

The authors use highly efficient catalysis (reaction yields 80–90%) to selectively install chemical groups at the ends of the monomers; these groups form the basis of the desired ‘break points’ in the polymers. The monomers are then polymerized using well-established methods. The authors find that using a particular co-monomer (diethyl carbonate) in the polymerization reaction enables the formation of high-molecular-weight polymers. This is essential for making a plastic that matches the thermal, mechanical and processing properties of HDPE.

Häußler and colleagues demonstrate that the new plastic can be processed using common industrial techniques such as injection moulding and 3D printing, and to include colourants or carbon fibres (which are widely used as additives to strengthen polymers). They also show that solvolysis of the new plastic occurs selectively when it is mixed with conventional plastics such as commercial polyethylene terephthalate (PET), which is widely used in drinks bottles and is also a candidate for chemical recycling by solvolysis. This proof-of-concept result hints that selective recycling of the new plastic might be possible in the future.

Although the findings hold great promise, it is important to recognize that this is still early-stage, fundamental research. Polymer-to-polymer recycling has been demonstrated for only 20 grams of the new material, and much work will be required to translate this into industrial-scale processes and products. Major engineering challenges remain to be solved in other parts of the polymer’s life cycle, including finding ways to produce the biomass-derived monomers at large scales and the development of industrial processes for making, forming and recycling the plastic.

Furthermore, economic considerations overshadow these endeavours. Plastics used in industry, such as HDPE, are produced on the multimillion-tonne scale, and usually sell at US\$1–3 per kilogram. It would be unreasonable to expect a new plastic to be cost-competitive immediately, but such price issues make the introduction of new plastics highly challenging.

Questions also need to be answered about how well the new plastic integrates with existing waste-management systems – if it is to replace HDPE, it must be shown to be compatible with all the methods used for separating waste plastics across multiple facilities and geographies. Unlike most current recycling strategies, the type of chemical recycling reported by Häußler *et al.* requires a chemical plant. Encouragingly, however, the reported chemistries seem well suited for use with industrial methods. Moreover, the reported system seems consistent with European legislation that requires manufacturers to take responsibility for the plastics in their

products after consumer use.

Häußler and colleagues’ work is exciting and inspiring, because it is extremely challenging to come up with plastics that can be derived from renewable resources, have outstanding properties, are compatible with large-scale manufacturing and processing techniques, and are fully recyclable – few materials meet all these criteria. The authors’ work is an excellent example of how scientific innovation can solve all the facets of a problem, rather than just individual components. The next step must be to build on the life-cycle assessments presented in the current work, to provide even greater improvements in sustainability. More broadly, society must also demand that manufacturers provide equivalent life-cycle assessments and evaluations of all the environmental impacts of currently used plastics, so that the priorities for replacements become clear.

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Evolution

The role and rule of relatedness

Andrew F. G. Bourke

Inclusive fitness theory shows that social partners must be related for altruism to evolve, yet some models suggest that relatedness is not needed. An analysis concludes that assumptions in those models build in a role for relatedness, after all.

Scientists aim to work on important, open problems: their papers and grant proposals tell us so, and, of course, such a focus is entirely proper. But if a field forever declares a problem to be open, it can give the impression that progress is never made. The study of social evolution runs this risk, because many researchers repeatedly assert that how altruism evolved remains an unsolved puzzle. In fact, in the early 1960s, the evolutionary biologist W. D. Hamilton came up with a solution to this ‘problem of altruism’ with his inclusive fitness theory^{1,2}, which shows that it is possible for altruism to evolve if socially interacting individuals are related. Writing in *Proceedings of the National Academy of Sciences*, Kay *et al.*³ conclude that multiple attempts to find alternatives to Hamilton’s solution have simply rediscovered it.

Biological altruism is defined as any social behaviour between individuals in which an action by an altruistic individual decreases its lifetime direct ‘fitness’ (that is, reduces the number of offspring it has) but increases

the lifetime direct fitness of the recipient. By contrast, another type of social behaviour, termed reciprocal altruism, does not qualify as altruism in this sense. Reciprocal altruism occurs when social benefits are exchanged between interacting individuals⁴, and such cooperation evolves only when both partners experience a net gain in lifetime direct fitness⁵.

A prime example of biological altruism is the case of eusocial insects (those that have a worker caste), such as bees (Fig. 1), and in some of these species the workers have lost their ability to reproduce entirely. Such cases encapsulate the problem of altruism. By what means can natural selection, a process based on out-reproducing competitors, lead to self-sacrificial sterility?

According to Hamilton^{1,2}, the answer lies in interacting individuals being positively related, meaning that they are genetically more alike than any individuals associating together randomly within a population. If altruism is directed towards relatives (kin),



Figure 1 | Altruistic insects. Buff-tailed bumblebees (*Bombus terrestris*) are prime examples of biological altruism. The worker bees reduce their own reproduction to boost that of another individual, the queen (the large bee in the middle of the lower half of the image). Kay *et al.*³ assessed papers proposing that altruism can evolve without relatedness, and conclude that the models presented are actually consistent with the long-standing idea¹ that interacting individuals must be related for altruism to evolve.

then, according to inclusive fitness theory, it can evolve by the process of kin selection. Considering this scenario mathematically, Hamilton demonstrated that an individual's aid to a sister, for example to produce b extra offspring at a cost to the individual of c offspring, can be favoured by selection if the individual's indirect fitness gain ($r \times b$) through its sister's extra offspring exceeds its direct fitness loss (c). In this formula, r stands for relatedness and equals the chance of a given gene being shared by the interacting social partners relative to the probability that two randomly selected individuals share the gene.

This condition, known as Hamilton's rule, is met in examples of altruism observed in nature⁶. Moreover, all cases of eusociality found since Hamilton's work involve family groups, and there are no known cases of altruism between non-relatives except for unicellular ants (ants living in populations of merged colonies of a given species)^{7,8}. However, unicellular ants descend from species that lived in separate colonies of relatives, and so their altruism originally evolved in those ancestral societies^{7,8}.

An individual that altruistically aids a non-relative ($r = 0$) loses direct fitness (c), but generates no compensating gain in indirect fitness (if $r = 0$, then $r \times b = 0$, whatever the value of b). Hence, Hamilton's rule shows that altruism directed towards unrelated recipients cannot evolve.

Since Hamilton's work, the theoretical understanding of kin selection and inclusive fitness theory (which encompasses the social behaviours of selfishness and spite, as well as

altruism and cooperation) has been enriched in key ways^{2,9}. However, inclusive fitness theory has also attracted controversy^{2,7,9,10}, one aspect of which concerns a large set of models that were used to claim that altruism can evolve without requiring relatedness. To assess the validity of this conclusion, Kay and colleagues systematically analysed the assumptions underlying these models.

The authors began with a list of 195 leading papers on the evolution of altruism and cooperation (generated from the top results of Google Scholar searches). Of these, 89 studies modelled the evolution of altruism; 46 of them attributed altruism to kin selection, whereas 43 did not. Within the set of 43, 17 papers explicitly denied a role for relatedness.

Kay *et al.* report that, on the basis of their analysis of the life cycles presented, the life cycle of the individuals in each of these 17 models did, in fact, generate positive relatedness, either positive genetic relatedness or its cultural equivalent (arising through individuals imitating one another's behaviour). Typically, this occurred because the life cycle involved low dispersal of offspring from their birthplace, and interactions happened mainly between neighbours. In such 'viscous' populations, as Hamilton recognized¹, social behaviours will be directed towards relatives, just as would be the case for humans if successive generations of one family filled up each street and people interacted mainly with those living next door.

The authors also assessed the 26 modelling studies that did not invoke kin selection but, rather than explicitly denying a role for

relatedness, attributed altruism to other processes. The explanation usually given in these cases was a mechanism described as spatial selection, a term derived from models that again involve altruists or cooperators clustering because of localized interactions under a regime of low dispersal. Kay *et al.* took a closer look at ten influential studies of this kind and conclude not only that spatial proximity served as the driver of positive relatedness, but also that the models converged on overtly kin-selection-based models because, in successive papers, the assumptions made grew closer to those made in kin-selection-based models.

Kay and colleagues did not attempt the essentially impossible task of reconstructing all the models examined to rerun them using variations of the assumptions or frameworks. The authors' critique is therefore based on inference and not on new modelling. However, they highlight several previous studies in which deep dives into a subset of the alternative models have demonstrated in detail their compatibility with inclusive fitness theory. Kay *et al.* therefore conclude that all models purporting to show altruism evolving in the absence of relatedness rather provide a 'backhanded' validation that endorses Hamilton's explanation of altruism. By extension, these models unwittingly provide support for inclusive fitness theory as a whole – beyond just supporting the theory's insights on the evolution of altruism.

The authors speculate candidly about why modelling studies repeatedly 'rediscover' existing results and present them as novel.

In drawing lessons from Kay and colleagues' valuable work, it is therefore instructive to step back and examine the implications for the entire field.

First, partly because of nature's complexity, evolutionary biology is particularly vulnerable to misplaced claims of novelty¹¹. Making such claims on the basis of modelling studies could be avoided if researchers always sought to link their work to existing theory, stated their assumptions explicitly, and avoided over-abstraction to explain the real-life behaviours or traits of organisms, thereby generating testable biological predictions. In this regard, modelling viscous populations remains worthwhile because, as Kay *et al.* point out, many real-life organisms, notably plants, live in fixed locations and so represent such populations.

Second, some issues remain to be fully resolved in inclusive fitness theory, not least how best to define inclusive fitness¹². More generally, there are many active research topics in the study of social evolution, such as understanding how social cheating is held in check. Therefore, although previous findings need to be acknowledged, continued exploration of the theory is valuable. Lastly, the theory has

nonetheless achieved notable successes, one of which is solving the problem of altruism^{3,7,9}. A legitimate desire to tackle important, open problems should not prevent the field from recognizing this.

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Plant biology

Multiple genomes give switchgrass an advantage

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The genome sequence of switchgrass (*Panicum virgatum*) sheds light on genetic mechanisms that have enabled the ancestors of this valuable biomass crop to adapt to cycles of climate warming and cooling. **See p.438**

Switchgrass (*Panicum virgatum*) is a keystone species of the North American tallgrass prairie. The habitats of switchgrass have undergone many cycles of contraction and expansion over time, owing to the advances and retreats of glaciers^{1,2}. This makes it a good species in which to study how plants adapt to varied and variable environments – a timely subject, given that Earth is experiencing what is projected to be the most rapid change in global temperature for at least the past 65 million years³. Moreover, given its high biomass yield and tolerance to drought, switchgrass has long been bred as a forage crop for livestock, and has been studied as a model bioenergy feedstock crop since 1992 (ref. 1). As such, the high-quality genome sequence for switchgrass now reported on page 438 by Lovell *et al.*⁴ is of great value.

Polyploidy – having more than two complete sets of chromosomes – is a common theme in plant evolution, and has been hypothesized to promote the generation and preservation of gene variants that can confer adaptation to new ecological niches^{5,6}. Like most polyploid plants, switchgrass arose from a cross between two species and a whole-genome duplication, thereby giving it four sets of chromosomes (a state called tetraploidy, involving two subgenomes, one from each parental species). Switchgrass plants have many different versions of each gene because progeny are typically produced from the mating of two genetically different individuals (they are outbred), rather than by self-pollination. Such complexity makes the genomes of polyploid outbred plants difficult to sequence, but Lovell *et al.* took advantage

of advances in long-read DNA sequencing technology to generate a complete and highly accurate reference genome for tetraploid switchgrass (varieties that have eight sets of chromosomes also exist, but were not included in the current study).

The authors used this genome to estimate that the two parental species of switchgrass diverged from a common ancestor about 6.7 million years ago, and that the two genomes came back together in a whole-genome duplication at least 4.6 million years ago. This places the evolutionary origins of switchgrass in the latter, and, on average, colder and more variable, part of the ongoing Late Cenozoic ice age, which began 33.9 million years ago. The parental species of switchgrass were probably from the tropics of Central or South America⁷; how a polyploid genome might have contributed to the northward migration of switchgrass to temperate latitudes during a time of increased climate change and low temperatures is a key question.

Currently, switchgrass has a vast natural geographical and environmental range, from the tropics of central Mexico in the south to Canada's James Bay and Labrador in the north, and from the Great Plains of the United States and Canada in the west to the Atlantic coast in the east¹. Lovell *et al.* proceeded to sequence a diverse panel of 732 switchgrass individuals that are representative of the species' distribution across the United States. This revealed three genetic subpopulations that were largely restricted to certain regions: Gulf (mainly located in the southern United States), Atlantic (along the East Coast) and Midwest (the most northerly of the subpopulations).

The authors estimated that these subpopulations diverged from one another about 1.1 million years ago. Thus, the current population structure long pre-dates the Last Glacial Maximum around 22,000 years ago, when populations whose habitats became covered in ice probably took refuge along the Gulf Coast and in the montane west. The researchers also showed that the population structure has been maintained through at least ten glacial cycles, rather than being erased by habitat loss and interbreeding of clustered populations during several glacial maxima.

Ecotypes are distinct forms of a species that occupy different habitats. Two ecotypes of switchgrass have long been recognized, namely lowland and upland; lowland typically has fewer, thicker and taller stems and wider leaves, and flowers later¹. The lowland ecotype is most commonly found in northern Mexico, the southern United States and along the Atlantic coast, whereas the upland ecotype predominates in the northern United States and Canada. However, intermediate forms, which Lovell and colleagues call 'coastal', are also common throughout the southern United States and along the Atlantic coast. One might