

NEWS AND VIEWS

Perspective

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Searching for the genetic footprint of ancient and recent hybridization

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Determining the long-term consequences of hybridization remains a central quest for evolutionary biologists. A particular challenge is to establish whether and to what extent widespread hybridization results in gene flow (introgression) between parental taxa. In this issue of *Molecular Ecology*, Jordan et al. (2018) search for evidence of gene flow between two closely related species of *Geum* (Rosaceae), which hybridize readily in contemporary populations and where hybrid swarms have been recorded for at least 200 years (Ruhsam, Hollingsworth, & Ennos, 2013). The authors find mixed evidence of ancient introgression when analysing allopatric populations. Intriguingly, when analysing populations of a region where the two species occur either mixed in the same population or in close proximity, and where hybrids are presently common, Jordan and colleagues find that the majority of randomly sampled individuals analysed (92/96) show no evidence of introgression (defined as individuals with admixture coefficients of <1%). The few individuals identified as hybrids are shown to likely be F1 or early-generation backcrosses, indicating that even in sympatric regions, hybridization does not penetrate beyond a few generations. Based on their findings, *Geum* seems to be an example of little to no introgression despite contemporary hybridization.

KEYWORDS

ecological barriers, hybridization, introgression, reproductive isolation

Among the >900 hybrid plant taxa that occur in the wild in the British Isles (Stace, Preston, & Pearman, 2015), intermediate avens (*Geum* × *intermedium* Ehrh., Rosaceae) is one of the most widespread and best known (Figure 1). This hybrid is the product of crosses between two species with contrasting ecologies and mating systems. Water avens (*G. rivale*) has purple, pendulous flowers, which is highly outcrossing, and is usually found in wetter soils and more open habitats. In contrast, wood avens (*G. urbanum*) is a yellow-flowered plant with more erect flowers that are highly self-fertilizing. *Geum urbanum* tolerates more shaded habitats in woodlands, usually occurring in better-drained soils. The hybrid *G. × intermedium* is geographically widespread (Stace et al., 2015), and previous genetic analysis in a single hybrid swarm indicates that 50% of all individuals sampled at the flowering stage are hybrids (Ruhsam et al., 2013). The widespread occurrence of *G. × intermedium* is not entirely surprising. Studies of natural hybrids indicate that F1 hybrids are viable and fertile and that

backcrosses can be readily generated (Ruhsam, Hollingsworth, & Ennos, 2011). Moreover, hybrids have similar fitness to parental taxa in a common garden, indicating that there are no strong intrinsic barriers to hybridization (Ruhsam et al., 2013). In this context, Jordan and colleagues set out to measure genetic introgression across multiple populations and significantly extend previous work on the system.

Detailed genetic analyses of *Geum* hybrid and parental taxa have been limited by the availability of genetic tools. The study of Jordan et al. (2018) represents a major step forward in developing such tools. Using an inbred, field-collected individual, they generated the first draft genome for *G. urbanum*. The genome size of *G. urbanum* and *G. rivale* is relatively large (1.2 and 1.6 Gb, respectively), and these taxa are ancient hexaploids, which complicates distinguishing among multiple paralogous regions during genetic analysis. In fact, the authors found that 90% ultraconserved genes are represented by more than one orthologue, with the number of orthologues



FIGURE 1 Flowers of parental and hybrid *Geum* (Rosaceae). (a) *G. rivale*. (b) *G. urbanum*. (c) F1 hybrid. (d), Backcross to *G. rivale*. All photographs were taken by R. Ennos

ranging between 3.39 and 3.82 per gene. Using the draft genome of *G. urbanum*, the authors developed a pipeline to genotype individuals from both parental species and their putative hybrids using double-digest restriction site-associated DNA sequencing (ddRAD-seq). Key to their genotyping approach was an aggressive filtering of potentially paralogous regions that could be mistakenly genotyped as the same SNP locus. After alignment to the *G. urbanum* genome, allowing for an empirically determined number of mismatches between the reads and the reference, Jordan et al. filtered out SNPs with high heterozygosity ($h > 0.5$) or negative inbreeding coefficients (F_{is}). Using this filtered data set, the authors searched for the genetic signature of introgression at two levels: (i) historical introgression, which could reveal the possibility that these taxa continued diverging while exchanging genes with one another (divergence with gene flow), and (ii) more recent introgression that could be occurring in geographic areas in which both taxa presently co-occur.

1 | ANCIENT INTROGRESSION

To test whether gene flow may have occurred before the formation of currently allopatric populations, the authors compared pairs of *G. urbanum* and *G. rivale* individuals from populations sampled across Europe, which have likely remained allopatric for at least 5,000 years. Jordan et al. (2018) found that the likelihood models (Lohse, Chmelik, Martin, & Barton, 2016) that best fit the data include introgression between species, although at a very low rate ($m = 0.04$ or 1 migrant every 25 generations). The authors argued that likelihood models detecting low levels of introgression may be flawed due to violations of the model assumptions and concluded that there is no strong evidence that introgression has characterized the divergence of these two species.

2 | INTROGRESSION IN AREAS OF PRESENT-DAY SYMPATRY

One of the most interesting findings of this study comes from the analysis of multiple populations in the south of Scotland where both species co-occur, and where mixed populations are often found (Stace et al., 2015). Jordan and colleagues genotyped 96 randomly sampled individuals from 39 populations, including 10 populations where both species co-occur. Admixture analysis of 188 SNPs showed that the majority of individuals (92/96) present little to no evidence of introgression. The few individuals (4/96) where hybridization was detected are thought to be early hybrids or backcrosses (to *G. rivale*), which is consistent with previous genetic analyses of hybrid swarms.

Despite the general lack of introgression in the sympatric region, Jordan et al. (2018) detected a section of unrecombined *G. rivale* genome segregating in *G. urbanum*. This finding is interesting, first, because it suggests that introgression has occurred from the outcrossing species into the selfing taxon, which is consistent with their genetic inferences of historical introgression (Jordan et al., 2018), but contrasts with the expectation that selfing species are better shielded against introgression due to their mating system (Smith & Rausher, 2007). Second, the introgressed block is associated with variation in morphology, mainly the angle in which the flower is presented to pollinators, as estimated using a principal component analysis. This raises the exciting possibility that even rare gene flow may enable adaptive introgression, although it is unknown to what extent floral orientation affects fitness in *G. urbanum*. Adaptive introgression is often invoked in discussions of how hybridization may positively contribute to rapidly increase the adaptive potential of populations (Hamilton & Miller, 2016).

To conclude, the study by Jordan et al. (2018) provides convincing evidence that present-day hybridization does not reflect the level of introgression detected in natural populations of *G. urbanum* and *G. rivale*. Their study supports previous work in this system showing that when hybrids occur, these tend to be early generation (Ruhsam et al., 2013). Given the lack of reduced viability, fertility and overall performance of hybrids relative to parents in common gardens, the question remains as to what mechanisms are keeping advanced generation hybrids rare, and these two parental taxa genetically apart. The obvious suspect is ecologically driven barriers, in other words, the fact that hybrids may be unfit when facing the ecological challenges found in natural habitats. Interestingly, at a 10×10 km scale, there are no records of the hybrid on its own, and it only very rarely occurs in the absence of one of the parental taxa (~2% of 10×10 km squares with only one parent; Stace et al., 2015). The answer to the mystery of why *Geum* hybrids are apparently ephemeral, at least over evolutionary time, may therefore require not only further genomic analyses, but a return to classic ecological experiments and measurement of fitness under field conditions.

AUTHOR CONTRIBUTIONS

M.V.-M. wrote the commentary.

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