The greenbeard effect

Andy Gardner

School of Biology, University of St Andrews

andy.gardner@st-andrews.ac.uk

What is the greenbeard effect?

The greenbeard effect is a driver of social evolution, and one of the three basic mechanisms of kin selection. It was first described in the 1960's, in the context of W. D. Hamilton's work on the evolution of altruism and other social behaviours. Hamilton noted that a gene encoding altruistic behaviour, and hence reducing the fitness of its carrier, can nevertheless be favoured by kin selection if the individuals who benefit from the altruism also carry copies of the same gene. The first two mechanisms of kin selection (kin discrimination and population viscosity) involve the beneficiaries of altruism being genealogically-close kin of the altruist, whereas the third mechanism (the greenbeard effect) can operate even when the altruist and her beneficiaries are not genealogical kin.

How does it work?

Hamilton hypothesised a gene (or a cluster of genes, inherited as a single unit) that encodes two separate phenotypes. First, it causes the carrier to exhibit a detectable phenotypic marker. Second, it causes the carrier to behave altruistically towards individuals who display this marker. In this way, the greenbeard gene is able to pick out which of its carrier's social partners carry copies of itself, and ensure that they are the ones who stand to benefit from the altruism. More generally, the greenbeard effect needn't involve genes that are physically linked together, so long as the component alleles are statistically associated with each other (i.e. "linkage disequilibrium"; Figure 1).

Why is it called the "greenbeard" effect?

The colourful name came more than a decade later, in the 1970's, with the publication of Richard Dawkins's book *The Selfish Gene*, which brought Hamilton's ideas to a wider audience. As a vivid illustration of Hamilton's third mechanism of kin selection, Dawkins described a gene that causes its carriers to both grow a green beard and also behave altruistically towards other individuals bearing green beards. This striking image caught the imagination of Dawkins's readers, and the name stuck.

Do greenbeard genes actually exist?

Hamilton formulated the idea of the greenbeard effect as a thought experiment, primarily for the purpose of demonstrating that kin selection is driven by genetic similarity rather than genealogical relationship *per se*. This insight shows that "kin selection" – like "linkage disequilibrium" – is something of a misnomer, as it emphasises only one of the ways in which the phenomenon can arise. Accordingly, it's not clear that Hamilton intended the greenbeard effect to be taken literally, as an empirical prediction. But a small number of real-world examples of greenbeard genes have subsequently been described, mostly in microbes (Figure 2).

Why aren't they more common?

The greenbeard mechanism only works whilst the component beard and behaviour alleles remain in linkage disequilibrium. A breakdown of this association leads to the appearance of "falsebeard" individuals who exhibit the beard but not the altruistic behaviour, and thereby gain a fitness advantage. That is, they enjoy all the benefits of membership of the greenbeard club (by receiving the altruism of others) without paying any of the fees (by providing no altruism themselves). And as these falsebeard genotypes overrun the population, the true greenbeard genotypes decline in frequency and are eventually lost. This inherent vulnerability of the greenbeard mechanism is the main reason for thinking it should be rare, and also for suspecting that will be relatively more common in asexually-reproducing organisms where there is less recombinational breakdown of linkage disequilibrium.

Are greenbeard genes purely altruistic?

Most of the literature on greenbeards has focused on altruism. Yet the basic logic also holds for other, darker social behaviours. Just as a gene can gain an evolutionary advantage by helping individuals who carry copies of itself, it can also gain an advantage by harming individuals who do not carry copies of itself – both strategies are ultimately ways of increasing the frequency of the focal allele in the population. Accordingly, greenbeards can also underpin spiteful behaviour. Moreover, the greenbeard effect also extends to behaviours that are not traditionally thought of in terms of altruism or spite at all. Indeed, a classic evolutionary hypothesis – R. A. Fisher's "sexy son" explanation for why females in many species prefer males with extravagant ornamentation – can be seen as an application of greenbeard logic to sexual selection. Specifically: assortative mating between choosy females and ornamented males results in their respective alleles being brought together in their offspring, such that ornamented males tend to carry the choosiness alleles; and, accordingly, when a choosiness gene induces its female carrier to mate only with ornamented males, it is actually helping out copies of itself.

Are greenbeard genes in conflict with the rest of the genome?

Because an individual's costly, greenbeard-driven altruism is directed towards beneficiaries who carry copies of the greenbeard gene but not necessarily copies of the other genes in the altruist's genome, it has long been argued that these other genes are favoured to suppress the action of the greenbeard. But the situation is not so clear cut, as although suppressing the greenbeard phenotype would stop the individual from enacting costly altruism, it would also stop them from receiving beneficial altruism. However, in some scenarios at least, greenbeard genes do appear to be in conflict with the rest of the genome. For example, if neighbouring individuals are closely-related kin, then whilst greenbeard genes are favoured to withhold altruism from their non-greenbeard neighbours, the other genes in the genome can be favoured to restore this altruism, and thereby provide a benefit to copies of themselves in their neighbours' bodies.

Where can I find out more?

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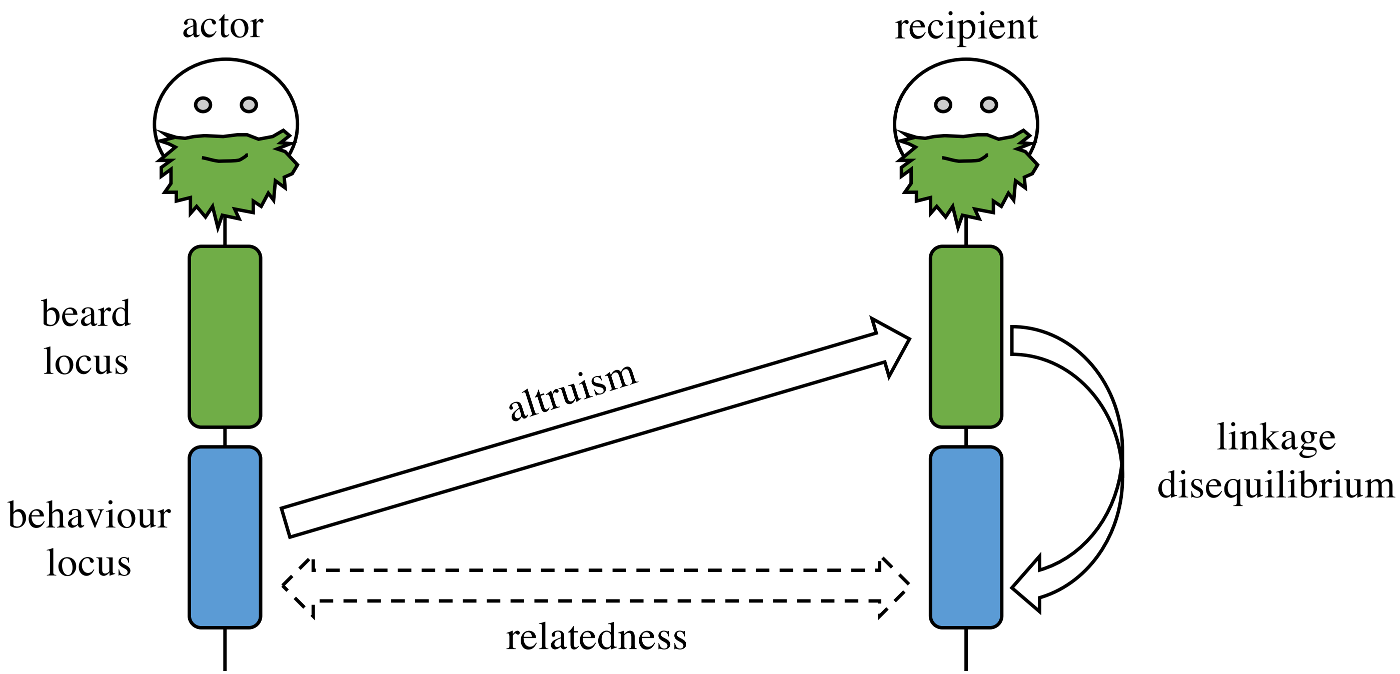
Figure 1 | The greenbeard effect. A carrier of the behaviour allele directs altruism towards a carrier of the beard allele who, on account of linkage disequilibrium between the two loci, is also likely to be a carrier of the behaviour allele. In this way, the greenbeard effect ensures that actor and recipient are genetically related at the behaviour locus, such that the altruistic behaviour is favoured by kin selection, even if the two individuals are unrelated at most other loci across their genomes.

Figure 2 | Empirical examples of the greenbeard effect. (a) Bacteriocins, produced by bacteria to kill other bacteria, have been conceptualised in terms of the greenbeard effect. In this image, filter paper discs soaked with regular antibiotic (left), bacteriocin (right) and the two in combination (bottom) create inhibition zones within which bacteria cannot grow (credit: S. Bakkal & M. Riley). (b) The *Ti* plasmid of bacterium *Agrobacterium tumefaciens*, responsible for gall-formation in plants, induces the host plant to manufacture opines that benefit only *Ti*-plasmid-carrying bacterial cells (credit: A. Grosscurt). (c) Cells of a GFP-labelled line (green) of social amoeba *Dictyostelium discoideum* assort during development while in mixed culture with an unlabelled isogenic line (black) carrying a different *Tgr* allele (credit: B Stewart & C. Thompson). (d) *doc* genes conferring communication-group specificity in filamentous yeast *Neurospora crassa* have been described as greenbeards (credit: L. Corrochano). (e) *Gp-9*-carrying workers of fire ant *Solenopsis Invicta* execute a non-carrying queen (credit: J. All & K. Ross). (f) The greenbeard gene FLO1 is responsible for flocculation in brewer's yeast *Sachharomyces cerevisiae*. Here, a yeast culture with overexpression of FLO1 (right) is contrasted with regular yeast of the same genetic background (left; credit: K. Verstrepen). See Gardner & West (2010) for an overview, and Heller et al (2016) and Gruenheit et al (2017) for more recent updates.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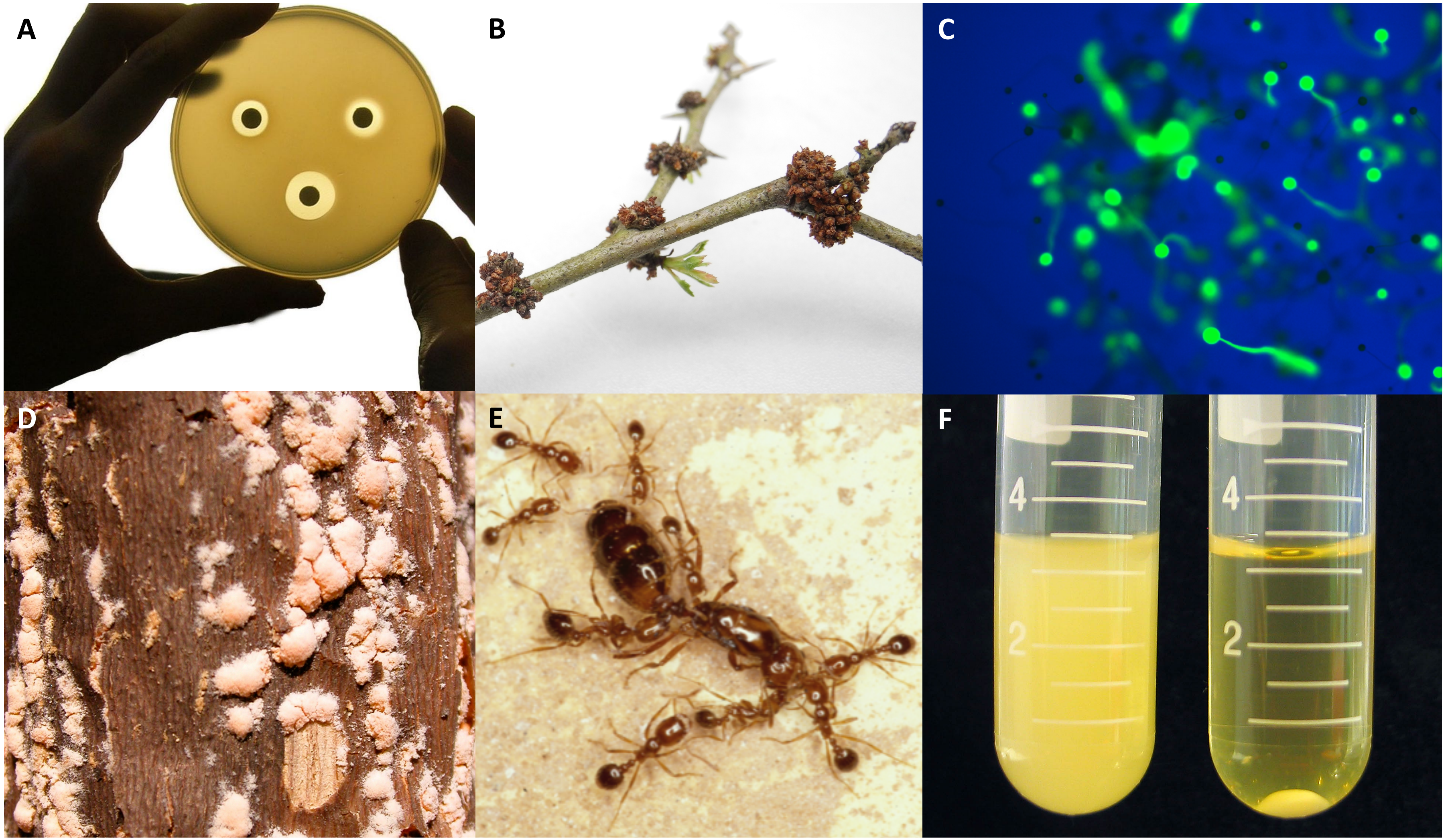
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