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 novelty[11]. 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 fitness[12]. 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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1. Hamilton, W. D. *J. Theor. Biol.* **7**, 1–16 (1964).
2. Gardner, A., West, S. A. & Wild, G. *J. Evol. Biol.* **24**, 1020–1043 (2011).
3. Kay, T., Keller, L. & Lehmann, L. *Proc. Natl Acad. Sci. USA* **117**, 28894–28898 (2020).
4. Trivers, R. L. *Q. Rev. Biol.* **46**, 35–57 (1971).
5. West, S. A., Griffin, A. S. & Gardner, A. *J. Evol. Biol.* **20**, 415–432 (2007).
6. Bourke, A. F. G. *Phil. Trans. R. Soc. B* **369**, 20130362 (2014).
7. Bourke, A. F. G. *Proc. R. Soc. B* **278**, 3313–3320 (2011).
8. Helanterä, H., Strassmann, J. E., Carrillo, J. & Queller, D. C. *Trends Ecol. Evol.* **24**, 341–349 (2009).
9. Marshall, J. A. R. *Social Evolution and Inclusive Fitness Theory: An Introduction* (Princeton Univ. Press, 2015).
10. Allen, B., Nowak, M. A. & Wilson, E. O. *Proc. Natl Acad. Sci. USA.* **110**, 20135–20139 (2013).
11. Welch, J. J. *Biol. Phil.* **32**, 263–279 (2017).
12. Fromhage, L. & Jennions, M. D. *Proc. R. Soc. B* **286**, 20190459 (2019).

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Plant biology

Multiple genomes give switchgrass an advantage

Erik J. Sacks

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 years[3]. 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 America[7]; 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 east[1]. 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 later[1]. 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

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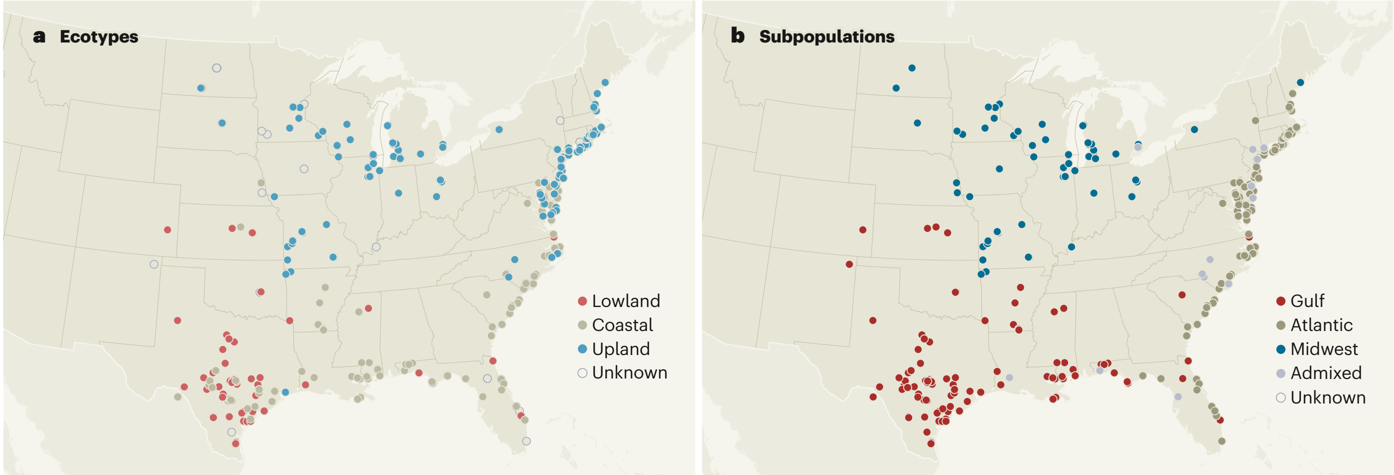

Figure 1 | Distribution of switchgrass (*Panicum virgatum*) across the United States. a, Switchgrass populations can be categorized as belonging to one of three 'ecotypes' on the basis of their morphology – lowland, upland, and an intermediate between the two known as coastal. Each of the ecotypes occurs naturally in different regions. Lovell *et al.*[4] studied 732 individual switchgrass plants from across the United States that had been assigned to ecotypes (those that could not be confidently assigned are labelled as unknown). **b**, The authors sequenced the genomes of these switchgrasses, and found that they mostly clustered into three genetically distinct subpopulations (some were admixed, containing genetic material from multiple subpopulations). Although the subpopulations were also roughly demarcated by geography, being found mainly in Gulf, Atlantic or Midwest locations, there were differences from the ecotype classification. This indicates that the two classifications are not in complete alignment. (Maps generated from data in Supplementary Information Table 4 of ref. 4.)

have expected lowland, coastal and upland ecotypes to correspond, respectively, to Gulf, Atlantic and Midwest subpopulations. But Lovell and colleagues found that the two classifications were not in complete concordance (Fig. 1).

For example, although the Midwest subpopulation was entirely upland, 37% of sampled upland ecotypes were part of the Atlantic subpopulation. The Atlantic subpopulation was 62% upland and 38% coastal. Similarly, all lowland plants belonged to the Gulf subpopulation, but 38% of the Gulf subpopulation showed evidence of gene exchange or substantial shared ancestry with the Atlantic subpopulation. These results reveal that the Gulf and Atlantic subpopulations contain more genetic variation than does any one ecotype.

Next, the researchers set out to learn how genetic diversity within switchgrass contributes to its adaptation to many environments. They asexually propagated their diverse panel of sequenced switchgrass plants at ten field-trial sites spanning 1,862 kilometres of latitude, from Texas to South Dakota, and collected data on biomass yield and winter survival. They then identified regions of the genome in which differences in sequence were associated with differences in winter survival, climate at the plant's original collection site, and biomass yield.

Notably, many of these associations were unique to a given subpopulation. If, through natural evolution or breeding programmes, some of these unique gene variants were to be combined, some of the progeny would probably have adaptation traits that exceed the range of variation in the parents. This might enable the progeny to fill new ecological niches or become outstanding cultivars – growing in colder environments, for instance, or having exceptionally high biomass yield. Thus, the problem of climate change might become a driver of evolutionary solutions for plant species.

Lovell *et al.* also found evidence that the Atlantic subpopulation obtained genes for winter survival from the Midwest subpopulation at the end of the Last Glacial Maximum, presumably when these populations came into contact along the Gulf Coast, having previously been isolated from one another. This genetic exchange subsequently enabled the Atlantic population to migrate to cold-temperate northern areas of the East Coast – an excellent example of how range contraction can promote gene exchange that benefits the species as a whole.

Genome duplication provides an opportunity for genes to take on new functions, subfunctionalize, or even reduce or lose functions, because there is less risk of the change being lethal than if it occurred in a species with only two sets of chromosomes. Lovell *et al.* observed that one of the switchgrass subgenomes (dubbed the non-dominant genome) had fewer upregulated genes, fewer functional genes and more mutations than the other. This type of difference is common in subgenomes of polyploids derived from crosses between species. But the authors demonstrated just how important this process might be for generating adaptive genetic variation. Notably, the non-dominant subgenome of switchgrass, which, on average, had fewer genes affecting physical traits than did the dominant subgenome, accounted for 76% of the genetic variants associated with altered biomass, and for 54% of the Midwest-derived variants in the Atlantic subpopulation that were associated with winter hardiness. This observation makes the current study one of only a few to identify genes for adaptation that arose as a result of genome duplication. It suggests that reduced dominance for one switchgrass subgenome allowed it to become a beneficial blackboard of evolution.

As climate change accelerates, wild plant populations will be challenged to migrate and adapt fast enough to avoid extinction, and crops will need to adapt quickly to new environments if humans are to avoid famines. Lovell and colleagues' work should lead to further insights into how plant species survive, and even thrive, during times of rapid environmental change. This, in turn, should help people to more effectively manage and conserve domesticated and wild plants. The future of human civilization could depend on it.

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1. Casler, M. D. in *Switchgrass* (ed. Monti, A.) Ch. 2 (Springer, 2012).
2. Augustin, L. *et al. Nature* **429**, 623–628 (2004).
3. Diffenbaugh, N. S. & Field, C. B. *Science* **341**, 486–492 (2013).
4. Lovell, J. T. *et al. Nature* **590**, 438–444 (2021).
5. Barabaschi, D. *et al. Mol. Biotechnol.* **50**, 250–266 (2012).
6. Nieto Feliner, G., Casacuberta, J. & Wendel, J. F. *Front. Genet.* **11**, 792 (2020).
7. Triplett, J. K., Wang, Y., Zhong, J. & Kellogg, E. A. *PLoS ONE* **7**, e38702 (2012).

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