

SHORT COMMUNICATION

Unexpected hybridization reveals the utility of genetics in native plant restoration

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Native plant materials (NPMs) are increasingly utilized during the restoration of disturbed plant communities. Here, we analyze next-generation genetic sequencing data for *Hilaria jamesii*, a dominant graminoid across drylands of the southwestern United States, and document that the species' only commercially-available NPM, "Viva," is a hybrid between *H. jamesii* and its sister species, *Hilaria mutica*. In fact, hybrids between these species are common where they geographically overlap. Furthermore, we show that the "Viva" hybrid has successfully been moved beyond the hybrid zone and into the core range of *H. jamesii*. The potential ramifications of introducing novel genetic material into *H. jamesii* are discussed, as well as the utility of genetic analyses to protect species' natural patterns of genetic diversity and help managers make informed decisions regarding the development and deployment of NPMs.

Key words: cultivar, genetic diversity, *Hilaria*, native plant materials (NPM), Poaceae, population differentiation

Implications for Practice

- Sourcing native plant restoration materials (NPMs) from hybrid zones, which may be common where the ranges of closely related species overlap, has implications for the genetic integrity and diversity of target species when restoration occurs away from hybrid zones.
- The "Viva" NPM is a hybrid between *Hilaria jamesii* and *Hilaria mutica* and should be treated as such.
- "Viva" has successfully been moved beyond the hybrid zone from which it was sourced and is now established in the core range of *H. jamesii*.
- Restoration programs would benefit from evaluating target species' genetics, both across their natural distributions and for available NPMs.

Introduction

Restoration treatments across western North America are increasingly implemented using native plant materials (NPMs) (Richards et al. 1998; Shaw et al. 2012; Oldfield & Olwell 2015), similar to many regions around the globe (e.g. Holmes et al. 2005; Offord & Meagher 2009; Tischew et al. 2011). Although there is a substantial debate on which NPMs are most appropriate for a given restoration site (e.g. McKay et al. 2005; Broadhurst et al. 2008; Johnson et al. 2010; Bucharova 2017; Massatti et al. 2020), utilizing NPMs remains a challenge because sufficient quantities of a diverse range of NPMs are limited (both in terms of species diversity and diversity of environments represented) (Dunne & Dunne 2002; Peppin et al. 2010). As a result, restoration practitioners often rely on readily

available NPMs (e.g. cultivars; Aubry et al. 2005) to facilitate restoration goals.

Depending on the plant material development strategy, NPMs can range from highly selected lineages (e.g. cultivars) to multi-source composites (Jones 2003; Kettenring et al. 2014). All strategies have constraints when attempting to restore native plant communities and functioning ecosystems (Bucharova et al. 2019). For example, a genetically depauperate NPM may not be well matched to habitats beyond its origin (Jones 2013) or highly disturbed areas (Lesica & Allendorf 1999). In addition, a depauperate NPM may not be adapted to future climates (e.g. Breed et al. 2016), which can limit plant establishment (Bischoff et al. 2010) and disrupt ecosystem functions (Kettenring et al. 2014). A genetically diverse NPM may be maladapted to the environment one seeks to restore (Byrne et al. 2011) and can cause ecological disruptions when it interbreeds with conspecifics at the restoration site (Schröder & Prasse 2013; Kramer et al. 2018). Sequencing-based techniques allow restoration species and their NPMs to be genetically characterized and compared (e.g. Shryock et al. 2017; Massatti et al. 2018; Tso & Allan 2019), under the premise that increased

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scrutiny of genetic diversity and adaptations (e.g. Gustafson et al. 2004; Smith et al. 2007) may increase restoration success and protect species' natural patterns of genetic variation (Massatti et al. 2020).

During the course of range-wide genetic analyses of *Hilaria jamesii* (Torr.) Benth. (Poaceae; common name: James' galleta grass; synonym: *Pleuraphis jamesii*) (Massatti & Knowles 2020), data were generated for the species' only NPM, "Viva" (NMSU et al. 1979), as well as for representatives of the closely related species *Hilaria mutica* (Buckley) Benth. and *Hilaria rigida* (Thurb.) Benth. Here, we report evidence of hybridization between *H. jamesii* and *H. mutica*, including in the "Viva" NPM. In doing so, we illustrate the utility of genetic investigations of priority restoration species. Our findings raise questions regarding the appropriate use of "Viva" in restoration treatments across the core range of *H. jamesii*, and we argue that increased knowledge of species' genetic patterns is essential to consider during NPM development and subsequent restoration activities.

Methods

Study Species

Hilaria jamesii is an outcrossing, C₄ bunchgrass that is perennial and can develop sprawling, woody rhizomes (Sohns 1956). It is native across interior western North America, where it occasionally overlaps with congeners (*Hilaria mutica* and *Hilaria rigida*; Fig. 1). "Viva" was released in 1979 by New Mexico State University, Colorado State University, and the USDA-NRCS (Natural Resources Conservation Service) Los Lunas Plant Materials Center. Seeds for cultivation were collected in 1944 near Newkirk, New Mexico by the Soil Conservation Service and were planted and tested in trials from 1958–1979 (NMSU et al. 1979). It is the only commercially available material for *H. jamesii* and has been utilized in many restoration efforts across the western United States (e.g. Warren et al. 1996; Monsen et al. 2004). "Viva" was originally described as being useful for soil stabilization and range revegetation (NMSU et al. 1979) and is currently marketed as being useful for binding soils and its drought tolerance (e.g. St. John et al. 2012). *Hilaria mutica* and *H. rigida* are also perennial, C₄ bunchgrasses that develop sprawling rhizomes. They are less cold tolerant and have higher drought tolerance than *H. jamesii* and, as such, are found in the warm Sonoran, Chihuahuan, and Mojave deserts (Fig. 1).

Analyses

Single nucleotide polymorphism (SNP) data were generated for 87 *H. jamesii*, six *H. mutica*, and seven *H. rigida* individuals (Fig. 1, Tables S1 & S2). *Hilaria jamesii* sampling sites were selected to represent its range where it does and does not overlap with *H. mutica* (Fig. 1). *Hilaria mutica* and *H. rigida* were represented by three field-collected and 10 herbarium specimens that unambiguously represented the defining morphological traits of these species (Barkworth 2003). This sampling scheme was informed by results reported in Massatti and Knowles (2020).

Raw data were generated by sequencing a RADseq library on an Illumina HiSeq4000, which produced 100 base pair, single-end reads. SNPs were identified utilizing STACKS v2.2 (Catchen et al. 2013; see Massatti & Knowles 2020 for processing details). The evolutionary history among the three species was inferred using SVDQuartets (Chifman & Kubatko 2014, 2015) as implemented in PAUP* v4.0a166 (Swofford 2003). SVDQuartets uses a coalescent-based species tree approach that estimates trees on each locus within a dataset, thereby allowing loci (which herein are represented by unlinked SNPs) to have independent histories. As such, this method alleviates complications from incomplete lineage sorting, which may be expected in recently diverged sets of species (Maddison & Knowles 2006). Our implementation of SVDQuartets allowed all possible quartets to be evaluated, included 100 bootstrap replicates, and used a multispecies coalescent tree model with distributed ambiguities.

Signatures of hybridization between *H. jamesii* and *H. mutica* were further investigated using STRUCTURE version 2.3.4 (Falush et al. 2003). We used a subset of individuals (Tables S1 & S2) in STRUCTURE analyses to mitigate the bias that may be introduced by including many *H. jamesii* and few *H. mutica* individuals (Shringarpure & Xing 2014). These analyses did not include *H. rigida* due to the lack of evidence of its admixture with either *H. mutica* or *H. jamesii*. Furthermore, we only investigated genomic patterns using a *K* value = 2 in line with the hypothesis that *H. jamesii* and *H. mutica* are discrete species that may hybridize in areas where they geographically overlap. All other methodological details are similar to Massatti and Knowles (2020).

Results

Illumina sequencing produced $>1.4 \times 10^8$ reads across 100 individuals (average = 1.46×10^6 reads per individual; Tables S1 & S2). Because of low coverage, three individuals were excluded from further analyses (Table S2). The STRUCTURE dataset included 44 individuals and 2,536 unlinked SNPs (average missing data per SNP = $9.1 \pm 5.5\%$; average missing data per individual = $5.1 \pm 5.5\%$). SVDQuartets was conducted on the variation represented by 404,512 SNPs as summarized by sampling sites; preliminary analyses on individuals instead of sampling sites resulted in similar relationships (data not presented). Loci for these analyses were determined by filtering values used in the STACKS program (see Massatti & Knowles 2020). Data generated during this study are available from the USGS ScienceBase-Catalog (Massatti & Winkler 2020).

Relationships among sampling sites are robust, as all nodes had 100% bootstrap support in the SVDQuartet cladogram (Fig. 2). *Hilaria mutica* and *H. jamesii*—Drake form a clade that is sister to a clade containing all other *H. jamesii* sampling sites. Notably, the "core" *H. jamesii* sampling sites (i.e. those that do not overlap geographically with *H. mutica*; Fig. 1) form a strongly supported clade nested within the phylogeny (Lees Ferry, Jesus Mesa, and Poison Spring; Fig. 2). STRUCTURE analyses illuminate patterns of admixture that explain the pectinate, or comb-like, structure of the cladogram. At *K* = 2, all *H. mutica* individuals are solely assigned to the one genetic axis (hereafter, the blue axis; Fig. 2),

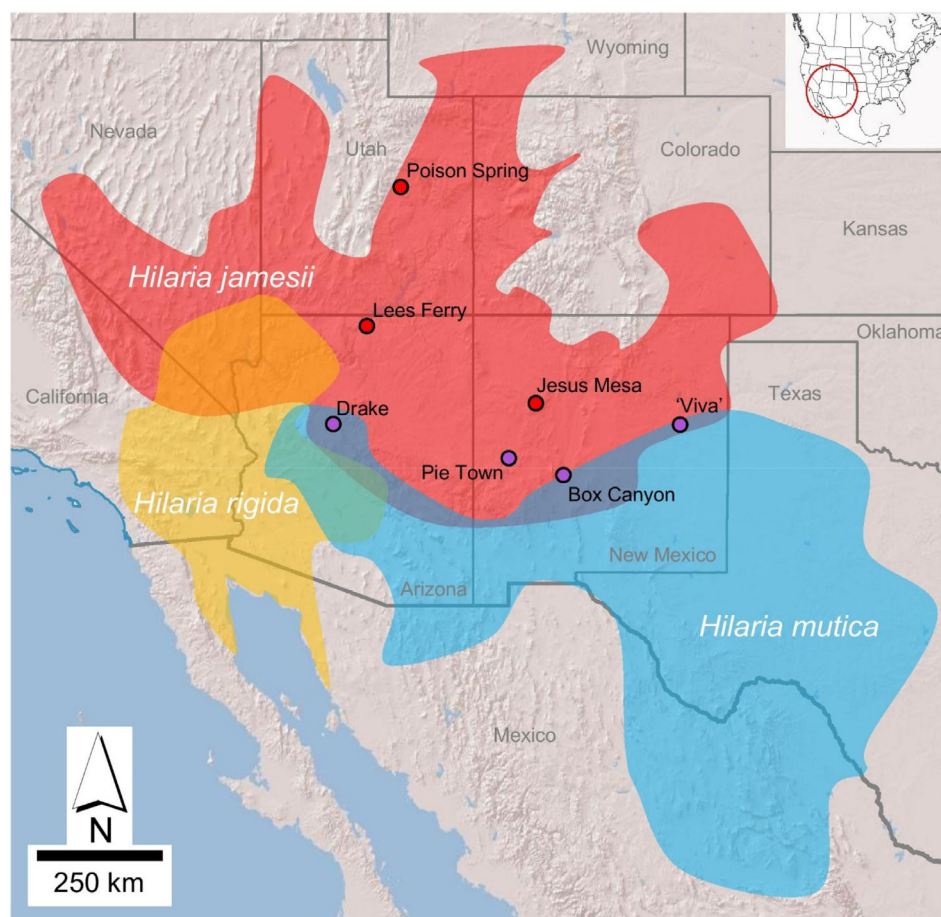


Figure 1. Geographic map of the southwestern United States depicting the distributions of *Hilaria jamesii*, *Hilaria mutica*, and *Hilaria rigida* (colored polygons). Distributions were mapped using georeferenced herbarium collections downloaded from SEINet (<http://swbiodiversity.org/seinet/>); they exclude outlier voucher specimens that may be misidentified, improperly georeferenced, or are in disjunct, otherwise rare habitat. Sampling sites showing no signal of admixture (i.e. exclusively *H. jamesii*) are represented by red circles, while those with individuals containing genetic signatures of both *H. jamesii* and *H. mutica* are represented by purple circles. Circle color corresponds to sample site name in Fig. 2.

while the core *H. jamesii* are solely assigned to the second genetic axis (hereafter, the red axis; Fig. 2). The *H. jamesii*—Drake sampling site, which unambiguously clusters with *H. mutica*, is composed of individuals dominated by the blue axis. *Hilaria jamesii*—Pie Town and “Viva” contain individuals showing very similar mixtures of the red and blue genetic axes. Finally, *H. jamesii*—Box Canyon individuals have a minor component of the blue genetic axis, and this sampling site is sister to the core *H. jamesii* sampling sites (Fig. 2).

Discussion

An increasing awareness of the impact plant materials may have on restoration treatment success, genetic resources and organisms in the local community, and overall ecosystem functioning (e.g., Lesica & Allendorf 1999; Hufford & Mazer 2003; Espeland et al. 2017) is driving the creation of new guidelines for the development and use of NPMs (Oldfield & Olwell 2015; Breed et al. 2018; Bucharova et al. 2019; Massatti et al. 2020). In particular, genetic sequencing is rapidly advancing NPM use and

development because patterns of genetic differentiation and diversity offer a look into species’ dynamics that has previously not been possible. Here, sequence-based analyses precipitated the identification of a previously unknown hybrid zone where two closely related species overlap, as well as admixture in the “Viva” NPM, which is the only restoration material available for *H. jamesii*. The parent material for “Viva” was sourced from an area near Newkirk, NM where the ranges of *H. jamesii* and *H. mutica* are in close proximity (Fig. 1). It is important to note our results do not allow us to infer whether the admixed genetic pattern is a product of the NPM development process or if it represents the genetic structure of individuals at the Newkirk sampling site. However, the identification of admixture at other sampling sites where the two species come into contact (Figs. 1 & 2) strongly suggests that “Viva” may be derived from a naturally occurring hybrid population. Natural hybrid zones are commonly found in intermediate or disturbed habitats where species’ ranges overlap (Rieseberg & Wendel 1993); sourcing NPMs from such zones can have unintended consequences on species’ non-admixed populations once hybrid materials are introduced (Grabenstein & Taylor 2018).

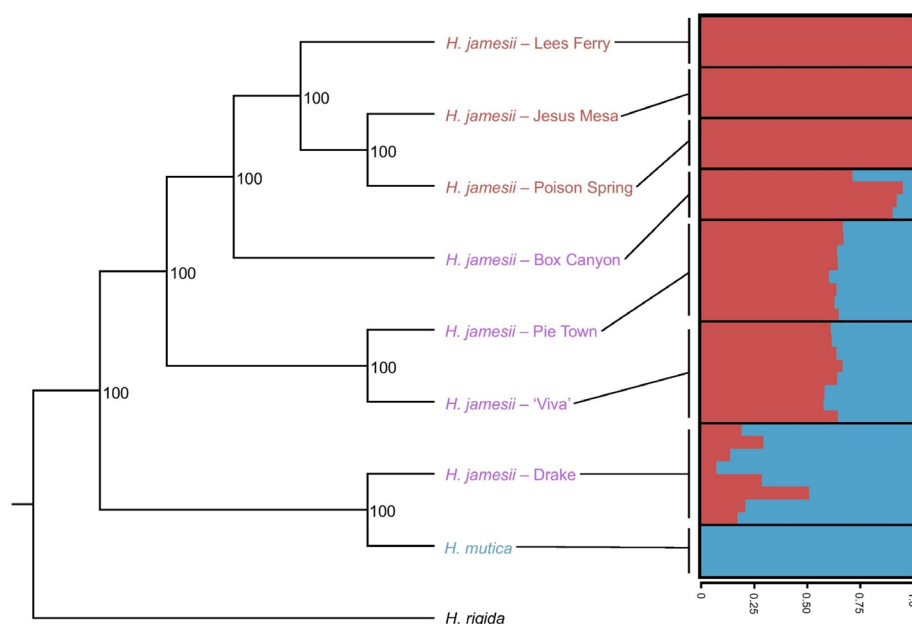


Figure 2. Cladogram inferred using SVDQuartets (left) and ancestry coefficients for individuals inferred using $K = 2$ in STRUCTURE (right). All nodes in the cladogram were highly supported, as measured using 100 bootstrap replicates. Sampling site names are colored by their dominant genetic axis, with red = *Hilaria jamesii*, blue = *Hilaria mutica*, and purple = admixture between *H. jamesii* and *H. mutica*. Colors correspond to those used in Figure 1.

Our genetic investigation also likely documented the establishment of "Viva" within the core range of *H. jamesii* (i.e. not overlapping with *H. mutica*; Fig. 1). We hypothesize that the remarkable similarity of admixture patterns between individuals representing "Viva" and the Pie Town sampling site (Fig. 2) result from our sampling a previously restored roadside where "Viva" was used. While our sampling scheme for all other sampling sites strictly avoided collecting plant tissues from areas close to obvious human disturbance, *H. jamesii* was not found in any of the adjacent, higher-elevation habitat near Pie Town. Correspondences with New Mexico Department of Transportation personnel support this hypothesis, as "Viva" has been used in roadside remediation throughout this area. The evolutionary implications of spreading *H. mutica* genes throughout *H. jamesii*'s range are largely unknown, but negative effects may include reduced fitness as a result of outbreeding depression, selection against adaptive traits and destabilization of wild populations due to introgression, and cryptic invasion of "Viva" genotypes (Rieseberg & Wendel 1993; Hufford & Mazer 2003), among others. Potential beneficial aspects of spreading *H. mutica* genetic material into the core range of *H. jamesii* must be carefully investigated and discussed, as this action would compromise the genetic integrity of an important, dominant graminoid across the Intermountain West.

Overall, our results demonstrate the importance of considering patterns of genetic variation in the development and use of NPMs. Although it is unknown how common human-mediated movement of hybrids is in restoration, the opportunity for deleterious genetic consequences implies that managers should exercise caution when using NPMs developed from potential hybrid zones; hybrid zones should be suspected wherever closely

related taxa overlap and taxonomic keys are difficult to use. Interestingly, future genetic analyses, especially if appropriately designed and executed, will illuminate and document how previous management decisions have shaped the genetic patterns of priority restoration species across their distributions. In turn, we may be able to learn from these miniature evolution experiments so that future restoration can be performed in a way that will protect integrity of restoration species and the organisms that depend on them (Bucharova et al. 2019). In conclusion, land management would benefit from incorporating genetic analyses into the development and use of NPMs so that future restoration treatments will promote sustainable land use and conserve biodiversity (Miller et al. 2017; Winkler et al. 2018).

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Details of sampling localities and data processing.

Table S2. Details of voucher samples included in analyses.

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