Hybridization as an invasion of the genome: Online Appendix 1. Notes on Table 1: Hybridization rates in the wild

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In Table 1, I show percentages of species known to hybridize in the wild with one or more other taxonomic species. Hybridization between taxonomic subspecies is excluded, thus excluding many classic "hybrid zone" studies. I have also attempted to exclude hybridization with introduced species, since these are hardly "natural". In the UK vascular plants example, I include all taxa marked as hybrids, but exclude allopolyploids and other species of hybrid origin that are now considered separate stable species (although these species may themselves be involved in hybridization, of course). Hybrids in this table have been identified almost exclusively via morphology.

Most of the examples of Table 1 are cases of hybridization between species that overlap in sympatry (for example, the mallard duck hybridizes with the wigeon). A lesser number represent hybrids between largely parapatric forms whose ranges abut, but are considered distinct enough, and produce few enough hybrids to be considered different species (for example the arctic hare and brown hare). Most of the sources of this table utilize a taxonomic version of the "biological species concept": parapatric forms are considered separate species only if hybrids are rare in the zone of contact, or if it is presumed that they would be rare if contact was made. If hybrids form a substantial fraction of the population, the two parental forms are considered conspecific. In contrast, the more recent "phylogenetic species concept" [A1.1] considers that distinct parapatric forms are separate species, even if they hybridize freely. Therefore, adoption of the phylogenetic species concept (provided the hybrids are excluded from consideration) can lead to inflation in the numbers of species [A1.2], and, because most such newly-elevated species hybridize with related taxa, to a higher fraction of species that hybridize.

One could estimate of rates of hybridization by the numbers of unique hybridizations (e.g. mallard x wigeon, mallard x eider, and divide by the total number of possible hybridizations, which is $S(S-1)/2$, where S is the total number of species sampled [A1.3-4]. Some workers have used this method. However, the method will have a variable bias depending on the breadth of the phylogenetic group covered, since the probability of hybridization declines in proportion to genetic distance between species, while the number of possible hybridizations goes up almost as the square of the number of species (see main text). Therefore comparisons within a genus will tend to give higher estimates of rates of hybridization than those within an order, say.

Instead, it seems best simply to count the numbers of species involved in hybridization (with each species counted only once, no matter with how many species each hybridizes), and divide by the total number of species in the group [A1.5]. This method was used for the estimates of hybridization rate per species in Table 1. This gives an estimate of the fraction of species in nature with blurred boundaries, or in other words, the fraction of species prone to introgression. The completeness of the species-level information required for estimating per species hybridization rates makes it difficult to include data from some well-known surveys, such as those in flowering plants and marine organisms [A1.3-4, 6].

For each group, I attempt also to give representative estimates of hybridization rates per individual in cases where hybridization occurs. These estimates vary widely between different species pairs and even in different parts of the range of the same species pairs, and are not generally well known. For instance, most *Heliconius* hybrids between sympatric sister species are rarer than one in 1000 individuals, but in the case of the parapatric *Heliconius himera* and *H. erato*, which overlap in a narrow contact zone, hybrids form about 5% of the population [A1.7]. Although *Papilio* hybrids are usually rare in populations, in some *Papilio* cases interspecific hybrids may locally exceed 80% of the total individuals [A1.8].

There is some variability in the per species hybridization rate, but many of the estimates seem to hover around 10% when measured over reasonably large groups. Four rates of hybridization per species seem significantly lower than the others, but I do not believe that any of them are particularly reliable:

(1) Mayr's analysis of the flora of Concord, Massachusetts [A1.9] gives a particularly low value of hybridization for flowering plants [A1.10, 11]. However, Mayr's purpose was to analyse the "validity of the biological species concept"; hybridizations that did not cause "obliteration of parent species" were overtly excluded.

(2) The low value of 1% of *Drosophila* species hybridizing is almost certainly due to poor knowledge of the vast majority of the over 1700 species described. Of the nine cases of hybridization known (18 species), four occur in the three groups of species most used as model organisms in evolution and genetics [A1.12, 13]; these systematically and genetically well-known species groups therefore have a higher per species hybridization rate than the average overall.

(3) The sylviid (Old World) warblers of the Western Palaearctic are not known to hybridize at all [A1.14], but it seems likely that hybrids would be missed easily given that that all the species have very similar morphologies. In contrast, the ecologically similar parulid (New World) warblers, which are brightly coloured and strongly divergent between species, hybridize at a rate of 24% of species [A1.15].

(4) The 6% rate of hybridization for European mammal species, which are very well-known, is probably accurate, but Europe is not a centre for diversity in this group; with so few species, the average interspecific relationships will be low. It seems likely, or at least possible, that more rapidly radiating mammals in tropical regions will show higher rates of hybridization, contributing to a higher rate of mammalian hybridization per species globally than the value documented here. It would not be surprising if world mammals hybridize at a rate similar to that of birds (9%).

What is the overall fraction of species involved in natural hybridization? For vascular plants, I could find only UK data where hybrids between species had been carefully listed, and the rate seems to be around 25%. Families such as Orchidaceae are renowned to be far more prone to hybridization, and the Orchidaceae is also the most species-rich family of plants world-wide [A1.11]. However, orchids are poorly represented in the UK, so the world average of hybridization in vascular plants could well be higher than 25%. For large groups of animals, the bird and butterfly estimates hover around 10%, and the mammal estimate of 6% from Europe does not seem much lower, given the low diversity and relatedness of most mammal species groups in Europe. Therefore it seems that on average, around 10% of all animal species are liable to hybridize in the wild. However, this is probably an underestimate because of the ascertainment bias against hybrids in the many morphologically uniform species-groups (see text).

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