Evil green beards: Tag recognition can also be used to withhold cooperation in structured populations

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HIGHLIGHTS

- We study the interaction between two mechanisms for the evolution of cooperation.
- We show that tag recognition and population structure interact in a non-trivial way.
- Low assortment leads to cycles with periods of tag based cooperation and defection.
- High assortment leads to cycles where tags are used to undermine cooperation.
- High assortment does not lead to indiscriminate cooperation if tags are available.

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ABSTRACT

Natural selection works against cooperation unless a specific mechanism is at work. These mechanisms are typically studied in isolation. Here we look at the interaction between two such mechanisms: tag recognition and population structure. If cooperators can recognize each other, and only cooperate among themselves, then they can invade defectors. This is known as the green beard effect. Another mechanism is assortment caused by population structure. If interactions occur predominantly between alike individuals, then indiscriminate cooperation can evolve. Here we show that these two mechanisms interact in a non-trivial way. When assortment is low, tags lead to conventional green beard cycles with periods of tag based cooperation and periods of defection. However, if assortment is high, evil green beard cycles emerge. In those cycles, tags are not used to build up cooperation with others that share the tag, but to undermine cooperation with others that do not share the tag. High levels of assortment therefore do not lead to indiscriminate cooperation if tags are available. This shows that mechanisms that are known to promote cooperation in isolation can interact in counterintuitive ways.

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1. Introduction

How costly cooperation can emerge, and how it can be maintained, is a fascinating question (Pennisi, 2005). Paying a cost for the benefit of others seems to be at odds with natural selection, and yet it occurs. Evolutionary theory provides an array of answers to this question. One set of explanations involves repetition, which can allow for cooperation to evolve hand in hand with direct (Axelrod and Hamilton, 1981; Boyd and Lorberbaum, 1987; May, 1987; Bendor and Swistak, 1995; van Veelen et al., 2012) or indirect reciprocity (Nowak and Sigmund, 2005). Another set of explanations involves assortment caused by population structure, which includes models of kin selection (Hamilton, 1964a; Rousset and Billiard, 2000; Rousset, 2004; van Veelen, 2007; Eshel and Cavalli-Sforza, 1982) and group selection (Wilson and Dugatkin, 1997; Traulsen and Nowak, 2006; Boyd and Richerson, 2009; Simon et al., 2013). In such models, interactions take place between individuals that share genes, or that are otherwise relatively likely to have inherited the same strategy (Eshel and Cavalli-Sforza, 1982; Tarnita et al., 2009).

Individuals can also self-assort, for instance through kin recognition. With kin recognition, individuals do not cooperate indiscriminately, but use cues of relatedness in order to differentiate

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between more and less related others. An even better way for cooperators to direct help to other cooperators would be a direct signal by which cooperators can identify each other. This possibility was suggested by Hamilton (1964b) and such a signal is known as a green beard (Dawkins, 1976).

A problem that Hamilton already recognized is that tag based cooperation is vulnerable to invasions of cheaters, that have the tag, but defect. Nonetheless, tag based cooperation is possible if it is either impossible to disentangle the tag and the behavior (Haig, 1996; Keller and Ross, 1998; Summers and Crespi, 2005), as a recurrent phase in a cycle (Riolo et al., 2001; Sigmund and Nowak, 2001; Roberts and Sherratt, 2002; Axelrod et al., 2004; Traulsen and Nowak, 2007; Rousset and Roze, 2007; Antal et al., 2009; Biernaskie et al., 2011), or in dynamics that allow different tags to coexist (Jansen and Van Baalen, 2006; Laird, 2011; Lee et al., 2012).

In this paper we study the dynamics that emerges from the interaction between tag recognition and assortment caused by population structure; henceforth, assortment. Both the availability of tags and the assortment are considered as assets for the evolution of cooperation (Hamilton, 1964a; Cohen, 2012). We show that the interaction between them implies that the availability of tags can actually cut both ways. Tags not only have the potential to help cooperation evolve in settings where it would not evolve without tags, but they can also undermine indiscriminate cooperation in settings where assortment alone would otherwise unambiguously favor it.

2. Model and results

2.1. Individual-based simulations in finite populations

We assume that fitness is determined by behavior in a prisoner's dilemma. In the simplest case, cooperators provide a benefit b to others at a cost c to themselves, while defectors pay no costs but may benefit from others cooperating. The resulting game is given by the following matrix:

$$\mathbf{P_1} = \begin{array}{c} D \\ C \end{array} \begin{pmatrix} 0 & b \\ -c & b-c \end{pmatrix} \qquad (1)$$

Without tags, the only available strategies are cooperate (C) and defect (D). If we allow for two tags, a strategy is now denoted by three bits. The tag (1 or 2), the action taken on meeting others with tag 1 and the action taken on meeting others with tag 2. As a result, we obtain eight strategies: (i) indiscriminate defectors that always defect (denoted $[1,(D,D)]$ for those with tag 1, and $[2,(D,D)]$ for those with tag 2), (ii) indiscriminate cooperators that always cooperate ($[1,(C,C)]$ and $[2,(C,C)]$), (iii) intra-tag cooperators that only cooperate with those that have the same tag ($[1,(C,D)]$ and $[2,(D,C)]$) and (iv) extra-tag cooperators that only cooperate with those whose tag is different ($[1,(D,C)]$ and $[2,(C,D)]$). For those eight strategies, an 8×8 payoff matrix $\mathbf{P_2}$ can be constructed from $\mathbf{P_1}$. Section 1 of the Electronic Supplementary Material – ESM – contains details on the strategy space and the complete payoff matrix $\mathbf{P_2}$.

Besides tags and conditional behavior, we also consider exogenous assortment. It is measured by a parameter r in the interval $[0, 1]$. This parameter controls population structure and can also be interpreted as relatedness (Eshel and Cavalli-Sforza, 1982). This way of modeling population structure is also used in, for instance, Bergstrom (2003), Jansen and Van Baalen (2006), van Veelen (2009), Alger and Weibull (2010, 2013). Its equivalence to other measures of population structure (e.g., Wright, 1921a,b) is established and discussed elsewhere (Bergstrom, 2013).

To analyze the interaction between tags and population structure, we first simulate a Wright–Fisher process with assortative matching in finite populations. Fitness is determined by a single interaction, and the Wright–Fisher process is adapted so that it creates interaction pairs with relatedness r. Details of this process can be found in van Veelen et al. (2012). With probability μ, each individual switches to a random strategy during reproduction. Simulations are based on a population of $N=1000$ individuals, with mutation probability set to $\mu=10^{-3}$. Averages are taken over 1,000,000 generations. Due to randomness in the simulations, the initial configuration does not affect our results. Section 5 of Supplementary Materials explores other simulation parameters.

Fig. 1 shows simulation results based on a prisoner's dilemma with a benefit-to-cost ratio $b/c=2$. Without tags, whether or not cooperation evolves depends on whether the level of r is below or above the threshold implied by Hamilton's rule (see Fig. 1). If r is
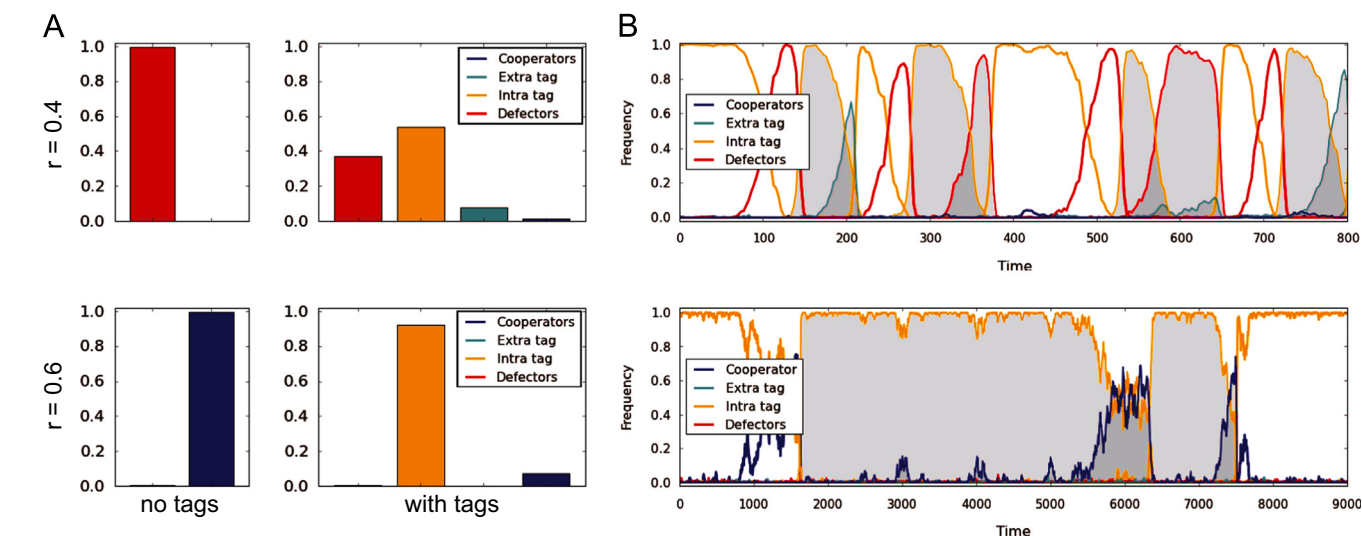

Fig. 1. Good and evil green beards in stochastic individual-based simulations. Individuals play a prisoner's dilemma with a benefit-to-cost ratio of 2. A cooperator gets a payoff of 2 if facing another cooperator, and 0 if the other defects. A defector gets 3 when meeting a cooperator or 1 if meeting another defector. A player with strategy S is matched with an opponent that also uses strategy S with probability $r+(1-r)x_S$, where x_S is the frequency of strategy S in the population. Panel (A) shows average frequencies of the different strategies for assortment $r=0.4$ (top) and $r=0.6$ (bottom) with (right) and without tags (left). Panel (B) shows parts of the runs with tags for low and high assortment. In both cases we see cycles, but in the first case indiscriminate defectors are invaded by tag-based cooperators, and in the second case it is indiscriminate cooperators that are invaded. In the right half of Panel (A), similar strategies with different tags are grouped together; for instance 1-C,D and 2-D,C both fall under intra-tag cooperators (see also Fig. 2). Panel (B) shows no shadows below strategies with tag 1, and shadows below strategies with tag 2.

below c/b cooperation does not evolve (as shown on the top of Fig. 1A, where $r=0.4 < 0.5$). If r is above c/b indiscriminate cooperation evolves (as shown on the bottom of Fig. 1A, where $r=0.6 > 0.5$).

How does the introduction of tags change this simple picture? For low values of r a considerable amount of intra-tag cooperation evolves, but this cooperation comes and goes. Indiscriminate defectors with one tag are invaded by intra-tag cooperators with the other tag. After the new tag is established in the population, intra-tag cooperators are eventually invaded by indiscriminate defectors that still have the same tag, but defect indiscriminately (see Fig. 1B).

For large values of r, surprisingly, we also see that a considerable amount of tag-based cooperation emerge. In this case, however, it is part of a different cycle that we will refer to as the evil green beard cycle. Indiscriminate cooperators with one tag are invaded by intra-tag cooperators with the other tag. Once tag-based cooperation is established, indiscriminate cooperators can drift into the population, and when they do, they open the door for a new invasion of tag-based cooperators with a different tag. With high r, tags therefore act against indiscriminate cooperation (see Fig. 1B).

In the conventional green beard dynamics, individuals use tags to channel help towards others that will return this help (see Fig. 2A). Departing from indiscriminate defection, tags allow individuals to single out copies of themselves, and evolve cooperation where it did not evolve before. These intra-tag cooperators are in turn invaded by indiscriminate defectors with the same tag, but cooperation can re-emerge again based on another tag.

For high levels of assortment or population structure, evil green beards undermine indiscriminate cooperation instead (see Fig. 2B). In that case, tags allow individuals to withhold cooperation. Departing from indiscriminate cooperation, a new tag still allows the new strategy to single out copies of itself, but now it uses the tag to restrict cooperation to the few who share their tag, while enjoying all benefits of indiscriminate cooperation from the majority of the population. In this case, tags are used to discriminate for the bad, not for the good.

2.2. Deterministic dynamics

In order to gain a deeper insight into these green beard dynamics, we analyze them mathematically using evolutionary game theory. To account for population structure we can study a transformed payoff matrix (Jansen and Van Baalen, 2006; van Veelen, 2011). This matrix is defined as $\mathbf{P}' = (1-r)\mathbf{P} + r\mathbf{Q}$, where $\mathbf{P}$ is the original payoff matrix and $\mathbf{Q}$ is defined as $\mathbf{Q}[i,j] = \mathbf{P}[j,j]$; i.e., the elements in the diagonal of $\mathbf{P}$ are copied to the entire corresponding row of $\mathbf{Q}$.

Let us first consider $r < c/b$. We start by excluding weakly dominated strategies, which reduces the strategy set from 8 to 4 strategies by removing unconditional cooperators and extra-tag cooperators. The transformed payoff matrix for the remaining strategies is given by

$$
\begin{array}{c}
\quad\quad [1,(D,D)] \quad [1,(C,D)] \quad [2,(D,D)] \quad [2,(D,C)] \\
\begin{array}{l}
[1,(D,D)] \\
[1,(C,D)] \\
[2,(D,D)] \\
[2,(D,C)]
\end{array}
\left(
\begin{array}{cccc}
0 & (1-r)b & 0 & 0 \\
(1-r)(-c)+r(b-c) & b-c & r(b-c) & r(b-c) \\
0 & 0 & 0 & (1-r)b \\
r(b-c) & r(b-c) & (1-r)(-c)+r(b-c) & b-c
\end{array}
\right)
\end{array}
$$

In this region as whole, there are two possible attractors: a neutrally stable edge made out of defectors, and a cycle with discriminate cooperators and defectors.

The first attractor consists of mixtures of unconditional defectors. In particular, a mixture with an α share of unconditional
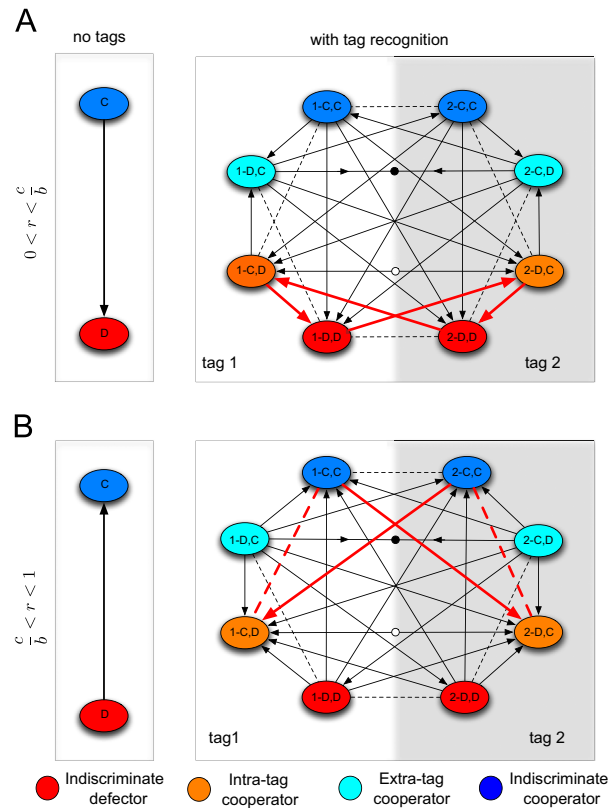

Fig. 2. Different cycles emerge for low assortment (A) and high assortment (B). With two tags, strategies are represented by three variables; one for which tag they are themselves (1 or 2), then a C or a D that indicates whether or not they cooperate with tag 1 individuals, and a C or a D that indicates whether or not they cooperate with tag 2 individuals. Between every pair of strategies, one can compute the direction of selection (see the ESM). This is reflected by the arrows. Dotted lines connect neutral pairs, and the red arrows give the typical cycles for normal and evil green beards. For low assortment (A), both at the transition from defection to tag-based cooperation, and at the transition from tag-based cooperation to defectors of the same tag, the new strategy has a selective advantage. For high assortment (B), only the transition from indiscriminate cooperators to tag-based cooperators is by selection, whereas the transition to indiscriminate cooperation is due to neutral drift. This implies a much slower cycling than in the case of low assortment (see also Fig. 1). (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

defectors with tag 1, and a $1-\alpha$ share of unconditional defectors with tag 2 will be neutrally stable if the following condition is satisfied:

$$
\left(\frac{b}{c}-1\right)\frac{r}{1-r} < \alpha < 1 - \left(\frac{b}{c}-1\right)\frac{r}{1-r} \tag{2}
$$

This holds for all $\alpha \in [0,1]$ if $r=0$, and it never holds for $r > c/(2b-c)$. For $0 < r < c/(2b-c)$ a range of α values will make the mixture neutrally stable.

The second attractor is the conventional green beard cycle (e.g. Jansen and Van Baalen, 2006), where conditional cooperators invade indiscriminate defectors with a different tag, and unconditional defectors invade conditional cooperators that have the same tag. Fig. 3A and B illustrates the resulting dynamics.

These results imply that for r lower than $c/(2b-c)$, the system evolves either to a mixture of indiscriminate defectors that can differ in the tag or to the conventional good green beard cycle, where waves of tag-based cooperation are followed by periods of indiscriminate defection. When r increases, the basin of attraction of the good green beard cycle expands at the expense of the basin of attraction of indiscriminate defectors. These findings remain valid if we include weakly dominated strategies (see ESM for details). Note that mixtures of unconditional defectors in the first
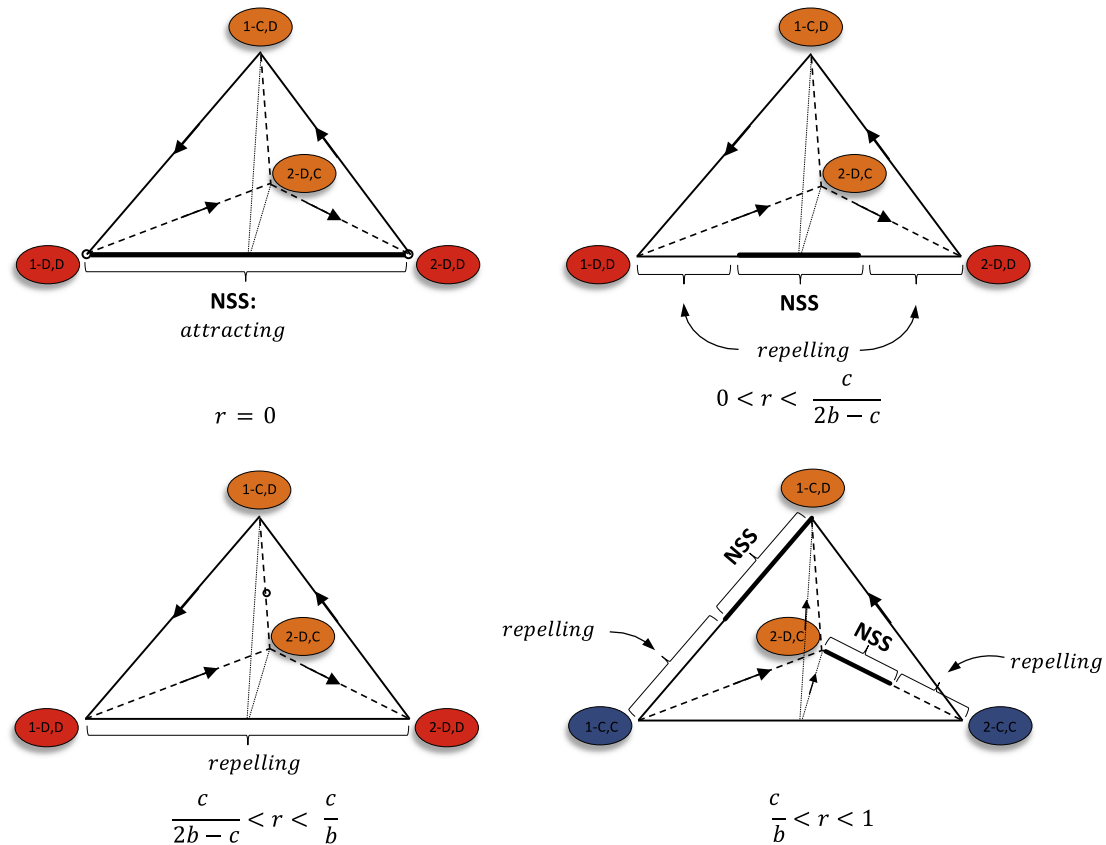
Fig. 3. Deterministic dynamics. (A) In a well-mixed population, for $r=0$, all mixtures of indiscriminate cooperators are neutrally stable. (B) This neutrally stable region shrinks, while the basin of attraction of the good green beard cycle expands, as r increases. (C) For sufficiently large assortment, mixtures of indiscriminate defectors are no longer neutrally stable and the good green beard cycle is prevalent. (D) If $r>c/b$, evil green beard cycles emerge, in which indiscriminate cooperation is short-lived and discriminate cooperation is prevalent.

attractor, although neutrally stable, can be replaced via indirect invasions (van Veelen, 2012). In particular, an indiscriminate defector may open the door for a discriminate cooperator if drift is present.

For intermediate levels of assortment, $c/(2b-c)<r<c/b$, mixtures of indiscriminate defectors are no longer neutrally stable. The only remaining outcome is the conventional good green beard cycle, as illustrated in Fig. 3C. In the more general case with k

available tags, the threshold level of r that is needed for this conventional green beard cycles to be the only outcome is $c/(c+k(b-c))$. A complete characterization of the general case for k tags is provided in the ESM.

This analysis shows that, while tag recognition itself is a mechanism that creates assortment in behavior, green beards need a little help from an external source of assortment to get off the ground. In Jansen and Van Baalen (2006), this external source is the local interaction structure. As shown in Section 4 of the ESM, it is even more difficult to escape uncooperative states if we consider the mutation-selection equilibrium (Bomze and Bürger, 1995). The threshold level required decreases with the

number of available tags, but even with many tags, there is a threshold.

Let us now focus on high levels of r, i.e., $r>c/b$. We again restrict ourselves to the set of four strategies that results from excluding weakly dominated strategies. For $r>c/b$ the set of strategies that are weakly dominated changes, and we now have to remove indiscriminate defectors and extra-tag cooperators. The transformed payoff matrix is then

$$\begin{array}{c} \\ [1,(C,C)] \\ [1,(C,D)] \\ [2,(C,C)] \\ [2,(D,C)] \end{array} \begin{array}{cccc} [1,(C,C)] & [1,(C,D)] & [2,(C,C)] & [2,(D,C)] \\ \left(\begin{array}{cccc} b-c & b-c & b-c & (1-r)(-c)+r(b-c) \\ b-c & b-c & (1-r)b+r(b-c) & r(b-c) \\ b-c & (1-r)(-c)+r(b-c) & b-c & b-c \\ (1-r)b+r(b-c) & r(b-c) & b-c & b-c \end{array} \right) \end{array}$$

Computing the expected payoffs on the basis of this matrix, it turns out that mixtures of indiscriminate cooperators and intra-tag cooperators, both with the same tag, are neutrally stable if

$$0 \leq \alpha < \frac{b-c}{b} \qquad (3)$$

where α is the share of indiscriminate cooperators, and $1-\alpha$ is the share of indiscriminate defectors. This is illustrated in Fig. 3D. The size of the neutrally stable region is determined by the maximum share of indiscriminate cooperators, which is $(b-c)/b$.

Leaving a neutrally stable mixture with a high share of tag-based cooperators is much harder than leaving a neutrally stable mixture

with a low share of tag-based cooperators. The former requires a stepping stone provided by drift, while the latter can happen directly. This implies that neutral drift can occasionally take the population from tag-based cooperators to indiscriminate cooperators, which are then quickly invaded by tag-based cooperators with the other tag. Indiscriminate cooperation is therefore relatively short-lived and on average, when the population size is finite, there will be more tag-based cooperation than indiscriminate cooperation.

Our analytical findings are summarized in Fig. 3. These results explain well the stochastic individual based simulations, where the two thresholds reappear. Fig. 4 reveals that for r below $c/(2b-c)$, the fraction of intra-tag cooperators increases quicker with r than above this threshold. The reason is that below this threshold, an increase in r has two effects, whereas above the threshold only one of them is left. The first effect is that within the conventional good green beard cycle, more time is spent in the phase where intra-tag cooperators are predominant. This effect is present both below and above the threshold. The second effect is present only below the threshold $c/(2b-c)$, where there is also a stable attractor with only defecting individuals. As r increases, the basin of attraction of this attractor shrinks, increasing the time spent in the conventional good green beard cycles.

As expected from the analysis of the replicator dynamics, for r above c/b, mostly intra-tag cooperators and some indiscriminate cooperators are observed, which is consistent with the evil green beard cycles.

In the ESM, we derive these results for general prisoner's dilemma games. We also generalize the analysis to the case with an arbitrary number of tags. With k tags there are two possible responses to any tag, which leads to a total number of $k \cdot 2^k$ strategies.

3. Discussion

Our model shows that the pattern of interaction between assortment caused by population structure and tag recognition is far from a simple linear combination of the two mechanisms. For very low assortment, there is hardly any green beard effect. At some point, assortment starts fueling the good green beard effect, and the frequency of intra-tag cooperators increases steeply. When r crosses the $c/(2b-c)$ threshold, the frequency of intra-tag cooperators increases less steeply. Over the next threshold, c/b, tag recognition makes indiscriminate cooperation unstable, resulting in a high share of intra-tag cooperators.

Below and above this last threshold, we see two different cycles. For assortment below c/b tags can help establish cooperation, which would not be established without tags there; for assortment above c/b tags undermine indiscriminate cooperation, while indiscriminate cooperation would in fact evolve in the absence of tags. We have therefore shown that there are two different evolutionary paths to green beards. This implies that if we find a green beard in nature, a pertinent question is whether is it a good or an evil one.

The distinction between normal and evil green beards is not the same as the distinction between facultative helping and facultative harming (Gardner and West, 2010), where Keller and Ross (1998) is an example of the latter. The behavior in our model is facultative helping, and the evil green beard effect occurs when facultative helping evolves, even though assortment is large enough for indiscriminate helping to evolve in the absence of tags.

It is also worth noting that neutral drift is not necessary for evil green beards to arise. While a modest amount of drift is indeed required to obtain complete evil green beard cycles, only a part of the cycle is needed to establish an evil green beard. Also without drift, tag-based cooperation takes over from indiscriminate cooperation when relatedness is high. Evil green beards will therefore be established with or without neutral drift, although drift is necessary to get a sequence of complete cycles. High relatedness is not necessary either, since a high benefit to cost ratio induces a low threshold such that the evil green beard effect can appear for modest levels of relatedness. These considerations suggest that the concept of evil green beards is likely to be empirically relevant.

Our model also implies that green beards need an exogenous source of assortment to work, and, more importantly, that the availability of tags is not only a force for good. When tags are available under high assortment, we should therefore expect tag-based, and not indiscriminate cooperation there. In addition, there is a temporary loss of cooperation when a transition to another tag occurs. If an external constraint prevents tag-based cooperators from fixating, the loss of cooperation can be long-lasting. One such constraint may be e.g. genetic architecture (Keller and Ross, 1998).
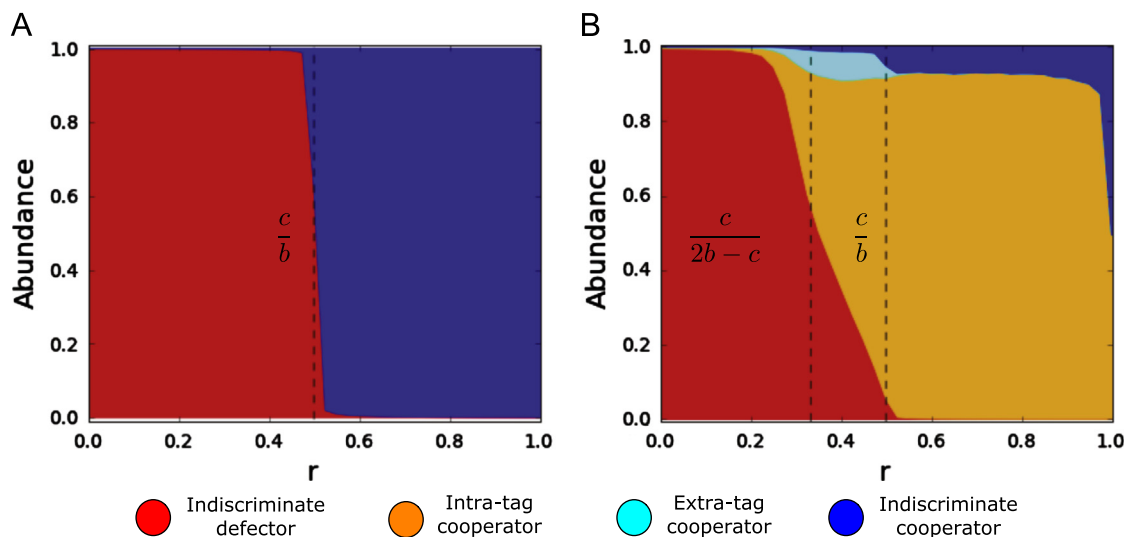

Fig. 4. The impact of tags for varying relatedness. (A) Without tags, cooperation is selected if and only if assortment is larger than $c/b = \frac{1}{2}$, as predicted by Hamilton's rule. (B) With tags, there is no tag-based cooperation for very low levels of assortment, but as r increases, we see increasing levels of intra-tag cooperators, and a distribution of strategies consistent with what we expect from the "normal" green beard cycles. The prevalence of tag-based cooperators however does not stop at assortment $r = c/b$. This is consistent with the "evil" green beard cycles in the replicator dynamics. Including extra-tag cooperators in the strategy space implies that for intermediate assortment, occasionally there is a cycle that includes this strategy in finite population dynamics. The reason is that for intermediate assortment, extra-tag cooperators can take the place of indiscriminate defectors as invaders of intra-tag cooperators, because both mutants keep the tag, but defect against the incumbent (Parameters as in Figs. 1 and 2).

Under low assortment, tags can lead to waves of tag-based cooperation where there is otherwise no cooperation at all. This has led to the idea that tags always promote cooperation. But when assortment is high, tags lead to tides of tolerance only, where without tags, full, indiscriminate cooperation would evolve. Thus, the interaction of mechanisms for the evolution of cooperation can lead to non-trivial results where too many cooks can spoil the broth.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtbi.2014.07.002.

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