

not proud of this, nor am I happy with it, but its a start and makes ideas easier to clean up

outline

- open with focus on introgression with endangered species, not just introgression as in hufford, but mention hufford paper as crop-wild
- move to background on rice evolution
- then into glumaepatula
- mention evidence of introgression in experimental settings for gluma and in wild for rufipogon
- mention lack of studies showing introgression of rice species, with focus on transgenes and weedy varieties
- why its important and what we show

Introduction

Hybridization and introgression have long been studied for their unique role in the promotion of variation (citation) and for curious questions regarding the ambiguity of species boundaries (citation). Many studies of introgression focus on fluid natural habitats and recently-diverged wild populations, with interest in mechanisms of speciation (citations). The rapid evolutionary responses of adaptive introgression are of particular interest. In plants, adaptive introgression has been shown to play a part in herbivore resistance (citation), highland adaptation (?), and drought escape (citation). These adapted hybrids may have higher fitness than their wild progenitors, leading to hybrid swarms (citation) that increase the mean fitness of a population and lead to rapid range and population size expansion (citation). This can be hazardous to endangered species whose mean fitness is lower than that of the hybrid swarm, threatening extinction of the wild population (citations). Anthropogenic disturbance in the form of domesticated and introduced species, habitat destruction, and environmental changes influence the hybridization and introgression in natural settings (citation). An extreme example is that of the wild California raddish, which is now extinct due to the introduction of different raddish species, with the hybrid of the two forming swarms that now dominate the states geography (citation). Despite the potential hazards of extinction via introgression, which are especially high in crop-wild settings where the wild species often populates areas surrounding fields, few studies have investigated the extent to which it occurs naturally.

One such species interaction may be evidenced in the *Oryza* species complex, which includes multiple endangered wild species (citations). The domesticated *Oryza sativa* is the most important crop in the history of agriculture, estimated to feed nearly 80

Similar in many ways to the wild ancestor of the sativas is the wild *O. glumaepatula*, which is morphologically indistinguishable from *O. rufipogon* (citation). However, sterility barriers exist (citations), as well as phylogentic evidence (citations) to suggest the two are a separate species. Through phylogenetic methods it has been shown that *O. glumaepatula* diverged from *O. rufipogon* and the sativas 1.2 MYA and is closely related to the African cultivated *O. glabberima*(citations). Native to South and Central America (citations) and predominantly found in Brazilian rivers (citations), *O. glumaepatula* shares a AA genome with the sativas (citation), and is a perennial species with a mixed though predominantly-selfing mating system (citations). Gene flow of the species primarily occurs through seed dispersal and uprooting of plants (citations), with pollen dispersal

highly limited by distance (citation), contributing to most variation existing between populations (citations), with higher variation in downstream populations due to seed and clonal dispersal (citation). Although most studies focus on Brazilian *O. glumaepatula* (citations), the species is found in Central America up to Cuba (citation?), and with most variation in the species existing between populations over geographical distance, *glumaepatula* in more Northern latitudes may exhibit differential variation when compared to its more Southern populations. *O. glumaepatula* is considered endangered (citations), along with *O. rufipogon* (citations), warranting the possible need for conservation to preserve the genetic diversity of the wild rice species as potential sources of useful natural variation for breeding (citations).

While crop-wild introgression has been shown to sparingly occur in nature between *rufipogon* (citation) and other wild species (citation), there is no evidence of natural crop-wild introgression with *O. glumaepatula*. Most studies of introgression in rice species have focused on the flow of transgenes from cultivated crops in an experimental setting (citation) or on the evolution of weedy rice species (citations). However, due to the shared AA genome in *glumaepatula* and *japonica*, as well as morphological features of *glumaepatula* such as completely protruding anthers and stigma and differential flowering time on the same panicle (Karasawa et al. 2007), there is reason to believe that natural introgression is possible. *Glumaepatula* and *sativa* have been successfully experimentally-crossed (citations), leading to the discovery of new potentially-useful genes (citation) along with multiple hybrid sterility loci causing pollen inviability in F1 offspring (citations). The possibility of inviable pollen in the natural setting causes worry for a decrease in mean fitness of populations in which introgression may have occurred, contrasting with the worry of hybrid swarms. Although female gametes show no functional deficit when homozygous for inviability loci (citation?), offspring of homozygous females with carry these loci, increasing their frequency in natural populations and decreasing the overall fecundity. Also, as seen in other crop-wild introgressions (citations), it is possible that domesticated loci may sweep in wild populations, possibly creating regions of increased diversity due to their low frequency in the wild population, counter to the traditional low-diversity signature of sweeps (citations), with potential adaptive consequences, again shining light of the danger of hybrid swarms.

Here we use statistical and population genomic methods using whole-genome sequencing of two Costa Rican populations of *O. glumaepatula* to show evidence of crop-wild introgression in a natural setting. We show that domestication loci, as well as hybrid inviability loci flow from cultivated *O. sativa* ssp. *japonica* into *O. glumaepatula*, giving rise to concern for the future viability of wild rice populations. Because of its genome compatibility with domesticated rice, *glumaepatula* is an important genetic resource for breeding applications, and its conservation should be considered. In situ conservation of *glumaepatula* requires blah blah blah. Our findings run counter to findings of gene flow from wild to cultivated species (Hufford), and show that crop-to-wild gene flow in nature is a threat for rice and potentially for other species with wild and cultivated species living in sympatry.