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REVIEWS

Hybrid speciation

James Mallet[1]

Botanists have long believed that hybrid speciation is important, especially after chromosomal doubling (allopolyploidy). Until recently, hybridization was not thought to play a very constructive part in animal evolution. Now, new genetic evidence suggests that hybrid speciation, even without polyploidy, is more common in plants and also animals than we thought.

Linnaeus stated in *Systema Naturae* that species have remained unchanged since the dawn of time, but he later experimented with hybrids and convinced himself that hybridization provided a means of species modification. One hundred and eighty years later, Lotsy[1] still argued that species were invariant genetic types, and that novel lineages could evolve only by means of hybridization. These peculiar ideas were overturned when the concept emerged of species as reproductively isolated populations[2–4]. In zoology, this concept discouraged the view that hybridization and gene flow (introgression) between species could be important evolutionary forces[2,5,6], even while botanists continued to argue for their significance[4,7,8]. Today, armed with new and abundant molecular marker data, biologists increasingly find new examples where hybridization seems to facilitate speciation and adaptive radiation in animals, as well as plants[8–12].

What is hybrid speciation?

‘Hybrid speciation’ implies that hybridization has had a principal role in the origin of a new species. The definition applies cleanly to hybrid species that have doubled their chromosome number (allopolyploidy): derived species initially contain exactly one genome from each parent, a 50% contribution from each, although, in older polyploids, recombination and gene conversion may eventually lead to unequal contributions. Furthermore, allopolyploids are largely reproductively isolated by ploidy. Recombinational hybrid speciation, in which the genome remains diploid (homoploid hybrid speciation), is harder to define. The fraction from each parent will rarely be 50% if backcrossing is involved. Homoploid hybrid species may be only weakly reproductively isolated, and are hard to distinguish from species that gain alleles by hybridization and introgression, or from persistent ancestral polymorphisms. Although hybrid speciation is sometimes inferred if any marker alleles originate from different parents, I here restrict the term to cases where hybrid allelic combinations contribute to the spread and maintenance of stabilized hybrid lineages generally recognized as species.

This raises the question of what exactly we mean by ‘species’. Hybrid speciation is only possible if reproductive isolation is weak; if hybrids are intermediate, hybrid species will be even more weakly isolated. In practice, we must recognize species as multi-locus ‘genotypic clusters’ (Box 1)[6,13]. A hybrid species will then be a third cluster of genotypes, a hybrid form that has become stabilized and remains distinct when in contact with either parent.

Hybridization can also influence speciation by means of ‘reinforcement’, where mating barriers evolve owing to selection against unfit hybrids[6,14,15]. Although hybridization contributes to speciation, I do not consider reinforcement to be hybrid speciation, because a third species does not form. A related and highly relevant phenomenon is ‘hybridogenesis’. The diploid or triploid edible frog *Rana esculenta* is a well known example: it is heterozygous for complete *Rana lessonae* and *Rana ridibunda* genomes[16]. Here, I exclude hybridogenetic species because they do not breed true.

Theory and background of hybrid speciation

Hybridization may be “the grossest blunder in sexual preference which we can conceive of an animal making”[17], but it is nonetheless a regular event. The fraction of species that hybridize is variable, but on average around 10% of animal and 25% of plant species are known to hybridize with at least one other species[18]. Hybridization is especially prevalent in rapidly radiating groups: 75% of British ducks (Anatidae)[18], for example. Recent, closely related species are most likely to hybridize, although hybridization and introgression

Box 1 | Species as genotypic clusters versus reproductively isolated populations

Species can be defined as distinguishable groups of genotypes that remain distinct in the face of potential or actual hybridization and gene flow[6,13]. This is similar to Darwin’s usage of species to divide biodiversity by means of gaps or troughs in the distributions of phenotypes and genotypes. A very likely reason why a pair of genotypic clusters in contact might remain distinct is, of course, ‘reproductive isolation’, but this becomes a means of achieving speciation and species maintenance rather than a definition of the species state itself. It might seem that autopolyploids (species resulting from chromosome doubling within a single parent species) cannot be recognized as genotypic clusters because they have initial gene frequencies like their diploid parents. Autopolyploids are, however, genetically distinct in heritable traits such as chromosome number and ploidy at individual loci. They can be regarded as distinct species provided that euploids (for example, diploids and tetraploids) form clusters that are more abundant than intermediates formed by hybridization between them (for example, triploids and aneuploids).

Such species have no guarantee of permanence. Two genotypic clusters might be stable for a long time, yet when ecological circumstances change, gene flow may exceed some threshold, eventually resulting in a single genotypic cluster that absorbs both species[13]. There are several examples of species fusion in the literature, for example in Darwin’s finches and cichlid fish[44,45]. ‘Despeciation’ itself could be classified as a form of hybrid speciation, as a new species has resulted from the fusion of two old species. I exclude despeciation here because, in my definition, hybrid species should remain distinct when in contact with either parent. Many have argued that permanent divergence is an important criterion of species[2]. However, dropping this a priori requirement seems reasonable to avoid the need to predict an often unpredictable future for distinct, existing taxa[6], and allows for extinction of species via genomic swamping, which seems as valid and potentially important as other forms of extinction, especially in human-altered environments[8].

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[1] Galton Laboratory, Department of Biology, University College London, 4 Stephenson Way, London NW1 2HE, UK.

may often persist for millions of years after initial divergence[18]. Hybridization is thus a normal feature of species biology, if at a rather extreme end of the natural spectrum of sexuality[5]; it is not merely an unnatural "breakdown of isolating mechanisms"[2]. At the population level, interspecific hybrids are, of course, unusual, forming <0.1% of individuals in a typical population[2,18]; they are also 'hopeful monsters', with hefty differences from each parent, no adaptive history to any ecological niche, and little apparent scope for survival (Fig. 1). Furthermore, hybrids are often sterile or inviable owing to divergent evolution in each species[2,6]. Even if a healthy hybrid is formed, it normally suffers 'minority cytotype disadvantage' because it encounters few mates of its own type, and backcrosses to the more abundant parent species will often be unfit. For example, a rare tetraploid hybrid will produce unfit triploid progeny with diploid parents[19].

Yet hybrid species exist. What advantages could outweigh the catalogue of difficulties? This innocent-sounding question plunges to the heart of controversies about adaptive evolution. Is saltational evolution possible? Are maladaptive intermediates and genetic drift involved? Common sense and prevailing opinion suggests that evolution normally occurs by small adjustments rather than saltation, and rarely involves maladaption[6]. It is therefore extraordinary that hybrid speciation can disobey both rules. Hybridization (or hybridogenesis) can act as a multi-locus 'macro-mutation' that reaches out over large phenotypic distances[5] to colonize unoccupied ecological niches or adaptive peaks (Fig. 1). Furthermore, random drift in small, localized hybrid populations provides a parsimonious solution to maladaptation, to enable local establishment, stabilization and ultimate spread[20].

Two principal types of hybrid speciation are treated here: allopolyploidy and homoploid hybrid speciation.

Hybrid speciation through allopolyploidy

Polyploidy is a well-established speciation mode in plants, although many aspects of polyploid evolution are only today being revealed[3,19,21,22]. Speciation can be via autopolyploidy (duplication of chromosomes within a species) or allopolyploidy (duplication of chromosomes in hybrids between species), although the boundary is blurred because of the 'fuzzy' nature of species. Polyploid species are reproductively isolated from their parents because when polyploids mate with diploids, progeny with odd-numbered ploidies, such as triploids, are produced. These offspring may be viable but typically produce sterile gametes with unbalanced chromosomal complements (aneuploidy)[3,4,22]. Polyploidy is thus a simple saltational means of achieving speciation[4]. The process may be repeated many times, leading to lineages with >80-fold ploidy in some vascular plants; 40–70% of all plant species are polyploids[3,21].

Allopolyploid speciation can result from somatic chromosome doubling in a diploid hybrid, followed by selfing to produce a tetraploid. This was the route taken by *Primula kewensis*, the allopolyploid that arose spontaneously in 1909 among cultivated diploid hybrids of *Primula verticillata* and *Primula floribunda*[22]. However, there are other possibilities, such as fusion of two unreduced gametes

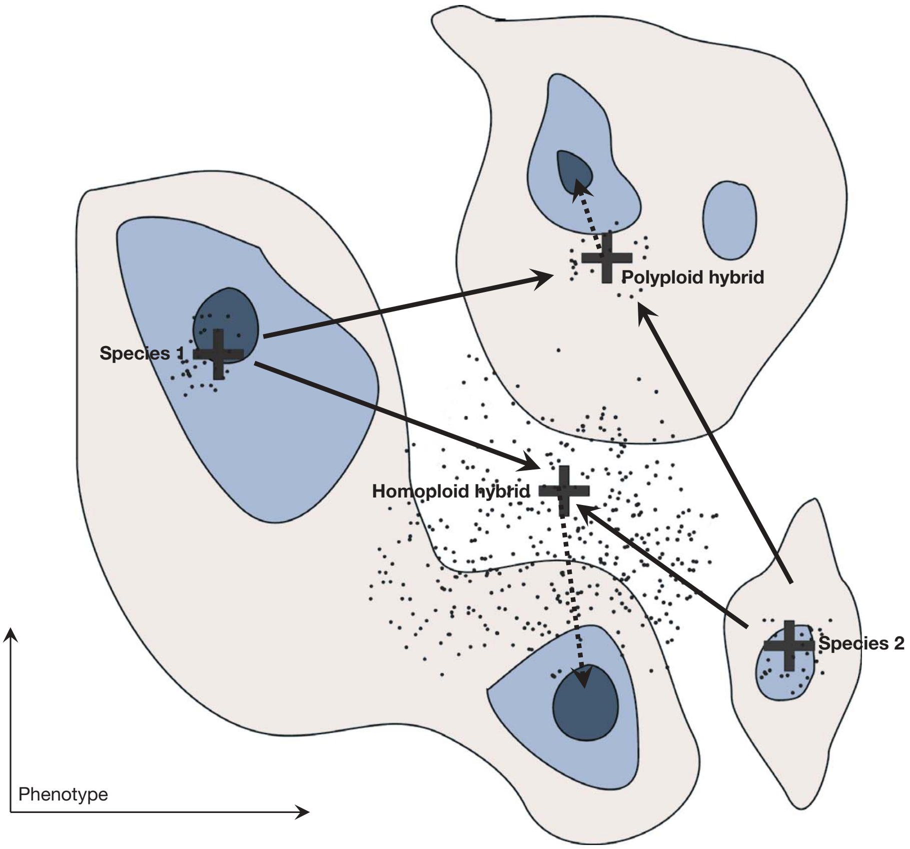

Figure 1 | Hybridization and the adaptive landscape. The hyperspace of possible phenotypes and genotypes can be represented as an adaptive landscape[20]. Fitness optima ('adaptive peaks') are coloured blue. Adaptive landscapes are not rigid, but are readily distorted by environmental or biotic changes, including evolutionary change. Mean phenotypes of species and their hybrids are shown as crosses, and offspring distributions as dots. Species 1 and 2 are adapted to different fitness optima. Natural selection acts mainly within each species, so hybrids are 'hopeful monsters', far from phenotypic optima (solid arrows). It is therefore hard to imagine how hybrids often attain new optima unless unoccupied adaptive peaks are abundant. Polyploid hybrids can have a variety of advantages over their parents, including heterozygote advantage, extreme phenotypic traits and reproductive isolation. Genetic variation in their offspring will initially be similar to that of non-hybrid parents if recombination between parental genomes is rare[4,22]; such hybrids will not spread unless already near an optimum. Homoploid hybrids have fewer initial advantages, but their progeny can have extremely high genetic variances via recombination, including phenotypes more extreme than either parent—transgressive variation (not shown here). This burst of variation can help homoploids attain new adaptive peaks (dotted arrow) far from parental optima[30,32].

after failure of reduction divisions in meiosis. A third route is the 'triploid bridge', in which rare, unreduced (diploid) gametes fuse with normal haploid gametes to form triploids. Triploids are normally sterile, but can contribute to tetraploid formation by themselves producing occasional, unreduced triploid gametes that can backcross with a normal haploid gamete to form tetraploid progeny[19,22]. This was the route used to engineer the first, and maybe the only, synthetic (that is, in the laboratory), self-sustaining bisexual animal polyploid strain, a hybrid between silk moths (*Bombyx mori* and *Bombyx mandarina*)[23].

After polyploid hybrids arise, they still face major hurdles. Diploid and triploid hybrids are strongly disfavoured because their aneuploid gametes are almost always sterile. Even when even-numbered allopolyploidy is achieved, chromosome pairing is rarely perfect[22]. Furthermore, assuming new polyploids are rare, they will mate mostly with incompatible parentals, leading to minority cytotype disadvantage[19]. These problems almost certainly explain why bisexual polyploid speciation is more common in plants than animals: (1) plants usually have indeterminate growth, and somatic chromosome doubling can lead to germline polyploidy; (2) plants are also often perennial or temporarily clonal, allowing multigenerational persistence of hybrid cell lines within which polyploid mutations can occur; (3) plants are more often hermaphrodites, allowing selfing as a means of sexual reproduction of rare polyploids, once formed; and (4) gene flow is weaker in plants than in animals, and local populations with unusual ploidy (whether by local drift or selection) can form more readily to overcome minority cytotype disadvantage. As expected, polyploidy is strongly associated with asexual reproduction, selfing and perenniality in plants, as well as in animals[11,21,23]. In clonal polyploid animals, reversion to out-crossing is rare, whereas in plants, with frequent alternation between clonal and sexual phases, bisexual polyploid species are common and themselves often give rise to further species. Thus, animal allopolyploids such as stick insects (*Bacillus*) and freshwater snails (*Bulinus truncatus*) are often, although not always, parthenogenetic or selfers[21]. Muller's theory[24] that sex chromosomes in animals prevent sexual polyploidy owing to sex:autosome gene dosage is no longer given much credence[6,21,23,25].

How common is polyploid speciation? Otto and Whitton[21] provided new insights from the over-representation of even-numbered chromosome counts. Recent polyploidy explains ~2–4% of speciation events in flowering plants and ~7% of speciation events in ferns[21], and these are probably underestimates[6] (40–70% of plant species overall are polyploid, but this includes the effects of much non-polyploid speciation within already polyploid lineages[3,21]). In animals, there is no bias towards even-numbered chromosomal counts, suggesting that animal polyploid speciation is very rare compared with other speciation modes[21].

Traditional dogma has it that allopolyploids arise more readily than autopolyploids because the latter are more prone to chromosome pairing problems in meiosis[4]; however, this view is no longer generally accepted. Newly arisen autopolyploids have levels of infertility and aneuploid gametes comparable to those of allopolyploids[22]. Furthermore, many autopolyploids probably lie unrecognized by taxonomy within diploid progenitor species[6]. Yet these discoveries give little insight into a more important question: what fraction of polyploids that spread successfully are allopolyploids? Autopolyploids may often be doomed to extinction, perhaps through competition with similar diploid relatives[6]. Opinions differ, but it probably remains true that allopolyploids are more successful than autopolyploids[6,26]; certainly allopolyploids are a sizeable fraction of well-studied crop cases, such as wheat, cotton and tobacco[7,26]. There are almost no surveys of entire floras, although a small-scale survey in the United States revealed that 79–96% of 28 polyploid species were allopolyploids[4]. Recently, the Arctic flora was surveyed, in which about 50% of the often clonal or selfing species are polyploids[27]. In Svalbard (Spitsbergen), 78% of the 161 species are polyploid, with the average level of ploidy approximately hexaploid. Every one of the 47 polyploid species studied genetically shows fixed marker heterozygosity, implying 100% allopolyploidy[27]. The Arctic is, of course, an extreme environment, but this remains the most comprehensive survey so far. If Svalbard is typical, most successful polyploids are also hybrid species.

After formation, novel allopolyploids face the usual 'hopeful monster' difficulties (Fig. 1). It helps if they can exploit a new ecological niche that is both vacant and also spatially separated to ameliorate minority cytotype disadvantage. For example, recent allopolyploid hybrids between introduced and native plants have successfully spread from sites of origin (for example, *Senecio cambrensis* in Wales[28] and *Spartina anglica* in England[29]). These invasive allopolyploids were able to exploit vacant ecological roles with relatively little evolutionary change (Fig. 1).

Stochastic drift may also be necessary to overcome minority cytotype and other disadvantages. A few polyploids, usually from the same hybridization event, must accumulate locally for the process to take off, probably involving chance or an unusual local selective regime. Stochastic effects are evident in nature. An independently derived Scottish population of *S. cambrensis* became extinct in Edinburgh some 20 yr after being discovered[28]. Of two origins, only the Welsh population now survives. Other allopolyploid hybrids can arise repeatedly from the same parents[26], but many widespread polyploids (for example, *S. anglica*) probably originated only once or a few times[21,28,29], even though parent species are in broad contact, again showing the importance of chance in the origins of hybrid species.

Recombinational and homoploid hybrid speciation

Homoploid hybrid speciation or recombinational speciation is well-known in flowering plants[4,7,30]. Speciation takes place in sympatry (by definition, as hybridization requires gene flow). Hybrids must then overcome chromosome and gene incompatibilities, while lacking reproductive isolation via polyploidy. For these reasons, the process is often considered unlikely[5,6,31].

However, hybridization can boost genetic variance[30,32], allowing colonization of unexploited niches (Fig. 1). Suppose + and − alleles at genes affecting a quantitative trait differ between species, so that each has fixed differences (+++−− and −−−++, say). Recombination can then liberate 'transgressive' quantitative variation[32], often more extreme than either parent (for example, −−−−− and +++++). Most early recombinants will be unfit, but extreme hybrids can colonize niches unavailable to parents. If ecological opportunities are partially separated from the parental habitat, if like hybrids tend to associate (for example, by means of seasonality or drift in small populations), or if selfing or inbreeding is common, gene flow between hybrids and parents will be reduced and hybrid speciation becomes more likely[7,32]. Successful hybrid species might also displace one or more parent species ecologically[30], and obliterate evidence of their own hybrid origin.

In plants, about 20 well-established homoploid hybrid species are known[31,33], but they are hard to detect and may be more prevalent. The best documented are the desert sunflowers *Helianthus anomalus*, *Helianthus deserticola* and *Helianthus paradoxus*, which all derive from hybrids between mesic-adapted *Helianthus annuus* and *Helianthus petiolaris*[30,33]. Selfing is rare and provides little assistance to establishment, but the three hybrid species survive drought better than their parents, suggesting recruitment of hybrid transgressive variation. Synthetic hybrid populations are readily recreated with karyotypic combinations like those in wild hybrid species, because selection repeatedly favours similar combinations of compatible chromosomal rearrangements. In addition, the wild contribution from each parent of extreme adaptive traits for morphology, physiology and life history of the hybrids (for example, small leaf size, seed dormancy, or tolerance of drought and salt) matches experimental predictions[32,33]. In *Helianthus*, recombinant genotypes and spatial separation have enabled the hybrids to flourish where their parents are absent.

Although bisexual polyploids are often barred in animals, there is no reason why homoploid hybrid species would be rarer in animals than in plants. The number of cases in animals is growing rapidly[10,33]. A recent example is the invasive sculpin, a hybrid fish derived from the *Cottus gobio* group from the Scheldt River (compare *Cottus perifretum*) and upper tributaries of the Rhine (compare *Cottus rhenanum*). Sculpins are normally restricted to clear, well-oxygenated cold waters in upper river tributaries across Europe. The Rhine and Scheldt rivers became connected as a result of earlier canal building, but invasive sculpins appeared in the warmer and muddier lower Rhine only in the past fifteen years. Morphologically, the invasive sculpin is intermediate, and its mitochondrial DNA, as well as nuclear single nucleotide polymorphisms and microsatellites, are characteristic of both Scheldt and Rhine forms[34]. The hybrid form meets upper Rhine sculpins in narrow hybrid zones, but remains distinct despite gene flow, suggesting that it is adapted mainly to the lower Rhine. Recent evolution and spread of the invasive sculpin, as well as intermediacy, provides convincing evidence of adaptive hybrid origin. A more ancient example is the cyprinid fish *Gila seminuda*, which inhabits the Virgin River, a tributary of the Colorado River (USA). This hybrid species contacts but does not overlap its parent species, *Gila robusta* and *Gila elegans*, from the Colorado River. *Gila seminuda* is morphologically and genetically intermediate, and similar to synthetic hybrids. Intermediacy may allow it to out-compete both parents in the Virgin River[35]. A similar case, with well-documented genetic intermediacy, is an unnamed form of the butterfly genus *Lycaeides*. This homoploid hybrid species uses a different host plant and inhabits high-elevation alpine habitats unoccupied by either parent[36].

Rhagoletis fruitflies provide another historically documented example. In 1997 flies were first found on introduced honeysuckle (*Lonicera* spp.). Molecular markers in the fly are a blend from the two parents: the blueberry maggot *Rhagoletis mendax* and the snowberry maggot *Rhagoletis zephyria*[37]. No F_1 genotypes are detected between the hybrid form and its parents where they overlap; the new fly is reproductively isolated. *Rhagoletis* flies mate on host fruits, and host choice ensures mating specificity. A different route to hybrid speciation can be inferred from the Colombian butterfly *Heliconius heurippa*[38]. This form has a colour pattern like that of synthetic hybrids between local *Heliconius cydno* and *Heliconius melpomene*. Microsatellite alleles are shared across all three species, but *H. heurippa* forms an allele frequency cluster distinguishable from either parent. The hybrid wing coloration of *H. heurippa* is a cue in mating discrimination, and directly causes reproductive isolation from both parents. Similarly, in the fish *Xiphophorus clemenciae*, the 'swordtail', a hybridization-derived trait, is involved in sexual selection and mate choice[39] and may be related to its speciation.

Hybrid speciation in animals is supported so far only by low-resolution molecular data. Genomic mapping of ecological or speciation-related hybrid traits, which so strongly supports hybrid speciation in *Helianthus*, is not yet available for any animal case. Many homoploid hybrid species fail to overlap with at least one parent species, and reproductive isolation is weak, so species status could be questioned (the *Lonicera*-feeding *Rhagoletis* is an exception). Nonetheless, in the cases surveyed here, hybrid traits often contribute strongly to maintenance or ecological expansion of the new form.

Is hybrid speciation important in evolution?

There are now many examples of hybrid species. We know that polyploidy is common in plants, giving rise to ≥2–7% of vascular plant species, but rarer in animals. Furthermore, ancient polyploidy has been found at the root of many plant and animal groups. Genome duplications probably facilitated the evolution of complex organisms (although this is debated)[21], and we can infer that successful genome duplications were mostly allopolyploid, provided that limited plant community data are reliable[4,27]. Hybridization would then be a catalyst not only for speciation but also for major evolutionary innovations.

Polyploid speciation leaves a clear genomic signature, but we have little idea how common homoploid hybrid species are. They could be abundant: most speciation involves natural selection[6]; natural selection requires genetic variation; genetic variation is enhanced by hybridization[12]; and hybridization and introgression between species is a regular occurrence, especially in rapidly radiating groups[9,12,18]. Enough suspected animal homoploid hybrid species exist to indicate that it may be at least as common as in plants, in contrast to the situation for polyploidy, where a variety of traits prevent its occurrence (see above). It now seems intuitively unlikely that all biodiversity arose as a result of recombination of existing diversity[1], but homoploid hybrid species might still represent a large fraction. Nonetheless, there are few convincing cases, probably, in part, because of the difficulty of demonstrating that hybridization has led to speciation. We clearly need more genomic analyses. As for hybrid species as a whole, we have observed recent speciation in the laboratory or nature in seven genera discussed here (*Helianthus*, *Senecio*, *Primula*, *Spartina*, *Rhagoletis*, *Bombyx* and *Cottus*), and there are many other cases. It would be hard to find another mode of speciation so readily documented historically and so amenable to experimentation.

That hybrid species exist at all reveals something perhaps unexpected about adaptive landscapes. If hybrid 'hopeful monsters', with all their problems, are ever to survive in competition with their parents, they must be able to hit (and for polyploid species, hit almost exactly) new adaptive combinations of genes (Fig. 1). This implies both that many adaptive peaks are scattered about in the adaptive landscape, and also that many are unoccupied. Liberal adaptive landscapes are further supported by the successes of many introduced species, and by fossil evidence: for insects, angiosperms and many other groups, diversity seems to have been increasing more or less continuously over geological time[40].

The ability of hybrid species to invade hitherto unoccupied niches also means that hybridization can contribute to adaptive radiations such as African cichlid fish and Darwin's finches[7,9,12]. This principle is well demonstrated by the 'domestication niche'. Humans have unwittingly created many allopolyploid and other hybrid crops and domestic animals while selecting for transgressively high yields[4,7]. Even our own species may have a hybrid genomic ancestry[41,42], although this is contested[43]. Whichever way the debate about humans is resolved, it would be hardly surprising if hybridization was one trigger for the origin of *Homo sapiens*, the most invasive mammal on the planet[42].

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