

Dear Editor,

Please find attached a revised version of our manuscript entitled "Why cooperation is not running away", that we would like to be considered for publication in Peer Community In Evolutionary Biology. We have submitted a previous version of this manuscript to PCI Evolutionary Biology where it was handled by the recommender Erol Akçay, and was asked for some revision.

Thanks to very insightful comments and critiques, we have been able to revise and, we believe, significantly improve our paper. The modifications we have made, together with our responses to all the points raised by the reviewers, are presented in detail below this letter.

We hope this new version of our manuscript will be worthy of the publication standards of Peer Community In Evolutionary Biology. In advance, we thank you very much for your kind attention in this matter.

On behalf of all authors, Félix Geoffroy.

## Recommender: Erol Akçay

In all what follows, the recommender's and reviewers' comments are written in black font and our responses in blue.

One issue that Reviewer 2 points out, and I agree, that considering quantitative evolution of cooperation (with diminishing benefits and/or increasing costs of cooperation) per se is a relatively weak argument for novelty. I don't think this is really the authors' intention, but at times the introduction does read like that is the main contribution. Even the more specific point of focusing on efficiency has been considered before, not least the McNamara et al. paper that looks at it in the precise setting of this paper, as do Akçay and Van Cleve 2012 (where it's in the title). It's true that continuous investment models are outnumbered by discrete strategy papers, but if the framing is "most papers ignore these issues," I think in fairness the papers that don't ignore them deserve mention in the framing, and the more specific contribution needs to be fleshed out. I think reviewer 2 in particular points to a helpful framing (their second paragraph), where the real contribution is investigating the effects of different mechanisms of choice on the level of cooperation.

We agree with both the Recommender and Reviewer 2 that the framing should emphasize on the specific contribution of the paper, namely the study of the runaway process of competitive altruism when cooperation jointly evolves with choosiness. We have re-written the review of the literature on partner choice models (lines 90-114). It is now more detailed, and it highlights the specific differences with our work.

I also find the main narrative of the paper to be somewhat misleading, or at least, incomplete. In particular, the abstract, introduction, and discussion are all state that the "base model" with non-plastic choice generates so much cooperation that it cancels out the benefits. This result is stated unconditionally in most places in the paper (e.g., abstract, l. 21-23, introduction l. 100-102, discussion l. 365-377). But Fig 2 shows that the zero-benefit cooperation result only obtains in the relatively large phenotypic variance limit. At least for medium and high market fluidity, there exists an intermediate level of phenotypic variation where ESS choosiness and cooperation seemingly reach efficient levels. It is true that the variance required to obtain near efficient cooperation is low in absolute value, so perhaps the authors would argue that biologically relevant levels of variance is high relative to these values, but this would need to be spelled out explicitly. As it is, the statements in the lines referenced above strictly speaking false, because they sound like there is an impossibility result, whereas all that there is cooperation evolving to one level or another depending on the parameter set. More generally, it looks like there is quantitative, rather than qualitative differences between the models in how much cooperation can be sustained in equilibrium. So I think this quantitative variation needs to be addressed in a more systematic fashion.

We agree that the interpretations of the results needed some clarifications and we have modified the abstract, introduction, results and discussion accordingly (lines 21, 114-119, 311-322, 410-414 and Fig. 2). We think that the results of the two models can still be considered as qualitatively and not only quantitatively different. In the first model, cooperation can reach levels with positive social payoffs only when the cost of partner choice is low (low market fluidity and low phenotypic

variation, Fig. 2). There is no evolutionary force that drives cooperation precisely towards the socially optimal level. When partner choice is cheap, only fruitless levels of cooperation evolve. In the second model, on the contrary, when partner choice is cheap, there is an evolutionary pressure favoring precisely the optimally efficiency level of cooperation.

Reviewer 1 and 2 both make a number of useful suggestions in both elucidating the results in more depth and also making the connections to the prior literature more explicit. I think the authors would do well to heed these suggestions. One question I had while reading the model was what would happen if choice was also noisy: after all, in a scenario where cooperation phenotype is noisy, choice being so as well (through errors in perception or execution of choice). In the fixed choice scenario, I can see this further relaxing the constraints to the evolution of cooperation, though intuition is a dangerous guide there. In any case, I feel like this is a relatively straightforward extension of the analysis that would also make the story in this paper more complete.

We thank the Recommender for this suggestion. However, we assume that cooperation is subject to phenotypic noise only because the existence of some variability of cooperation is a necessary feature for any partner choice to take place. Without variability in cooperation, indeed, there is no evolutionary pressure for choosing one's partner in function of their cooperation level (see McNamara and Leimar 2010 for a detailed discussion and review on this point). Put differently, our aim is not to study the effect of noise per se but rather to capture in the simplest possible manner the existence of some stable variation in a trait (cooperation) that makes it adaptive to choose one's partner in function of this trait. For this reason, variability in choosiness is not, in our view, such an important possibility to consider (see also Foster and Kokko 2006; Song and Feldman 2013) and we fear that considering such a variability might introduce some unnecessary complexity and confusion for the reader. Hence, we have preferred not to follow the recommender's suggestion on this point.

## Reviewer 1

For hard-wired choosiness the authors use the framework of adaptive dynamics to numerically compute exact trajectories. The main result is that cooperation evolves beyond what is socially optimal at the group level. This is interesting but not very surprising because selection is acting on individuals, not collectives. I would certainly not call this paradoxical. I find the choice of language also a little confusing, because choosiness is changing in this model and not fixed.(lines 113-115)

We agree with the reviewer that, in itself, observing that the social optimum is not reached by evolution is not a paradox at all. However, we insist on describing the result for our first model as an "apparent paradox" because in usual cases (that is, not in apparently paradoxical cases) natural selection leads to a level of cooperation that is too *low* in comparison with the socially optimal level, and the difficult thing is thus to find out a selective force able to *increase* cooperation. In our paper, quite on the contrary, we observe (i) that partner choice leads to a level of cooperation that is too *high* in comparison with the socially optimal level and (ii), what is worst, in most cases this level of cooperation is so high that its cost entirely cancels out its benefit, which is at odd with the idea that partner choice is a selective force that can improve social efficiency. Hence, for these reasons, we believe that our first result can be called an "apparent paradox".

Regarding the choice of language, we have adopted the term "hard-wired choosiness" to differentiate between the case where individuals unconditionally express a level of choosiness and the case where choosiness is plastic. We have tried to make it as clear as possible that, in both cases, choosiness in an evolving trait.

I like the idea of this paper but I have a few basic concerns:

1. I wonder if this is the simplest model to get to the main result. I find the need for  $S$ ,  $\tau$  and interactions through time not core to the argument. Why do we need them?

Accordingly, we have changed the model description and the figure legends to remove the parameter  $S$  as its effect is of little interest. We thank the reviewer for this suggestion.

We have considered the parameter  $\tau$  and the fact that the interactions take place through time because it is a convenient and common method to introduce search frictions on the partner choice process. It has been used both in the biological literature on partner choice (Aktipis 2004, 2011; McNamara et al. 2008), and in the economics literature on search and matching models (Smith 2006, Chade et al. 2017). The parameter  $\tau$  is important because of its role in the fluidity of the market. Even in a biological market where individuals rarely encounter each other, if they interact for a very long period of time (long-term relationships in mutualisms for instance), the expected outcome is that individuals will be very choosy.

2. I would have liked to have a more in depth study of the first model, using adaptive dynamics. How do the results depend on the choice of the payoff function? I find the efficiency argument is interesting, but rather underdeveloped. Is it only due to diminishing returns to cooperation?

We have chosen a simple and general payoff function that shows diminishing returns to cooperation. Although not shown in the paper, we have also checked that the model yields similar results with another payoff function that also entails diminishing returns ( $\Pi(x_i, x_j) = 1 - e^{-x_j} - x_i$ ). In general, when the payoff function has diminishing returns (regardless of its precise mathematical form), the runaway process should always slow down and eventually stop when the benefit of cooperation becomes very close to 0 (that is, at the "wasteful threshold"). The reason is that, at this very point, it becomes just as beneficial to remain solitary without any partner than to invest into cooperation in order to be chosen by a partner.

On the other hand, if we chose a payoff function with constant or accelerating returns, the runaway process would continue indefinitely, since it would always be adaptive to compete for the most generous individuals, because more cooperation is always worth it. In this case, the level of cooperation would increase indefinitely, with no limit, which is not biologically realistic.

3. How can we be sure that the results of the model with plasticity do not arise from noise alone? I understand that the evolution of functional traits is hard to tackle analytically, but numerical results are sometimes attainable, see for example reference 2. I would love to see a more robust theoretical underpinning for the simulations, or in lack of that, a more detailed analysis of the simulations results. Since the evolving traits are  $x$  and a function of  $x$ , one wonders why do the results differ from the first model when  $x$  and  $y$  vary freely. Under reasonable assumptions with minimal noise I would expect these to be very similar.

We agree with Reviewer 1 that it would be preferable to use analytical tools in both models, but unfortunately we didn't find a way to do so. Search and matching models from the economics literature are difficult to solve numerically and, in any case, they only address one part of the problem: the optimal choosiness strategy. They cannot be used to derive the evolution of the mean cooperation level. Nevertheless, their predictions concerning the optimal choosiness strategy make us confident that our simulation results do not arise from noise alone.

Since the evolving traits are  $x$  and a function of  $x$ , one wonders why do the results differ from the first model when  $x$  and  $y$  vary freely. Under reasonable assumptions with minimal noise I would expect these to be very similar.

It is true that, if variability on the cooperation level is low, both models yield the same result. At the evolutionary equilibrium, the choosiness  $y^*$  would be the optimal strategy in a population with a cooperation level  $x^*$ . However, for significant levels of variability in cooperation, both model yield very different results. In the second model, individuals have the possibility to evolve the optimal choosiness strategy  $y^*(x)$  for every possible values of the cooperation level  $x$ . Thus, plasticity allows the emergence of a correlation between the level of cooperation and choosiness, which was not possible in the first model.

I would hope the authors can revise the paper to address this suggestions or queries.

Other minor details:

- The abstract talks about ESS, but there is not ESS calculation, only adaptive dynamics. I would not expect these to be equivalent in general.

This sentence has been re-written.

- Other studies have combined simulations with adaptive dynamics to look at the coevolution of traits (e.g., Reference 1). How simulations match predictions – in the same setup, is a useful way to produce robust results. How does this paper relate to those?

For the first model, the complementary agent-based simulations yield qualitatively similar results than the adaptive dynamics models. Quantitative differences are expected given the necessity of having a large enough mutation rate in the simulations. Our model is based on the assumption that the cooperation level is variable at the phenotypic level, and not at the genetic level (as in McNamara et al. 2008). Hence, the adaptive dynamics better fits our needs than the agent-based simulations do.

For the second model, we have highlighted the fact that the choosiness strategy in the agent-based simulation seems to converge to the prediction of matching models when the market is very fluid (strict positive assortative matching, lines 361-363)

#### References

1. "It takes grouping and cooperation to get sociality." *Journal of theoretical biology* 264.4 (2010): 1240-1253.
2. "The adaptive dynamics of function-valued traits." *Journal of theoretical Biology* 241.2 (2006): 370-389.

## Reviewer 2

My main critiques are relatively minor. First, I think that the emphasis in the Abstract, Introduction, and elsewhere in how the paper looks at the quantitative level of cooperation instead of just whether cooperation is possible (e.g., lines 61–63) is unnecessary; its true that some models have used discrete strategies (cooperate or not or “all-or-nothing”) but others have used continuous ones and even the discrete strategy models can provide results on the precise level of cooperation evolved. Its also not clear, as claimed on lines 94–95, that other models lack diminishing returns of cooperation. However, the main point that these other models neither focus on the runaway process due to competitive altruism nor find a way to inhibit it without adding additional costs remains. Thus, I suggest that the authors simply point to this result as the main feature/point of the paper rather than that the paper looks at the quantitative level of cooperation (which of course it does, but this isn't the differentiating feature of the paper).

Reviewer 2 proposes to re-frame the Introduction to point out the contribution of the paper. We have changed lines 90-110 to make it clear that our contribution is not the study of cooperation as quantitative trait, but rather the study of the runaway of both cooperation and choosiness in a partner choice framework with considerations for social efficiency. We thank Reviewer 2 for this helpful comment.

Second, the paper points to a few previous papers for inspiration, such as the ones by Debove et al (2015) and McNamara et al (2008). These papers essentially provide much of the framework for the current paper where the McNamara et al sets up the coevolution of cooperation and choosiness and the Debove et al papers look at cooperation in another game, the ultimatum game, using a similar partner choice mechanism. I think the authors could do more in the discussion to talk about the connection between these prior works and the current paper. In particular, they can highlight how the Debove et al. papers find similar results about Pareto optimality and market fluidity for the ultimatum game. Also I'm not sure the stuff about the McNamara et al paper starting on line 417 is exactly right; McNamara et al do show (or claim at least) that in the prisoner's dilemma game with linear costs the Pareto-optimal investment evolves. While they do use accelerating costs, its only in the snowdrift game. The authors provide data in the SI for why the McNamara et al model might not obtain Pareto-optimal investment, essentially mutation load is costly, but this is really about how mutation load may be less efficient than phenotypic plasticity. Here, the authors could

strength that analysis by looking at lower and higher values of  $\sigma_{mut}$ ; they should be able to reduce the relative effect of the load and get closer to Pareto-optimal investment. More generally, its not entirely clear (to me at least) why McNamara et al get Pareto-optimal investment in the prisoner's dilemma at all with linear benefits and costs, which would seems to me to generate a runaway process even with linkage between cooperation and choosiness.

Reviewer 2 proposes to clarify the link between our study, Debove et al. (2015), and McNamara et al. (2008).

Our partner choice framework in this paper is similar to the one in Debove et al. (2015). However, in the ultimatum game, any division of the benefit is Pareto optimal. Thus, Debove et al. have not addressed the question of the social efficiency of the interaction. Still, it is true that both results (social efficiency and fairness in sharing) can be explained by partner choice if individuals interact in a biological market that is fluid enough (485- 489). Thank you for the suggestion.

We have clarified the paragraphs on McNamara et al. (2008) on lines 104-110, 461-462, and in the Supplementary Information as well. With linear benefits and costs, the social optimum is an infinite level of investment into cooperation. Hence, in their study, McNamara et al. (2008) obtained a runaway toward the maximum value of cooperation they authorized (Figure 3 in McNamara et al. 2008: " $x_{max} = 1$ "). For a function with diminishing returns, the socially optimal level is a finite and positive number. They used a snowdrift game payoff function and found that cooperation never exactly reached the socially optimal level (Figure 1 in McNamara et al. 2008).

Reviewer 2 also suggests that we run complementary simulations to be sure that this result is not caused by a too high or too low value of the mutation effect  $\sigma_{mut}$ . We have run additional agent-based simulations based on this suggestion (added in the SI). The results remain identical for higher and lower values of mutation effect  $\sigma_{mut}$ . The reason for this result is the same: mutations always generate maladapted mutants that are too generous and not choosy enough.

Finally, I'm a little unclear about a piece of the partner choice mechanism that is described in more detail in the SI of Debove et al (2015 Proc B). The ODE described there, above equation (1) in the SI, is purely linear in fraction of individuals in a pair and solitary. However, this doesn't seem to me to fit a mass-action kinetic where two solitary individuals must interact to become a pair and this should occur at rate proportional to  $S_i^2$ . I don't know how this changes the partner choice model and whether it changes results about the role of  $\beta/\tau$  in controlling "market fluidity", but I suggest that the authors address this point.

Reviewer 2 asks for clarification on the meeting dynamics. We have modified the text (lines 132, 145-155) and the SI. We have run additional simulations as well.

When modeling a market with search frictions, several assumptions can be made concerning the occurrence of meetings. In a seminal paper of the search and matching theory, Diamond and Maskin (1979) have distinguished two extreme cases of what they called the "search technology":

- The "quadratic search technology" corresponds to the mass-action kinetics used in epidemiology. The probability for a solitary individual to meet another one depends on the mass of solitary individuals in the population. It is more suited for low density populations.
- The "linear search technology" is more suited for high density populations. On the contrary, the probability for a solitary individual to meet another one does not depend on the mass of solitary individuals.

We have used the "linear search technology" because of its simplicity and the high density of human cooperative networks. However, the "quadratic search technology" yields qualitatively similar results (SI).

Diamond, P., and E. Maskin. 1979. An Equilibrium Analysis of Search and Breach of Contract, I: Steady States. *The Bell Journal of Economics* 10:282–316.

Finally, I have a few specific comments below. SPECIFIC COMMENTS

- Line 121: I'm not sure I quite get how choosiness is best when  $\beta/\tau$  is high. When its high, the pool of unpaired individuals is very small, so there are few individuals to choose from. In contrast, when  $\beta/\tau$  is low, the pool of unpaired individuals is large and choosiness should yield better returns. Maybe the authors could address what's wrong with this intuition.

We have added a new section in the Supplementary Information to address Reviewer 2's question.

Under the assumption of a "linear search technology", the answer is straightforward: the probability of meeting a solitary individual does not depend on the proportion of solitary individuals in the population.

With the "quadratic search technology" (mass-action kinetics), the effective encounter rate of a solitary individual depends not only on  $\beta$ , but also on the proportion of other solitary individuals in the population. A high value of  $\beta$  (or a low value of  $\tau$ ) indeed has a negative feedback effect on the effective encounter rate by lowering the proportion of solitary individuals. In the SI, we have derived the effective encounter rate and studied the effect of  $\beta$  and  $\tau$  on the market fluidity.

- Line 360: "analytically": more precisely, "numerically" since the solutions are not analytical.

We have followed the suggestion.

- Line 398: "effective units of selection". Cite Akçay and Van Cleve (2012) here who discuss levels of selection and assortment explicitly.

We have added the citation.

- Line 485–486. The paper here presents a continuous prisoners dilemma. The relevant difference with the paper here is simply the mechanism of conditional behavior.

We have clarified the sentence (lines 507-508).

- Line 496: Akçay and Van Cleve (2012) actually do not show that relatedness is required for socially optimal cooperation levels in general; rather they find this for a specific preference function. Its really an open question worth exploring how the preference mechanism in that paper can or cannot generate socially optimal behavior.

We have clarified the statement (lines 533-535).