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Epigenetics and the success of invasive plants

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Keywords: adaptation, biological invasion, biotic interactions, clonal reproduction, metabolomics, polyploidy

Summary

Biological invasions impose ecological and economic problems on a global scale, but also provide extraordinary opportunities for studying contemporary evolution. It is critical to understand the evolutionary processes that underly invasion success in order to successfully manage current invaders, and to prevent future invasions. As successful invasive species sometimes are suspected to rapidly adjust to their new environments in spite of very low genetic diversity, we are obliged to re-evaluate genomic level processes that translate into phenotypic diversity. In this paper, we review work that supports the idea that heritable trait variation, within and among invasive populations, can be created through epigenetic or other non-genetic processes, particularly in clonal invaders where somatic changes can persist indefinitely. We consider several processes that have been implicated as adaptive in invasion success, focusing on various forms of “genomic shock” resulting from exposure to environmental stress, hybridization and whole-genome duplication (polyploidy), and leading to various patterns of gene expression re-programming and epigenetic changes that contribute to phenotypic novelty. These mechanisms can contribute to transgressive phenotypes, including hybrid vigor and novel traits, and may thus help to understand the huge successes of some genetically impoverished clonal plant invaders.

Keywords: biological invasions, clonal plants, DNA methylation, hybridization, polyploidy, rapid evolution

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Introduction

Phenotypic variation fuels successful response of organisms to environmental challenges, and a lack thereof would thus seem to be a universal obstacle for introductions of species to new habitats (Sakai *et al.* 2001; Allendorf & Lundquist 2003). Species are generally thought to be introduced to new ranges by only limited numbers of individuals and therefore to undergo genetic bottlenecks that reduce genetic variation compared to their native range. This type of bottleneck is expected to result in inbreeding depression and decreased evolutionary potential, presenting a “genetic paradox” for understanding the successful plant invaders and their adaptation to new habitats (Allendorf & Lundquist 2003; Estoup *et al.* 2016).

Our understanding of the importance of genetic bottlenecks is rooted in the Modern Synthesis of evolutionary theory, which asserts that genes (defined by DNA sequence) are the sole source of heritable phenotypic variation, and that inheritance of environmentally-induced non-genetic variation is impossible (Keller 2014; Bonduriansky & Day 2018; Müller 2017; Stoltzfus 2017). The recovery of genetic variation has therefore long been considered an important driver of successful invasions (Baker & Stebbins, 1965). However, applications of genomics approaches have revealed the actual genetic make-up of invasive populations and refined our views of genetic diversity and evolutionary processes during invasions. First, comparative studies in the native and introduced species ranges suggest that the genetic paradox may not be as severe as initially thought because many invasive populations undergo only modest reductions in genetic variation due to multiple introductions or hybridization (Estoup *et al.* 2016). Moreover, loss of diversity measured by molecular markers does not necessarily reflect loss of quantitative trait variation, or may reflect successful response to selection to the novel habitat from an initially higher diversity of founding genotypes. Genetic bottlenecks can also contribute to performance by purging deleterious alleles, revealing beneficial cryptic variation or creating new beneficial interactions among genomic elements (Colautti & Lau 2015; Dlugosch *et al.* 2015; Estoup *et al.* 2016; van Kleunen *et al.* 2018).

In addition to genetic marker studies, accumulating whole-genome sequence data from various species allows us a more nuanced understanding of genome dynamics. One important insight is the prominence of genomic redundancy, largely resulting from multiple episodes of genome duplication (polyploidy) followed by genome fractionation and diploidization processes (Doyle *et al.* 2008; Freeling 2009; Wendel *et al.* 2016), which play a major role in plant diversification and adaptation (Van de Peer *et al.* 2017). Duplicated genes (homeologs) can exhibit various patterns of non-additive expression compared to their homologous genes in parental species, creating intragenomic functional plasticity even in the absence of inter-individual genetic variation. Another area of progress is on the effects of the “genomic shock” resulting from interspecific hybridization and polyploidy, which creates gene expression re-programming and phenotypic novelty (McClintock 1984; Comai 2005; Chen & Yu 2013; Wendel *et al.* 2016). However, despite abundant DNA sequence information for a variety of organisms, and information about broad patterns of genetic diversity on the landscape, biologists generally have only a limited understanding of the actual molecular underpinnings (*e.g.* the 'black box') of organismal responses to complex biotic and abiotic factors (Pigliucci 2010; Keller 2014).

Ultimately evolutionary response to challenging environmental conditions relies on *heritable* phenotypic variation, regardless of the underlying mechanisms of heritability, and we now have evidence that the structural and functional dynamics of genomes along with a variety of epigenetic and other non-genetic effects can affect heritable variation and thus contribute to adaptation (Johannes *et al.* 2009; Kooke *et al.* 2015;

Richards *et al.* 2017; Bonduriansky & Day 2018). Recent efforts have particularly addressed the ‘black box’ of the translation from genotype to phenotype by exploring intermediate molecular-level phenomena. For example, genome-level processes are often mediated by epigenetic changes (chromatin modifications, DNA methylation, small RNAs), which can vary among individuals within populations and be selected for, much like genetic variation, and serve as an additional source of heritable variation (Becker & Weigel, 2012; Richards *et al.* 2017). Changes in DNA methylation are known to be associated with allopolyploidization (*e.g.* Madlung *et al.* 2002; Salmon *et al.* 2005; Sehrish *et al.* 2014; Li *et al.* 2019), exposure to environmental stress (Verhoeven *et al.* 2010), different habitat types or shifts in species ranges (Xie *et al.* 2015; Foust *et al.* 2016; Gugger *et al.* 2016; Keller *et al.* 2016), and with variation in plant phenotypes (Cortijo *et al.* 2014; Kooke *et al.* 2015; Zhang *et al.* 2018). Epigenetic variation in turn can regulate differential gene expression and transposable elements (TE) activation or repression (Underwood *et al.* 2017; Niederhuth & Schmitz 2017; Cavé-Radet *et al.* 2020). The importance of TE activity in the context of biological invasion is still largely unexplored (reviewed in Stapley *et al.* 2015; but see Niu *et al.* 2019), but several studies have explored how differential gene expression underlies variation in ecologically important traits (reviewed in Alvarez *et al.* 2015; *e.g.* Hodgins *et al.* 2013; Turner *et al.* 2017; Xu *et al.* 2019). Particularly relevant in the context of biological invasions, changes in gene expression can translate into variation in secondary metabolism, which combines into complex phenotypes that can be finely tuned and provide a diverse array of appropriate responses to environmental challenges (Kooke & Keurentjes 2012; Kooke *et al.* 2019).

These possible contributions of genome dynamics to phenotypic variation and adaptation are particularly intriguing and relevant for invasion biology because some extremely invasive clonal plant species have almost no detected genetic diversity even after they become well established, *e.g.* knotweeds in the US (Richards *et al.* 2012) and Europe (Parepa *et al.* 2014; Zhang *et al.* 2016; Holm *et al.* 2018), alligator weed (*Alternanthera philoxeroides*) in China (Xu *et al.* 2003; Geng *et al.* 2007), *Spartina anglica* in Europe (Baumel *et al.* 2001; Ainouche *et al.* 2004) and water hyacinth (*Eichhornia crassipes*) outside of South America (Zhang *et al.* 2010). Researchers attempting to explain the huge success of these species often argue for the importance of phenotypic plasticity (“general-purpose genotype”; Baker 1965; Loomis & Fishman 2009; Oplaat & Verhoeven 2015), which could be mediated by epigenetic effects that translate into gene expression and changes in plant chemistry and other phenotypes (Nicotra *et al.* 2010; Richards *et al.* 2010a, 2017; Sultan 2015; Banta & Richards 2018; Kooke *et al.* 2019). Many of the hypotheses that attempt to explain variation in invasion success involve genetic or plastic response to novel biotic interactions, often associated with changes in secondary metabolites (Müller-Schärer *et al.* 2004; Joshi & Vrieling 2005; Lankau *et al.* 2009; Mitchell *et al.* 2006; Macel *et al.* 2014).

In the present paper, we take advantage of work done in plant invaders to outline how epigenetics may impact phenotypes and adaptation of species in their native versus introduced range. We specifically discuss how epigenetic variation can translate into transcriptomic and metabolomic variation, with a special focus on the biotic interactions of invasive plants and how epigenetic mechanisms can facilitate plant invasion by providing sources of variation to clonal plants, or novelty through hybridization and polyploidization.

Rapid adaptation during plant invasion

In spite of all of the progress on understanding genomic level processes during species introductions, the ultimate goal of invasion biology is to understand successful invasions, and for this we need to also consider the traits of invaders, their biotic interactions, and how these are linked to the fitness advantages of invaders,

and thus adaptation. Below we briefly summarize some of the key ecological-evolutionary hypothesis for plant invasion success, and suggest links to underlying genomic processes.

Several hypotheses in the invasive species literature have examined how biotic interactions contribute to increased fitness of invasive species in their introduced ranges. The Enemy Release Hypothesis (ERH; Keane & Crawley, 2002) proposes that escape from native herbivores and other specialist enemies explains the success of many exotic species. In complement, the Evolution of Increased Competitive Ability hypothesis (EICA; Blossey & Nötzold, 1995) assumes that after enemy release the invasive plants reallocate resources and rapidly evolve toward less defended but more vigorous ecotypes, as reported e.g. in *A. philoxeroides* (Zhang *et al.* 2019b).

An extension of EICA is the shifting-defense hypothesis (SDH; Müller-Schärer *et al.* 2004, Müller, 2018). The SDH postulates an evolutionary shift towards plant defenses against generalist instead of specialist herbivores (*i.e.* secondary plant metabolites like flavonoids or glucosinolates; through a trade-off from quantitative to qualitative defenses). Several metabolomic analyses have found invasive species to harbor more total secondary metabolites in invasive populations than in their native range (*e.g.*, Thelen *et al.* 2005; Macel *et al.* 2014; Lin *et al.* 2015; Zhang *et al.* 2018b; Wan *et al.* 2019).

While the shifting-defense hypothesis was an improvement over the EICA hypothesis, the evolution of plant defenses during invasions is even more complex. On the one hand, plant defense can involve both resistance and tolerance mechanisms, where resistance generally reduces damage to plants (Strauss *et al.* 2002), but tolerance mitigates the fitness impact of the damage, *e.g.* through rapid re-growth (Strauss & Agrawal 1999). On the other hand, resistance mechanisms can be either constitutive, *i.e.* constantly present, or only induced by herbivore attack (Karban & Baldwin 1997). Previous EICA or SDH studies have rarely evaluated the entire breadth of defense mechanisms (Liu *et al.* 2020), but those that did usually found more complex evolutionary changes. For instance, a recent SDH study on invasive *Spartina alterniflora* in China found increased resistance (= poorer herbivore performance) but lower tolerance to generalist herbivores in invasive populations (Ju *et al.* 2019).

Evolutionary changes in the chemistry of invasive plants can contribute to so-called ecological or evolutionary traps for native species where animal populations can show maladaptive behavior in response to the introduced plants (Schlaepfer *et al.* 2002, 2005; Battin 2004; Hale & Swearer 2016; Robertson & Blumstein 2019). For instance, when invasive plants are more attractive than native host plants, then herbivores in the invaded range may experience reduced fitness. The phenomenon was recently described for invasive *Spartina alterniflora* and the native herbivorous moth *Laelia coenosa* in China, where the levels of alkaloids and phenolics in *S. alterniflora* compared to the native host *Phragmites australis* were associated with reduced herbivore performance (Sun *et al.* 2020). Sun *et al.* (2020) suggested that volatile organic compounds (VOCs) attracted insect oviposition, but plant nutritional and defense (secondary metabolites) traits ultimately reduced the fitness of these natural enemies. In another example, cardenolide concentrations of an introduced *Asclepias* species were associated with reduced fitness of the specialist herbivore *Danaus plexippus* (Faldyn *et al.* 2018). A recent meta-analysis by Yoon & Read (2016) reported numerous additional studies supporting the idea of such ecological traps during plant invasion.

Ultimately, we would like to understand the genomic mechanisms that underly the responses to novel biotic interactions described above, and in particular the potential contribution of epigenetic processes. Although so far, to our knowledge, no study exists that fully encompasses genomic and epigenomic data to metabolome, biotic interactions and plant fitness, we have evidence for several important pieces of this puzzle.

For instance, numerous transcriptomic, epigenetic and metabolomic profiling studies have supported the correlation of these mechanisms with herbivory. In *Arabidopsis thaliana*, herbivory-induced changes in gene expression involved up- and down-regulated genes in plant secondary metabolism networks, hormone signaling pathways or plant defense related genes (Ehrling *et al.* 2008; Davila Olivas *et al.* 2016). Changes in expression patterns of genes involved in plant defense against herbivory were also observed in *Populus* (Babst *et al.* 2009) and *Solanum* (Kariyat *et al.* 2012; Lortzing *et al.* 2017) and in the invasive species *Ambrosia artemisiifolia* (Hodgins *et al.* 2013) and *Solidago canadensis* (Xu *et al.* 2019). Likewise, some studies in non-invasive species have linked epigenetic variation to herbivory. Herrera & Bazaga (2011) found methylation polymorphisms to be correlated with herbivory damage in *Viola cazortensis*, and Kellenberger *et al.* (2016) reported herbivory-associated changes in DNA methylation in *Brassica rapa*. In herbivore-infested plants and when herbivory was simulated by methyl jasmonate exposure, DNA demethylation was correlated with changes in floral signaling to pollinators. Similarly, in *A. thaliana* response to plant defense hormones like jasmonic acid and salicylic acid were shown to be correlated with differences in DNA methylation among epigenetic recombinant inbred lines (epiRILs; Zhang *et al.* 2018a; Latzel *et al.* 2012). Other studies in *A. thaliana* have shown that histone modifications, DNA methylation, or RdDM (RNA-directed methylation by small RNAs) are correlated with the expression of chemical defenses such as glucosinolates and flavonoids (Rasmann *et al.* 2012; Shen *et al.* 2012; Xue *et al.* 2015; Aller *et al.* 2018), supporting a role of these epigenetic mechanisms in shifting defenses.

The idea that epigenetic signatures may correlate with invasion relies partly on the assumption that changes in DNA methylation are involved in the regulation of gene expression, particularly since methylation of gene promoters has been associated with gene silencing (reviewed in Paun *et al.* 2019). However, studies over the last 10 years do not always support this idea since many transcription factors show increased DNA binding affinity for methylated DNA (de Mendoza *et al.* 2020). Although DNA methylation of the 5-prime end of genes has been correlated with gene silencing in plants, the functional relevance of gene body methylation varies by context and across taxa, and it is not always correlated to gene expression (Niederhuth *et al.* 2016; Bewick & Schmitz 2017; Niederhuth & Schmitz 2017). Changes in gene expression have also been shown to cause variation in patterns of DNA methylation (Meng *et al.* 2016; Feldman *et al.* 2013), *e.g.* in nearby TEs (Secco *et al.* 2015).

Considering that many of the interactions between plants and herbivores are mediated by secondary chemistry, metabolomic approaches could provide an opportunity to better understand the translation of genomic variation into plant success in novel environments. With appropriate experimental designs, metabolomic analyses can provide information on how plant secondary chemistry is induced by abiotic and biotic environmental challenges and is a functional readout of genome-level processes complementary to transcriptomic studies. Metabolomics approaches have already offered mechanistic support for the SDH hypothesis through surveys that showed herbivory impacts on the production of defense metabolites (Macel *et al.* 2014; Tewes *et al.* 2018; Müller *et al.* 2020). Still, how genomic and epigenomic variation translates into

variation in metabolites and, as a consequence, interactions with herbivores and invasion success, has been largely unexplored. This is partly because interactions between transcriptomic and metabolomic changes can be difficult to identify since the relationships between gene networks and metabolite pathways are complex.

In *Arabidopsis*, studies of epiRILs have identified epigenetic QTL underlying response to herbivore attack, providing evidence that methylation is involved in the control of secondary metabolism (Kooke *et al.* 2019). Differences in glucosinolates, flavonoids, and additional metabolites among epiRILs support the importance of variation in DNA methylation in plant responses to herbivory. In *Brassica* hybrids, the integration of transcriptome and metabolome data allowed for investigation of enhanced flavonoid and glucosinolates production, but no details about epigenetic variation were surveyed (Zhang *et al.* 2019a). Such analyses are much more challenging in non-model species without extended genomic resources, but more restricted approaches such as methylation sensitive AFLP or epigenotyping by sequencing (epiGBS) coupled with untargeted metabolomics could nevertheless provide important insights (Thiebaut *et al.* 2019). Combining (epi)genomic and metabolomic analyses in an integrative approach will reveal new understanding of the molecular mechanisms underlying exotic species responses to biotic interactions.

Clonal plant invasions

Besides a possible general contribution to plant adaptation, another main reason why epigenetics could play a role in plant invasions is that epigenetic changes are much more persistent in clonal plants, and clonal growth is particularly common among invasive plant species. If epigenetic variation can provide a source of phenotypic variation within clones, which translates into fitness differences, it could contribute to invasion success (Figure 1). Some of the world's most successful invasive plants are thought to be entirely genetically uniform in their introduced ranges. Among the 468 invasive plants from the IUCN Global Invasive Species Database (<http://www.issg.org/database>) 70% reproduce clonally. Out of the 37 plants included in the well-known list of 100 worst invasive species (Luque *et al.* 2014), 30 reproduce clonally, and for nine it is the main mode of reproduction in their introduced range. In a survey of invasive plants in China, Liu *et al.* (2006) found that almost half (44%) of the 126 invasive plants studied were clonal, and among the 32 most invasive ones the fraction of clonal plants was even 66%. The high frequency of clonality among invasive plants suggests that this mode of reproduction is beneficial for plant invasion.

One of the best-known cases of an invasive clonal plant is Japanese knotweed (*Reynoutria japonica* aka *Fallopia japonica*), where a single octoploid clone has spread aggressively through a broad range of habitats in temperate Europe and North America (Beerling *et al.* 1994; Bailey & Conolly 2000; Grimsby *et al.* 2007; Gerber *et al.* 2008; Bailey *et al.* 2009; Richards *et al.* 2012). In the United States, Richards and colleagues found only individuals of the same single AFLP haplotype of *R. japonica* that is the only one present throughout Europe, while 12 other populations were made up of only a few haplotypes of the hybrid hexaploid species *R. ×bohemica* (Richards *et al.* 2012). They reported that some individuals of each haplotype were found in beaches and marshes— novel habitats from the perspective of Japanese knotweed— with epigenetic variation correlated to the different habitats (Richards *et al.* 2012; Robertson *et al.* 2020). Another study across central Europe confirmed that all individuals of *R. japonica* belonged to one haplotype, but different populations harbored significant epigenetic and phenotypic variation which was associated with climate of origin and thus possibly related to adaptation (Zhang *et al.* 2017).

Another group of clonal species that provides intriguing cases of successful invasion is represented by several members of the polyploid genus *Spartina*. The molecular evolutionary history of the *Spartina* genus has been investigated well by Ainouche and colleagues (Baumel *et al.* 2002; Fortune *et al.* 2007; Rousseau-Gueutin *et al.* 2015; Salmon & Ainouche 2015). Cases of well-documented intercontinental invasions are illustrated in *S. alterniflora*, *S. anglica*, and *S. densiflora* (Ainouche *et al.* 2009; Strong & Ayres 2013; Ainouche & Gray 2016). Unlike in the case of Japanese knotweed, the hexaploid *S. alterniflora* has been studied extensively in its native range (North American Atlantic and Gulf Coasts), providing some insight into the potential mechanisms underlying its invasive abilities (Pomeroy & Weigert 1981; Pennings & Bertness 2001). *Spartina alterniflora* is a critical foundation species that supports fisheries, provides storm protection, and has a broad environmental tolerance (Pennings & Bertness 2001; Richards *et al.* 2005). The species is adapted to anoxic and salt conditions, and is highly tolerant to reduced, sulfidic sediments, and oil/PAH pollution (Pennings & Bertness 2001; Maricle *et al.* 2006, 2009; Robertson *et al.* 2017; Alvarez *et al.* 2018, 2020; Cavé-Radet *et al.* 2019). Like other marsh species, *S. alterniflora* exhibits extensive variation in these traits across habitats, and a range of ecological studies have shown that traits of native *S. alterniflora* are correlated to the environmental heterogeneity of salt marshes (Bertness & Ellison 1987; Pennings & Bertness 2001; Richards *et al.* 2005). More recently, several studies have also found correlations between DNA methylation and habitat or oil pollution (Foust *et al.* 2016; Robertson *et al.* 2017; Alvarez *et al.* 2020).

From the Atlantic North American Coast, *S. alterniflora* colonized the South American Atlantic Coast (Argentina), where it is now well-established (Bortolus *et al.* 2015). The species was also introduced to California (Strong & Ayres 2013), Western Europe (Ainouche *et al.* 2009), South Africa (Adams *et al.* 2012), and China, where its spread is particularly spectacular (Li *et al.* 2009). Clonal propagation seems to have contributed to the spread of this otherwise wind-pollinated perennial species in many cases (Davis *et al.* 2004; 2019; Maebara *et al.* 2020; but see Qiao *et al.* 2019; Shang *et al.* 2019). Although Chinese populations appear to be genetically diverse (Qiao *et al.* 2019; Shang *et al.* 2019), the introduction from China to Japan so far has resulted in a lack of diversity in the Japanese populations suggesting both founder effect and predominantly clonal propagation (Maebara *et al.* 2020). Other invasive *Spartina* species spread extensively by clonal means, such as *S. patens* (syn. *S. versicolor*; Baumel *et al.* 2016) introduced from North America to Europe (Sanchez *et al.* 2019) and *S. anglica*, which has expanded in Europe and is now introduced on several continents (Baumel *et al.* 2001; Ainouche *et al.* 2009). However, this allododecaploid species may maintain high intra-genomic diversity, which can contribute to the evolution of gene expression repatterning even within a single clone (Ainouche *et al.* 2012; Chelaifa *et al.* 2009; Feirreira de Carvalho *et al.* 2017).

Other prominent examples of nearly genetically uniform clonal plant invaders are the South American alligator weed (*Alternanthera philoxeroides*; Geng *et al.* 2007), “Bermuda buttercup” (*Oxalis pes-caprae*; Ornduff 1987), hawkweed (*Hieracium aurantiacum*; Loomis & Fishman 2009), crimson fountain grass (*Pennisetum setaceum*; Le Roux *et al.* 2007), and water hyacinth (*Eichhornia crassipes*; Zhang *et al.* 2010). There are many more successful clonal plant invaders that have not yet been studied at the molecular level, even though clonality has been found to be overrepresented among invasive plants (*e.g.* Liu *et al.* 2006).

Several authors have argued that epigenetic mechanisms could be particularly important for invasive species that are clonal or have low genetic diversity since they could provide a non-genetic source of heritable variation (Figure 1), and because clonal reproduction “bypasses” the resetting of epigenetic effects that is

thought to occur through meiosis (although this resetting is not universal, see Feng *et al.* 2010; Herrera *et al.* 2013, 2014; reviewed in Verhoeven & Preite 2014; Douhovnikoff & Dodd 2015; Liebl *et al.* 2015; Rollins *et al.* 2015; Richards *et al.* 2017). However, although there are compelling arguments for the importance of epigenetic effects in invasive clonal plants (Verhoeven & Preite 2014; Douhovnikoff & Dodd 2015; Richards *et al.* 2017), so far all studies of clonal plant invasions have been limited by a lack of genomic information. This is important because whole genome studies in the model plant *Arabidopsis thaliana* and in human cancers showed how quickly novel epigenetic variation can be generated, and can be dramatically shaped by *de novo* sequence mutation. For example, we know that even single nucleotide polymorphisms can have a remarkable impact on the methylome (Becker *et al.* 2011; Timp & Feinberg 2013; Dubin *et al.* 2015; Feinberg *et al.* 2016; Sasaki *et al.* 2019). Therefore, the low levels of somatic mutations cannot be dismissed, and could contribute to the rapid generation of epigenetic variation in natural clonal lineages. This is particularly true since several studies have reported that high rates of somatic mutation may allow asexual species to maintain abundant genetic variation and adapt to changing environmental conditions (Lynch *et al.* 1984; Gill *et al.* 1995; Schoen & Schulz 2019).

Deciphering the contributions of genetic and epigenetic variation to invasion success is consequently complicated even in clonal plants (Richards *et al.* 2017; *e.g.* Robertson *et al.* 2020). A recent study described somatic mutation within a single tree of *Populus trichocarpa* to be only slightly lower than the seed-to-seed mutation rate observed in *A. thaliana* lines (Hofmeister *et al.* 2019). Other studies have reported that structural and regulatory mutations can have large effects on phenotype, and mutation may be common enough to fuel adaptation even in the short time frame of an invasion (Colautti & Lau 2015; Dlugosch *et al.* 2015; Stapley *et al.* 2015). This is thought to be particularly true for the multi-locus traits which have increased opportunities for mutations to occur (Lande 2015). Dlugosch *et al.* (2015) argued that in the introduced range a greater range of mutations may be advantageous, and fast population growth provides more opportunities for new mutations to become fixed. They also argue that copy number variation (CNV) mutations occur almost as often as point mutations but more frequently contribute to beneficial phenotypes (Dlugosch *et al.* 2015; Estoup *et al.* 2016). Further, transposable elements activated by environmental stress can involve epigenetic processes, create novel genetic variation and further contribute to adaptation (reviewed in Stapley *et al.* 2015; Estoup *et al.* 2016).

Contribution of hybridization and polyploidy to invasive potential

Hybridization and polyploidy are known to be significant drivers of speciation and genetic diversity in plants (reviewed in Soltis *et al.* 2009; Wendel 2015; Van de Peer *et al.* 2017) and occur frequently throughout plant evolution (Wood *et al.* 2009; Alix *et al.* 2017). Like the pervasiveness of the clonal reproductive strategy in invasive plants, a growing number of studies have emphasized the potential importance of these genome level processes in invasions (Schierenbeck & Ainouche 2005; Pandit *et al.* 2011; Bock *et al.* 2015; Colautti & Lau 2015). In a systematic review and meta-analysis, Hovick & Whitney (2014) found that in 14 established hybrid plant taxa, the hybrids were significantly more fecund and larger than their parental taxa. In a global analysis of plant species, Pandit *et al.* (2011) compared ploidy level and chromosome number in 81 invasive species and 2356 of their congeners, and found that invasive species were disproportionately likely to be polyploid, while rare and endangered plants are generally more likely to be diploid (see also Dar *et al.* 2020).

Hybridization is generally thought to facilitate successful invasions through the transgressive segregation of traits, whereby extreme novel phenotypes are produced through the recombination of parental alleles (te

Beest *et al.* 2012; Gallego-Tévar *et al.* 2018; Kagawa & Takimoto, 2018; Qui *et al.* 2020). Even intraspecific hybridization can facilitate successful invasions through increasing genetic diversity and heterosis (*e.g.* *S. alterniflora*; Strong & Ayres 2013; Qiao *et al.* 2019; Shang *et al.* 2019). Kagawa and Takimoto (2018) modeled transgressive segregation in theoretical hybrid species and found that adaptive radiation into suitable novel niches was most likely to occur in hybrid offspring from parental species with moderate genetic differentiation (Kagawa & Takimoto, 2018; Qui *et al.* 2020). However, several recent studies support that hybridization between closely related lineages within species, between more divergent lineages within species or between species can contribute to standing levels of diversity, transgressive segregation, increased heterozygosity or purging of deleterious alleles (Bock *et al.* 2015; Colautti & Lau 2015). In addition, introgression following recurrent backcrosses between hybrids and the parental species can contribute to the invasion process (Currat *et al.* 2009), which has been particularly well-documented in European oak species (*Quercus petraea* and *Q. robur*; Petit *et al.* 2004). The vigorous introgressant hybrids between *S. alterniflora* and the native *S. foliosa* in California exhibited greater male fitness (viable pollen production of the hybrid was 400 times that of the native plants) and they rapidly invaded the San Francisco Bay area (Ayres *et al.* 2008).

Broad ecological tolerance is also generally reported in polyploid species (Stebbins 1985; Levin 1983; te Beest *et al.* 2012; Rosche *et al.* 2016; Nagy *et al.* 2017; Dar *et al.* 2020), and may be attributed to a large range of mechanisms, involving intrinsic (*e.g.* history and genome dynamics) or external (*e.g.* selective) evolutionary forces. Polyploids may arise from diverse pathways in natural populations (Ramsey & Schemske 2002), ranging from autopolyploidy (genome duplication within species) to allopolyploidy (hybrid genome duplication), resulting in duplication of more or less divergent genomes (Doyle *et al.* 2008). The relative abundance of auto- versus allopolyploids has been much debated (reviewed in Barker *et al.* 2016), but ecological success and invasiveness has been widely correlated with allopolyploidy. For example, major grassland ecosystems of the planet appear to be dominated by allopolyploids (Estep *et al.* 2014). Allopolyploids combine the heterosis effects that are a consequence of hybridization, with the fertility, genetic redundancy and plasticity provided by genome duplication. At the genomic level, these two components of the allopolyploid speciation process (namely differentiated genome merger and genome redundancy) have important, though different consequences, particularly with regard to epigenetic consequences.

In practice, the importance of hybridization and polyploidization in invasions can be difficult to tease apart (Bock *et al.* 2015), particularly since some estimates suggest that greater than 70% of angiosperms have undergone polyploidization in their evolutionary history (Wood *et al.* 2009) and allopolyploidy involves both hybridization and genome duplication (Salmon *et al.* 2005; Salmon & Ainouche 2015). The formation of hybrids and polyploids results in wide-scale genomic changes sometimes referred to as 'genomic shock' due to the processes involved in the merging of genomes or whole genome duplications, as well as subsequent deletions of genomic regions, and chromosomal rearrangements (Chen 2007; Otto 2007). While these alterations are often maladaptive, occasionally these processes can mask deleterious mutations through gene redundancy, release constraints on gene function, or result in offspring that exhibit heterosis, thereby increasing the potential for adaptive radiation and invasion success (Chen 2007; Sémon & Wolfe, 2007; te Beest *et al.* 2012; Kagawa & Takimoto, 2018; Qui *et al.* 2020).

Young hybrid and polyploid complexes appear to be particularly relevant in rapid range expansion (*e.g.* in knotweeds, Mandák *et al.* 2005; Bailey *et al.* 2009; Walls 2010; in *Phragmites australis*, Clevering & Lissner 1999;

Lambertini *et al.* 2012; Saltonstal *et al.* 2014; Liu *et al.* 2020; in *Spartina*, Ainouche *et al.* 2009; Strong & Ayres 2013; Ainouche & Gray 2016), which suggests a major immediate ecological consequence of hybridization and genome doubling. The recent hybridization and genome duplication events that occurred in genus *Spartina* provide an excellent opportunity to explore such questions. Comparisons between the F1 hybrid *S. x townsendii* (resulting from hybridization between the hexaploids *S. maritima* and *S. alterniflora*) and its allododecaploid derivative *S. anglica*, which formed in the 19th century, allow for distinguishing the effects of hybridization and genome duplication *per se* (Ainouche *et al.* 2004). During the allopolyploidization process, hybridization (rather than genome doubling) appears to have induced major DNA methylation alterations in *S. x townsendii*, which were transmitted to the invasive allododecaploid *S. anglica* (Salmon *et al.* 2005). Most of these changes affected regions flanking transposable elements (Parisod *et al.* 2009), but post-transcriptional gene regulation (via microRNAs), as well as repeat-associated small interfering RNA (targeting repetitive sequences) changes were also detected following genome merger and genome duplication (Cavé-Radet *et al.* 2020).

The parental hexaploid genomes have similar repetitive DNA contents (*c.a.* 45%) but higher amounts of transposable elements are found in *S. maritima* (*c.a.* 751 Mb/2C) than in *S. alterniflora* (724 Mb/2C; Giraud *et al. in press*). Transcriptomic analyses indicated transposable element repression following hybridization and genome duplication, which is congruent with previously reported changes in DNA methylation (Giraud *et al. submitted*). Epigenetic control of transposable elements has been shown to affect the expression of neighboring genes (*e.g.* Hollister *et al.* 2010), and in *Spartina* both hybridization and genome doubling entailed gene expression evolution, with non-additive parental expression patterns affecting genes involved in stress tolerance and epigenetic regulation (Chelaifa *et al.* 2010, Giraud *et al. submitted*). Non-additive patterns of parental expression contributed to enhance gene expression plasticity and adaptive responses to fluctuating environments observed in the allopolyploid populations (Ferreira de Carvalho *et al.* 2017). The increased tolerance to xenobiotic stress recently reported in *S. anglica* compared to its parental species could also be partly due to these novel expression patterns (Cavé-Radet *et al.* 2019)

Other studies in *Spartina* suggest that these species have high stress tolerance and increased phenotypic variation and tend to occur more frequently in newly created, harsh, and recently disturbed environments (Grewell *et al.* 2016). Further, phenotypic plasticity in newly formed hybrids promotes niche expansion (Ainouche & Jenczewski 2010; te Beest *et al.* 2012; Grewell *et al.* 2016; Banerjee *et al.* 2019). The vigorous intercontinental invader *S. densiflora* is a heptaploid created from hybridization between a hexaploid and a tetraploid species, and is native to the south-American Atlantic coast (Fortune *et al.* 2008). Grewell *et al.* (2016) reported high phenotypic plasticity in response to salinity in invasive populations of *S. densiflora* on the Pacific Coast of North America, but an examination of the F1 offspring of *S. maritima* and *S. densiflora* showed that *Spartina* hybrids have even greater tolerance to salinity than their parental species (Gallego-Tévar *et al.* 2018). In California, where *S. densiflora* hybridized with the native *S. foliosa*, the hybrids exhibit higher salt stress tolerance than their parents (Lee *et al.* 2016). *Spartina densiflora* has also invaded the southern coasts of Iberian Peninsula, hybridized with the native *S. maritima* and produced hybrids that grow better than the parent species in most cases (Castillo *et al.* 2010).

Precisely how polyploidy and hybridization might influence invasion success is highly dependent on introduction histories, the stages through which an invasion proceeds, and whether these microevolutionary

processes exist within a founding population or arise later as a result of introduction and the subsequent stress of competing in a novel environment (te Beest *et al.* 2012; Suda *et al.* 2015). The apparent association of hybridization or increased ploidy with traits that appear to impart invasiveness may not reflect causal linkages. Detecting these linkages may be challenging since traits with high adaptive potential at one life stage could be deleterious either at another life stage or under diverse environmental conditions (Suda *et al.* 2015; Martinez *et al.* 2018). Ploidy level and hybridization are both known to affect cell size and biomass (Bashir *et al.* 2014; Corneillie *et al.* 2019; Wu *et al.* 2019), as well as changes in seed weight and size, suggesting that each could play a role in vegetative and reproductive trait variation (Song & Chen, 2015). Polyploidization is also known to result in changes in flowering phenology between diploid and polyploid cytotypes (te Beest *et al.* 2012). This partitioning influenced the persistence of a novel cytotype of *Anacamptis pyramidalis* that might otherwise have been outcompeted by its diploid progenitor (Pegoraro *et al.* 2019). Niche differentiation of allopolyploid species relative to their progenitors could help explain the abundance of invasive allopolyploid hybrids (te Beest *et al.* 2012).

A growing body of evidence supports that these evolutionary phenomena are important for successful plant invasions (Schierenbeck & Ellstrand, 2009; te Beest *et al.* 2012; Welles & Ellstrand, 2016; Rosche *et al.* 2017; Wu *et al.* 2020). Anthropogenic forces such as the global plant trade, increased land use change, habitat fragmentation, and climate change have been proposed to increase opportunities for hybridization and polyploidization events that lead to invasiveness (Schierenbeck & Ellstrand, 2009). These forces create novel environments and shape new ecological niches that existing and novel hybrids and polyploids may exploit (Van de Peer *et al.* 2017; Banerjee *et al.* 2019). New tools and approaches are now available for better understanding of the molecular mechanisms underlying hybridization and polyploidy in plant invasion success; such studies so far remain limited to a few model systems or rely mostly on phenotypic associations that accompany changes in ploidy without identifying the underlying molecular mechanisms (Van de Peer *et al.* 2017).

Conclusions

In studies of natural populations and through ecological experiments, we have some level of information about how genomic and epigenetic mechanisms (mainly DNA methylation) may contribute to organismal response to environmental challenges, but these ideas have only rarely been applied to the understanding of secondary chemistry or invasions. Further, most of our knowledge about ecological epigenetics is fairly coarse grained and lacking critical fine-scale genomic context and understanding of the dynamics involved in processes of hybridization and polyploidization— processes that are often involved in invasion. Better understanding of the other molecular epigenetic mechanisms, like the action of small RNAs, chromatin modifications, and cellular location is required to truly flesh out how epigenetic mechanisms interact with each other to contribute to heredity along with genetic and other non-genetic mechanisms that ultimately translate into organismal performance (Keller *et al.* 2014). In addition, we know little about the translation of genomic and epigenomic differences into other molecular level phenotypes like gene expression and metabolites. Unravelling the role of epigenetics in plant biotic interactions is challenging, and has received particularly little attention in studies of plant invasion (Alonso *et al.* 2019). Although the genetic and epigenetic bases underlying defense mechanisms of invasive plants are virtually unexplored, increased access to omics approaches and tools to analyze (epi)genetic markers are providing novel insights for this perspective. Integrating epigenetics, expression, and defense chemical production (*i.e.* metabolome) to predict

molecular level mechanisms involved in invasion could provide novel insights for understanding plant defense strategies in response to native enemies.

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Genetic and non-genetic information contributes to phenotype

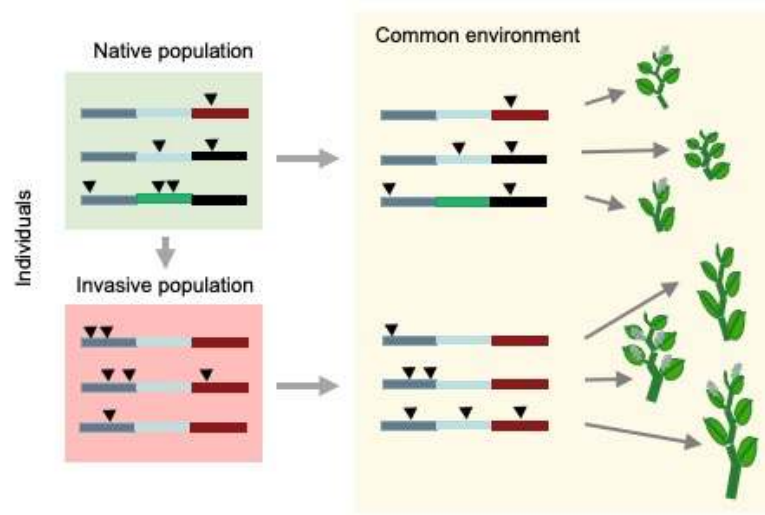


Figure 1. Hypothetical relationships between genetic, epigenetic, and phenotypic variation in invasive compared to native populations. Three segments of the genome are shown for each of three individuals from native (top panel) and invasive (lower panel) populations. The horizontal bars are the DNA, with differences in DNA sequence indicated by different colors. Epigenetic modifications at a particular gene are indicated by the black triangles. Natural epigenetic variation may be found within or between ranges. Epigenetic variation can be independent of or confounded with genetic variation. Some epigenetic variation in natural populations may be plastic and may therefore be non-heritable, i.e. it will not persist in a common environment. If independent epigenetic variation persists in a common environment, this is evidence for epigenetic inheritance. If this heritable epigenetic variation translates into phenotypic and fitness differences (as illustrated above), it could contribute to invasion success (modified from Bossdorf et al. 2008).