results show that under some conditions, innovative cheating can enhance stable coexistence of species in mutualistic communities, instead of destabilizing them. The average results presented in Fig. 2 explained ~51% of the variance in the effect of cheating on network persistence. The residuals effects of cheating on network persistence were positively correlated to the average growth rates of plants and animals (Fig. 3a) suggesting that cheating is more likely to have a positive effect on persistence when plant and animals depend weakly on each other than when this dependence is strong. The residual effects of cheating on persistence were also significantly linked to network structure, namely, connectance, nestedness and modularity (Fig. 3b-c). On average, the effect of cheating was more positive (less negative) when initial mutualistic interaction networks were more connected, more nested and more modular (Fig. 3), suggesting that the consequences of cheating were partially mediated by the structure of the underlying mutualistic network. Even if effects of the nestedness on the consequences of cheating were apparent in some conditions (Fig. S5), those structural variables explained only ~23% of the variance of residual effects of cheating on persistence. This result suggests that they were not the main determinant of how cheating affects network persistence, explaining why results were qualitatively similar over different connectance values (Fig. S1 & Fig. S6).

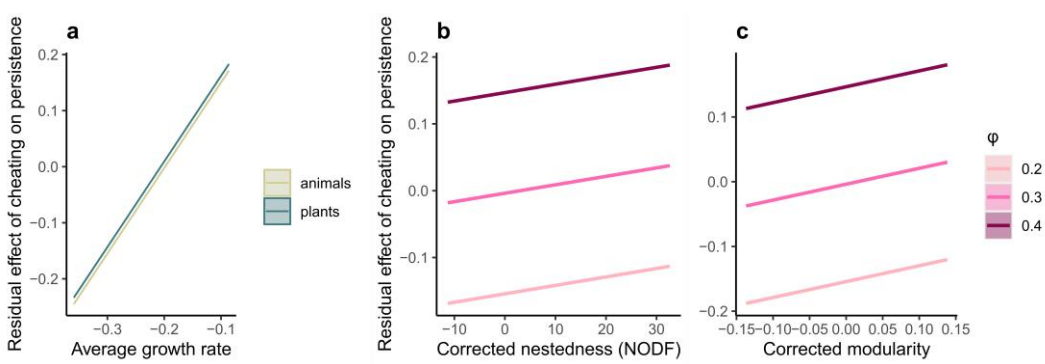

Figure 3: Effect of cheating on persistence is linked to plant-pollinator dependency and to network structure. *Residual effects of cheating on persistence as a function of (a) average plants and animals' growth rates, (b) connectance and nestedness, and (c) connectance and modularity of the initial mutualistic network (I_M, cf. Methods). Residual effects of cheating are calculated by subtracting the average effect corresponding to the respective parameter combination from the effect observed for each individual simulation. Positive values indicate effect of cheating on persistence above average effect while negative values indicate the opposite. In (a), more negative growth rates indicate*

stronger dependency to the other guild. Lines represent model predictions. Nestedness and modularity measures were corrected by connectance (φ) to disentangle their respective effects.

Considering the theoretical results developed above, empirical patterns of cheating should follow these conditions to maximize community persistence: (i) cheaters should be mainly specialists species, (ii) illegitimate interactions should mainly occur out of the mutualistic niche of cheaters (innovative cheating), (iii) proportion of cheaters can be high but the overall level of cheating, measured as $\overline{\Delta} \times \Omega$, should stay low (<0.5) and decrease with costs associated with mutualism, (iv) cost associated with mutualism should not be too high.

To evaluate if these conditions are met in natural communities, we used a unique dataset of empirical interaction networks between flowering plants and pollinating birds, over 17 sites in two countries, Costa Rica and Ecuador. We found patterns consistent with the conditions in which cheating has a positive effect on persistence (Fig. 4). First, cheaters tended to be specialist species (Fig. 4b, χ^2= 4,34, p-value = 0.037), a result that was consistent across countries (χ^2< 0.00, p-value = 0.96 for the interaction). Second, birds tended to cheat mostly in an innovative way (Fig. 4c), *i.e.* outside of the niche defined by the morphological traits of their mutualistic partners (*cf.* Methods). Third, even if the proportion of cheaters was high in some cases (Fig. 4d), the overall level of cheating was low and strongly decreased with the elevation (Fig. 4e, χ^2= 9.16, p-value = 0.002), partially because the proportion of cheaters also decreased with elevation (Fig. 4d, χ^2= 4.56, p-value = 0.03). Elevation is likely a proxy of cost associated with mutualism because it increases physiological constraints on plants and birds, likely increasing the cost of nectar production for plants and flight for birds. These trends were not significantly different between countries (*cf.* Table S1). It was not possible to evaluate the fourth condition because cost associated with mutualism was not estimable from the data. Nonetheless, the three first conditions were highly consistent with the theoretical patterns of cheating that maximize network persistence.

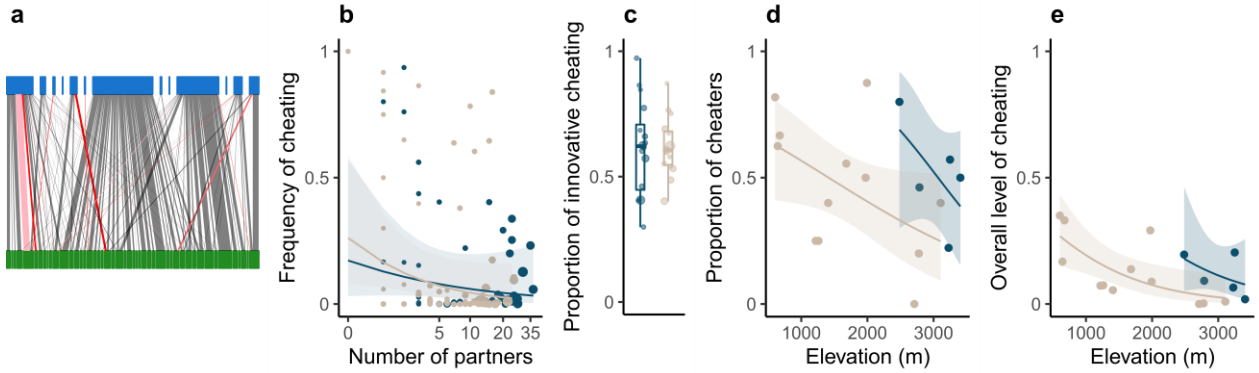

Figure 4: Empirical cheating patterns in plant-bird interaction networks fit theoretical conditions to maximize network persistence. *(a) An empirical network of interactions between plants (green) and birds (blue) from Ecuador for a given site. Thickness of the lines is proportional to interaction frequency, while colour of the lines represents cheating frequency, grey (only legitimate) and from pink (low cheating frequency) to bright red (only illegitimate). (b) Frequency of cheating as a function of mutualistic partner diversity, for each combination of bird species and site, for datasets from Costa Rica (beige) and Ecuador (dark blue). The size of the point represents the total number of interactions of the species in the given site. The solid lines show predictions of a generalized linear mixed-effects model with associated 95% confidence interval. (c) Proportions of innovative cheating, where each point is a bird species who cheated at least once. The size of the point represents the total number of interactions of the species summed over sites. (d) Proportion of cheaters and (e) overall level of cheating, for each site, as a function of elevation (in meters above sea level). The solid lines show predictions of generalized linear models with associated 95% confidence intervals.*

To close the loop between theory and data, we also used these empirical networks to parametrize our dynamic model and perform simulations over a gradient of model parameters that were not estimable from data (*cf.* Methods, Fig. 5). We confirmed that observed cheating patterns increased network persistence of empirical network, when the cost associated with mutualism was low (Fig. 5). Effects of cheating on network persistence in empirical networks became negative when considering high levels of per-interaction benefits

and cost associated with mutualism, but were positive for low and intermediate costs (Λ) and per-interaction benefits (α), which is likely to be the case in nature (22, 23).

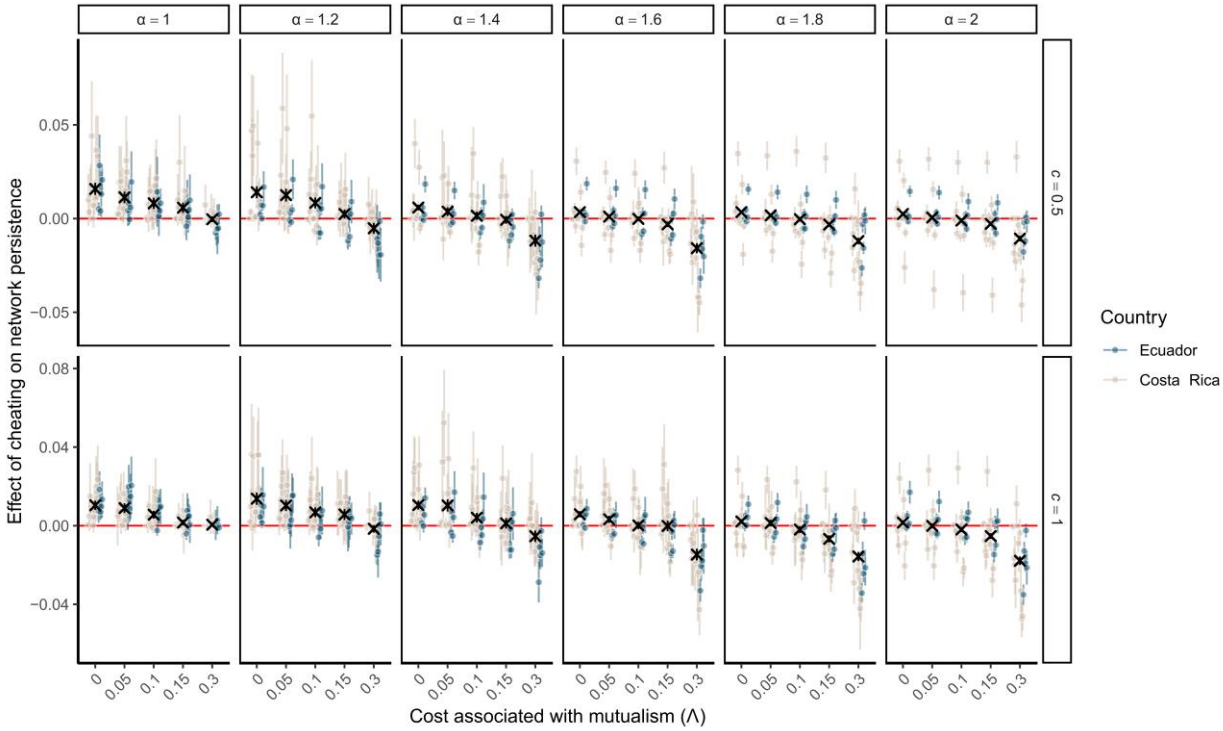

Figure 5: Parametrizing theoretical models with empirical data reveal that cheating can increase network persistence, when cost associated with mutualism is low. *Effect of cheating on network persistence when parametrizing the model with empirical patterns of cheating, as a function of per-interaction benefit (α), strength of competition for mutualistic partners (c) and cost associated with mutualism (Λ). Points represent the average effects over the 100 simulations performed over different growth rate vectors, while error bars represent the standard deviation. Black cross represents the overall average (over sites) and associated 95% confidence interval (vertical error bars, often hidden because too small). Note that the x-axis is not linear, there is a jump between Λ = 0.15 and Λ = 0.3.*

Discussion

We described two different kinds of cheating in mutualistic systems: conservative cheating arising when a species profits from a mutualistic partner, and innovative cheating, when a species profits from a species that is not a mutualistic partner. Highlighting these nuances in cheating and giving them distinct names allowed us to unify in a common theoretical framework two different conceptions of cheating: a concept inherited from game theory in which species cheat to escape cost (conservative cheating, see *ref.* 9 & 14) and empirical observation of nectar robbing in which species cheat to access new resources (innovative cheating, see *ref.* 18). Here we show that these nuances in cheating are important because they have different consequences for community stability. While conservative cheating always negatively affects network persistence, innovative cheating, the most prevalent kind of cheating in our empirical dataset, can have a positive effect on network persistence. In our empirical study case of plant-bird interactions, simulations and data analyses consistently show that cheating can increase the number of species able to coexist at ecological equilibrium. Evolutionary theory has proposed answers to the paradox of the persistence of mutualism in presence of cheaters (9, 24). Here we show that these cheaters are not rare in nature, and that they can enhance the ecological stability of mutualistic communities instead of destabilizing them.

Most empirical studies focusing on cheating in mutualistic networks have used indirect proxies of cheating, such as marks on flower corollas left (20, 25) or heterotrophic status of plants in plant-mycorrhizal networks (5). Although these proxies are valuable, they do not allow to characterize cheating as conservative

or innovative, because cheating is defined at the species level. Here, by using camera traps we were able to characterize each interaction as legitimate or illegitimate, and thus define cheating at the interaction level, allowing to estimate the relative importance of conservative and innovative cheating. Our analyses of this unique empirical dataset show a continuum gradient between cheating and mutualism: cheaters are common (up to 60% of the bird species, Fig. 4d) but they often cheat at a low frequency. Using theoretical simulations, we show that such low cheating frequency can dramatically affect network persistence, negatively or positively depending on the context (innovative *vs* conservative, cost and identity of cheaters). Previous work has shown that this continuum from mutualistic to antagonistic interactions, embedded in mutualistic networks, is important for community stability (7, 26). We extended these results by showing the distribution of the antagonistic links *vs.* mutualistic ones has important consequences for stability. When considering overlapping commensalistic/antagonistic and mutualistic links (*i.e.* conservative cheating) network persistence is lower than when commensalistic/antagonistic and mutualistic links occur between different species pairs (*i.e.* innovative cheating).

Our theoretical results highlight four conditions that can turn cheating into a factor increasing network persistence: (i) cheaters should be mainly specialists species; (ii) illegitimate interactions should mainly occur out of the mutualistic niche of cheaters (innovative cheating); (iii) the proportion of cheaters can be high but the overall level of cheating, measured as $\overline{\Delta} \times \Omega$, should be low (<0.5) and decrease with costs associated with mutualism; and (iv) costs associated with mutualism should not be too high. Parametrizing our model according to these rules led to ecological equilibriums that were in average more diverse than other parameter combinations. However, since our model did not include evolution, the question remains whether these ecological equilibriums are also evolutionary stable, that is can we expect to find them in nature.

Our analyses of empirical data suggest that patterns of cheating following the four conditions described above can be found in nature. Indeed, studied empirical communities appeared to be in the parameter window in which cheating tends to optimize ecological stability. Strong cheaters were specialist species, cheaters mainly cheated in an innovative way and the overall level of cheating was relatively low and decreased when costs associated with mutualism are likely to increase (with elevation). However, the cost associated with mutualism is a key parameter that determines the outcome of cheating on community stability, but we were not able to assess it from empirical data. Assessing this cost would require complex physiological measurement on birds and plants, that currently have been only rarely done (27, 28), and never on both guilds simultaneously. Although these missing measures of cost associated with mutualism add a layer of uncertainty on the effect of cheating on community stability, our theoretical results show that even with a cost reaching 20% of the mutualism benefits, innovative cheating can still have a stabilizing effect, in a very narrow parameter combination (Fig. 2b & S2).

The empirical patterns observed are the result of an interplay between community assembly processes and evolutionary dynamics (29), suggesting that, against what we could have expected, eco-evolutionary dynamics have shaped cheating patterns in a way that it increases community stability. The selection for innovative cheating in specialist species could be explained by the ability of species to select partners, that could lead to a competitive disadvantage for cheaters, strong enough to prevent generalists to become conservative cheaters, but still allowing specialists species to evolve as innovative cheaters. It has been shown recently that the coexistence of cheaters and mutualists can be evolutionary stabilized because of the ability of species to select the partners to which they give benefits (10). This ability to choose can be itself evolutionary stabilized by the presence or emergence of cheaters at each generation (30), thus leading to a loop of eco-evolutionary feedbacks that could explain the empirical patterns observed here. However, it is hard to substantiate this idea because studies focusing on cheating and evolution of mutualism considered conservative cheating only (8–10, 24, 30). Given the importance of innovative cheating for community stability, our results stress the need to revisit eco-evolutionary theory of cheating in a network context (11, 31). This future direction would provide new insights on the astonishing faculty of evolutionary processes to sometimes create structures that promote ecological stability at the community level.

Finally, since our theoretical model went through a necessary step of oversimplifying natural systems, we likely neglected subtilities in the way species cheat that could affect the consequences of cheating for community stability, for example behavioural changes of pollinators due to robbers (32). It has been shown that many opportunistic pollinators use already existing holes in flower corolla (16, 33). In this case, there is likely a difference of cost for plants between the primary cheating event, degrading the floral parts that involve an additional cost for plants, and secondary cheating events that only involve the cost associated with mutualism (*i.e.* nectar production). In addition, consequences of such flower degradation likely depends to when it occurs, after of before pollination, suggesting that the sequential order of these mutualistic/antagonistic interactions is likely to drive the overall effect of cheating on lifetime fitness, as suggested in plant-ant interactions (34). However, our results offer a new perspective on cheating in a mutualism context, extending the classic view inherited from the game theory, to describe a kind of cheating, innovative cheating, that was previously neglected in theoretical works. We derived a set of simple conditions turning cheating in a mechanism enhancing species coexistence, showing that antagonistic interactions embedded in mutualistic networks can play a key role in community stability. While previous studies on evolution had shown that mutualism and cheaters can coexist in the same communities, here we show that this mixture can increase the number of species coexisting in nature.

Materials and Methods

Theoretical model

We used a generalized Lotka-Volterra model with two guilds, plant (P_i) and pollinator (A_j), modelling temporal variations of abundance for each species. We incorporated four parameters ($\bar{\Delta}$, Ω, Ψ, Λ) that control respectively for the proportion of species cheating, proportion of links affected by cheating for each cheater (cheating frequency), the proportion of innovative cheating (*vs* conservative cheating) and the cost associated with mutualism.

We generated a gaussian morphological trait for each species, to define an initial binary interaction matrix (I_M) with a given connectance (*cf.* Supplementary Methods). $I_{M_{ij}}$ was the pairwise interaction strength between plant *i* and pollinator *j*, and equaled either zero (no interaction) or one (mutualistic interaction). $I_{M_{\cdot j}}$ defined the mutualistic niche of pollinator *j*, *i.e.* all partners with which pollinator *j* interacted mutualistically. The mutualistic niche of plant *i* was given by $I_{M_{i\cdot}}$. To store the information of species not being in the mutualistic niche of species in a convenient way for next steps, we also built another matrix, I_O, using $I_{M_{ij}} = 1 - I_{M_{ij}}$.

Each species of pollinator was defined by a binary state, cheaters (1) *vs* non cheater (0), stored in the vector Δ. The number of cheaters was defined as $round(\bar{\Delta} n_A)$, $\bar{\Delta}$ being the proportion of species cheating. To define cheaters, we used two different scenarios, one in each of those cheaters are the most specialist species and one in which they are the most generalist species (*cf.* Supplementary Methods). Each cheater cheated with a frequency Ω of their initial legitimate interactions. This amount of cheating was divided in conservative cheating $(1 - \Psi)\Omega$ and innovative cheating $\Psi\Omega$. The cost associated with mutualism was set by parameter Λ, which could vary on $0 \leq \Lambda < \alpha$ to be in a mutualism case.

Thus, a plant *i* interacted in a legitimate way with pollinator *j* with a strength $M_{ij} = I_{M_{ij}}(1 - \Delta_j\Omega)$. The same pair of species interacted illegitimately (with benefits only for the pollinator) with a strength $C_{ij} = \Delta_j\Omega\left((1 - \Psi)I_{M_{ij}} + \Psi I_{O_{ij}}\right)$, where $\Delta_j\Omega(1 - \Psi)I_{M_{ij}}$ was the conservative cheating and $\Delta_j\Omega\Psi I_{O_{ij}}$ the innovative cheating.

The model was described by the following system of differential equations for the plants and the pollinators, respectively:

$$\frac{dP_i}{dt} = P_i\left(r_{P_i} + \frac{(\alpha-\Lambda)\sum_{j=1}^{n_A} M_{ij}A_j}{1+\beta\sum_{j=1}^{n_A} M_{ij}A_j + c\sum_{k=1}^{n_P}\Pi_{ik}\times P_k} - \frac{\Lambda\sum_{j=1}^{n_A} C_{ij}A_j}{1+\beta\sum_{j=1}^{n_A} C_{ij}A_j + c\sum_{k=1}^{n_P}\Upsilon_{ik}\times P_k} - \sum_{k=1}^{n_P} c_{P_{ik}}\times P_k\right) \quad (1)$$

$$\frac{dA_j}{dt} = A_j\left(r_{A_j} + \frac{\sum_{i=1}^{n_P}[\alpha(M_{ij}+C_{ij}) - \Lambda M_{ij}]P_i}{1+\beta\sum_{i=1}^{n_P}(M_{ij}+C_{ij})P_i + c\sum_{k=1}^{n_A}\Theta_{jk}\times A_k} - \sum_{k=1}^{n_A} c_{A_{jk}}\times A_k\right) \quad (2)$$

The between parentheses part of equation (1) can be divided in four parts.

First, r_{P_i} was the basal growth rate of the focal species. Growth rates were scaled between -0.5 and -0.001, and drawn randomly from a beta distribution, to sample a wide variety of possible vectors of growth rates (*cf.* Supplementary Methods).

The second part modeled the balance between benefits and cost associated with mutualistic interactions. To have mutualistic interaction we fixed that the benefits were higher than cost ($\alpha > \Lambda$), so overall benefits increased and saturated with the product of legitimate interaction strength (M_{ij}) and abundance of the interaction partners by a rate $\alpha - \Lambda$ and β, respectively. Benefits also saturated because of competition among plants for shared pollinators, by a rate c, Π_{ik} being a vector of interaction similarity between P_i and P_k (*cf.* Supplementary Methods).

The third part modeled the cost of cheating interactions only, regardless of their kind, innovative or conservative. For the costs of illegitimate interactions for plants, we used a similar functional response than for mutualistic interactions. Similarly, costs of illegitimate interactions increased and saturated with the product of the amount of cheating in interactions C_{ij} and abundance of the interaction partners by a rate Λ and β respectively. Costs also saturated because of dilution of cheaters among plants sharing cheaters (Υ_{ik}, *cf.* Supplementary Methods), by a rate c.

Finally, the fourth part modeled the competition among plants, independent from mutualistic partners, for example competition for space.

Equation (2) can be divided in analogous parts, except that the third part described in equation (1) is absent, as the cost-benefit balance associated with mutualism and cheating could be grouped in one functional response, because all interactions with plants, regardless of their legitimate or illegitimate status, participated to competition among pollinators.

Numerical simulations

We created 500 different set of species, with different traits and growth rates, while fixing $n_A = n_P = 20$. For each of these initial conditions we solved the model numerically, for the 3630 chosen possible combinations of cheating parameters (Δ, Ω, Ψ, Λ, Table 1). For each of these combinations and initial conditions we applied two scenarios, one in which cheaters were the generalist pollinator species, another one in which they were the most specialist species (*cf.* Supplementary Methods). We also performed all these simulations with three different values of initial connectance (cf. Table 1). That led to 500 × 3630 × 2 × 3 = 10,890,000 simulations. We stopped a simulation when the variance of species abundance over the last 10 time steps was lower than 10^{-14} or when the number of iteration reached 8,000. In >99,98% of the simulations this was enough to reach a stable steady equilibrium (all eigen values of the jacobian matrix have negative real parts).

Table 1: Parameter values and initial values for variables for simulations. SM = Supplementary Methods

Parameter or Variable	Meaning	Value	Vary with parameter combination	Vary among initial conditions
$P_{i_{t=0}}$	Initial abundance of plant species *i*	1	No	No

$A_{j_{t=0}}$	Initial abundance of pollinator species *j*	1	No	No
α	Per-mutualistic interaction benefit	1.5	No	No
β	Per-interaction handling time	1	No	No
r_{P_i}	Plant basal growth rates for species *i*	ϵ [-0.5, -0.001], *cf.* SM	No	Yes
r_{A_j}	Pollinator basal growth rates for species *j*	ϵ [-0.5, -0.001], *cf.* SM	No	Yes
$c_{P_{ik_{k\neq i}}}$ $c_{A_{jk_{k\neq j}}}$	Strength of inter-specific competition strength for space, within guilds	0	No	No
$c_{P_{ik_{k=i}}}$ $c_{A_{jk_{k=j}}}$	Strength of intra-specific competition for space	1	No	No
n_P	Number of plant species	20	No	No
n_A	Number of pollinator species	20	No	No
$I_{M_{ij}}$	Per-capita interaction strength between plant *i* and pollinator *j*	0/1, *cf.* SM	No	Yes
$\bar{\Delta}$	Proportion of species cheating in pollinators	0.1 -> 1 per 0.1	Yes	No
Ω	Frequency of cheating for cheaters	0 -> 1 per 0.1	Yes	No
Ψ	Proportion of innovative cheating	0 -> 1 per 0.1	Yes	No
Λ	Per-interaction cost associated with mutualism	0/0.15/0.3	Yes	No
φ	Initial connectance of I_M	0.2/0.3/0.4	No	No

Networks metrics

To understand how the initial structure of the network affects persistence we measured the nestedness and the modularity of the initial binary interaction matrix (I_M), using NODF index (35) and Newman's modularity measure (36), respectively. The Newman's modularity measure is the likelihood-equivalent of the final proposed module structure after optimization, which was done using the algorithm proposed by Beckett (2016) as implemented in R package *bipartite* (38).

We evaluated network stability at the equilibrium, as network persistence. Network persistence was measured as the percentage of persisting species at equilibrium, with an abundance greater than 10^{-5} at the equilibrium, other species being considered as extinct, for each community and simulation.

To understand how cheaters affect other pollinators at equilibrium, we also evaluated direct and total effects that species have on each other, using analytical formula developed in *ref.* 34 (*cf.* Supplementary Methods).

Analyses of theoretical results

We presented theoretical results either as the absolute values of network persistence over parameters and scenario values (Fig. S1 for example), or as the difference between the case without cheating and the focal simulation for similar initial conditions (Fig. 2). The later one directly represents the effect of cheating on network persistence. These absolute or difference measures were averaged over the 500 initial conditions.

To determine the proportion of variance explained in cheating effect on persistence by our parameter and scenario combinations (group), we calculated the overall variance of network persistence over all simulations (V), and the variance within group (V_g), corresponding to the variance of centered persistence values for each group (minus the average persistence of that group). These centered values represent the residual effects of cheating on persistence, once we have accounted for parameter and scenario combinations. Then we estimated the proportion of variance explained in cheating effect on persistence by our parameter and scenario combinations as 1- V_g / V.

To understand what drives the residual cheating effect on persistence, we used a linear model to explain the residual effect of cheating by: average growth rates of animals and plants and connectance, modularity and nestedness of initial mutualistic interaction matrix. To break the correlation between connectance and nestedness and between connectance and modularity, we centered values of nestedness and modularity by the average nestedness and modularity, respectively, for each of the connectance values.

Empirical dataset

To assess the conservative/innovative character of cheating in empirical communities we used data of interactions among flowering plants and birds, hummingbirds (Trochilidae) in Costa Rica and hummingbirds and flowerpiercers (*Diglossa sp.*) in Ecuador. Sampled sites were located over an elevation gradient in the tropical forests of Costa Rica and Ecuador (Table S2), in which interaction were recorded along transects using camera traps, as described in Graham & Weinstein (2018, *ref.* 35). With each recorded interaction, the information of the interaction status, legitimate (bird bill entering the corolla opening) *vs* illegitimate (bird piercing the corolla), was recorded. Thus, here we assumed that illegitimate interactions do not bring any benefits to the plants and that when a bird bill enters the corolla the interaction is legitimate. Previous results have shown that even interaction that seem illegitimate can participate to pollination and thus be mutualistic (41). However, because piercing is often done at the base of the corolla, robbing interaction described here are likely to be non-efficient in terms of pollination, so as cheaters, although a strict classification would require fitness estimate (24).

Data from Costa Rica includes 18,146 interactions from 12 different sites, sampled monthly between June 2019 and May 2021. Data from Ecuador includes 15,586 interactions from 5 different sites, sampled monthly between February 2017 and December 2019. To obtain interaction frequency independent from the sampling pressure, each interaction count was divided by the number of hours of sampling on the corresponding plant, then multiplied per 24 to get interaction frequencies in interaction.day^{-1}, for legitimate and illegitimate interactions. Then, in both datasets, we aggregated interactions over time to get one interaction network per site (Fig. S7 & S8).

Estimation of empirical cheating parameters

To compare empirical patterns with our theoretical results, we estimated the 3 parameters related to cheating in our model: the proportion of pollinator species cheating ($\overline{\Delta}$), cheating frequency of these cheaters (Ω), the proportion of innovative cheating *vs* conservative cheating (Ψ). The estimation of these 3 parameters is detailed below.

To estimate the proportion of cheaters in each site, we calculated the proportion of species with at least one illegitimate interaction.

To estimate the cheating frequency for each bird species in each site, we calculated the proportion of illegitimate interactions for each species for each site, as the frequency of illegitimate interaction divided per the total frequency of interaction, both summed over all the partners of the focal bird species in the given site.

To estimate the proportion of innovative cheating, we first built a 2-dimensional mutualistic niche for each bird species. To do so, we used 2 plant traits measured on flowers (*cf.* Supplementary methods), the length of the corolla and its curvature. When values were missing and when it was possible, we inferred them using a random forest model that includes other traits and taxonomy as predictors (*cf.* Supplementary methods). After that step, we had to exclude 28 plant species over 253 because of missing trait values. For each bird species we then calculated a 2D kernel density distribution of mutualistic partners, over corolla length and curvature, weighting each plant by the legitimate interaction frequency with the focal bird species. This 2D density distribution models the mutualistic niche of the bird. We then did the same manipulation, but weighting the density by the illegitimate interaction frequencies, to obtain the space in which bird are cheating. Each density distribution summed to one. The overlap between the density function, measured as the area under the minimum of both functions, corresponds to the proportion of conservative cheating. It equals to one when bird cheat only within their mutualistic niche, and zero when bird cheat only outside of their mutualistic niche. To obtain the proportion of innovative cheating we simply took one minus this overlap, because the proportion of innovative cheating equals one minus the proportion of conservative cheating.

Finally, to estimate the overall level of cheating in each site ($\bar{\Delta} \times \Omega$), we calculated the average proportion of illegitimate interactions across all species of the focal site, as the frequency of illegitimate interactions divided by the total frequency of interactions, both summed over all pairs of plant and bird species in the given site.

Statistical analyses of empirical patterns

Finally, since elevation negatively affects net primary production of plants (42), it is expected to be positively correlated with the cost of nectar production, especially because of temperature-mediated effects on photosynthetic activity (43). Elevation is also known to increase flight cost for birds, especially hummingbirds (28, 44). These elements make elevation a good proxy of costs associated with mutualism. To assess how the proportion of cheaters and overall level of cheating varied over elevation, for each of these response variables we used a generalized linear model with a quasibinomial error distribution and a logit link function, where we included elevation as predictor and its interaction with country..

To assess how cheating frequency varies with the level of generalization/specialization of birds, we used a generalized linear mixed-effects model with a binomial error distribution and a logit link function. This model explains cheating frequency of each bird species in each site per the logarithm of their diversity of mutualistic partners, in interaction with the country. We also included random site and bird effects on the intercept. Diversity of mutualistic partners was calculated as the number of plants with which at least one legitimate interaction was recorded, for each bird species and site.

Numerical simulations with empirical networks

To test if the observed patterns of cheating were likely to increase network persistence, we parametrized our dynamic model with empirical patterns of cheating. First, we estimated the proportion of cheating among bird j and plant i (C_{ij}) by dividing the frequency of illegitimate interactions per the total number of interactions. Then we estimated the ability of this species pair to interact in a legitimate way using $M_{ij} = I_{ij}(1 - C_{ij})$, where I_{ij} is a binary state describe if species interacted at least once mutualistically (1) or never (0). We used a binary interaction matrix as a mutualistic backbone rather than a quantified interaction matrix because we assume that they reflect ability of species to interact in a mutualistic way, while interaction frequencies depend much more on abundance. In our model abundances were modelled a part of the

interaction matrix, thus this interaction matrix should reflect only the ability to interact, and not interaction frequencies.

Parameters from the functional response could not be inferred from the data: the per-interaction benefit (α), sometimes called mutualistic strength (45, 46), the cost associated with mutualism (Λ), the handling time (β) and the strength of competition for mutualistic partners (c). To overcome this limitation, we performed simulations over a gradient of possible values, even if it is hard to give an empirical meaning to those parameters. We thus perform simulations from low ($\alpha = 1$) to high per-interaction benefits ($\alpha = 2$) by steps of 0.2, for 3 different values of cost associated with mutualism ($\Lambda \in [0, 0.05, 0.1, 0.15, 0.3]$) and two different values of competition, intermediate (c = 0.5) and high competition strength (c = 1). For each of these per-interaction benefit and cost combinations we generated 100 different combinations of growth rate vectors, using equation (S1, *cf.* Supplementary Methods). For each of the 17 site, 100 initial conditions and 60 parameter combinations, we performed simulations with all empirical interactions, or without cheating interactions (setting $C_{ij} = 0$, for all i and j).

This part led to 204,000 new simulations. To analyze these simulations, we measured persistence at equilibrium, as explained above, and we subtracted the value of the simulation set without cheating to the value of the corresponding simulation with all interactions. This allowed us to obtain the effect of cheating on network persistence, presented in Fig. 5.

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