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The effects of genome duplications in a community context

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Summary

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Whole-genome duplication (WGD), or polyploidy, has important effects on the genotype and phenotype of plants, potentially altering ecological interactions with other organisms. Even though the connections between polyploidy and species interactions have been recognized for some time, we are only just beginning to test whether WGD affects community context. Here I review the sparse information on polyploidy and community context and then present a set of hypotheses for future work. Thus far, community-level studies of polyploids suggest an array of outcomes, from no changes in community context to shifts in the abundance and composition of interacting species. I propose a number of mechanisms for how WGD could alter community context and how the emergence of polyploids in populations could also alter the community context of parental diploids and other plant species. Resolving how and when these changes are expected to occur will require a deeper understanding of the connections among WGD, phenotypic changes, and the direct and indirect effects of species interactions.

I. Introduction

Whole-genome duplication (WGD) has long been recognized as a fundamental mechanism of diversification in plants. Polyploidy, or the state of having more than two chromosome sets, is exceedingly pervasive throughout the history of plant evolution. For example, all extant angiosperms can be traced to a polyploid ancestor (e.g. Jiao *et al.*, 2011), and 15% of plant speciation events are linked to WGD (Wood *et al.*, 2009). Although WGD does not appear to

increase speciation rates within polyploid lineages (Otto & Whitton, 2000; Meyers & Levin, 2006; Vamossi & Dickinson, 2006; Mayrose *et al.*, 2011; Arrigo & Barker, 2012; Estep *et al.*, 2014; Scarpino *et al.*, 2014; Puttick *et al.*, 2015), this process does fuel the accumulation of nascent lineages that can subsequently evolve, diverge, and diversify. Duplicate allele copies can be released from selective constraints, allowing genes to neofunctionalize, that is, to gain new or alternate functions (e.g. Hughes *et al.*, 2014; van den Bergh *et al.*, 2016). Furthermore, changes in gene expression,

gene loss, hybridization (allopolyploidy), and chromosomal rearrangements all contribute to the complex genetic pathways that shape the phenotype (e.g. Birchler, 2012; Soltis *et al.*, 2014a; Yoo *et al.*, 2014; Wendel *et al.*, 2016). Ultimately, the resulting genetic and phenotypic changes associated with WGD directly influence the ecology of polyploid lineages (Levin, 2002; Ramsey & Ramsey, 2014).

Although there are clear links between WGD and plant ecology, comparatively few studies have assessed how polyploidy changes the ecological context of a plant. We understand far more about the genome-level alterations that follow WGD (e.g. Birchler, 2012; Soltis *et al.*, 2014a; Yoo *et al.*, 2014; Wendel *et al.*, 2016) than about how these effects filter down to impact how an individual performs in its abiotic and biotic environment. For instance, WGD-induced changes in water-use efficiency could impact whether a plant has the physiological ability to persist in dry environments (e.g. Garbutt & Bazzaz, 1983). Likewise, WGD can affect interactions with other organisms, including those with pollinators, herbivores, and pathogens, while also potentially altering the ecology of these species in return (Segraves & Anneberg, 2016). These reciprocal effects could have far-reaching consequences for the ecology and evolution of the species that live within a community (Fig. 1). Similar to throwing a pebble into a still pool of water, the ripples caused by WGD could be experienced throughout an entire community. The strength of the disturbance in the pool will depend on a number of factors, including the genetic composition of polyploids, whether hybridization is involved in polyploid formation, the extent to which the phenotype is altered by WGD, as well as the strength of interactions that are present within the community.

The challenge in understanding the effect of WGD in a community context is that while a number of studies have

documented how polyploidy impacts interactions with a few species, it is comparatively rare to find studies of the collective species within a guild, such as all herbivore species that attack a polyploid plant. Moreover, no single study has documented the simultaneous effects of multiple guilds. I echo the frustration of others (e.g. Ramsey & Ramsey, 2014; Soltis *et al.*, 2014b) that the current paucity of data on polyploidy makes piecing together a well-supported perspective premature. Instead, I use the available information to offer a prospectus on the factors that may contribute to how WGD impacts community context. I define community context as the ecological setting in which a focal organism lives. Specifically, I focus on the interactions with other organisms and how this community changes geographically and through time. The ultimate goal of this review is to explore where genome duplication might fall on our community disturbance scale. Is the impact equivalent to the ripples caused by a grain of sand? A pebble? A boulder?

To accomplish this goal, I begin this review by discussing the available evidence on whether WGD impacts community context. Given the diverse results from a handful of studies, I propose a series of predicted mechanisms by which WGD could mediate changes in the surrounding community. I then offer approaches for testing these mechanisms, touching on some of the challenges that are inherent to the study of community context. Next, I consider hypotheses on how recurrent formation could affect community context. Finally, because the presence of polyploids in a community might also affect other plant species, I switch the viewpoint to examine how WGD alters community context from the perspective of other plant species within a community. These endeavors emphasize a strong need for additional work that draws clear connections among WGD, phenotypic change, and community context.

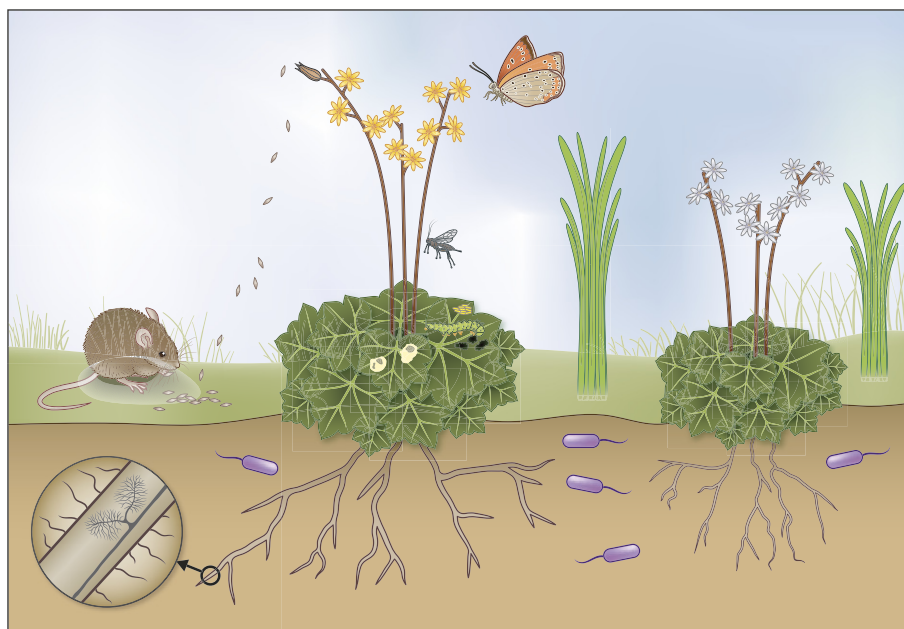


Fig. 1 Ecological interactions of polyploid plants within a community. Polyploids (large, yellow-flowered plant) will interact with a range of above-ground community members, including seed dispersers, pathogens, herbivores, and pollinators, as well as the diploid parents (smaller, white-flowered plant) and other plants in the community (grass-like plants). Below-ground, polyploids interact with mycorrhizal fungi (inset), bacteria (purple), and soil herbivores and pathogens. There will also be higher-order interactions such as tritrophic interactions with parasitoids.

II. Impact of WGD on community context of polyploids: from the ground up

Given the varied ways in which WGD can impact phenotype, it is not a stretch to imagine how changes in phenotype could lead to shifts in the communities of organisms that interact with polyploid plants. Even subtle phenotypic changes could pose a barrier for some community members, causing reduction or complete cessation of an interaction or, alternatively, WGD could offer an opportunity for some community members to expand their repertoire of interactions, potentially creating novel associations (Thompson *et al.*, 1997). The changes occurring in one interaction can then flow into other types of interaction, moving up or down through trophic levels via direct effects and indirect effects that are mediated through other members of the community. Consequently, we expect to observe changes in the collective assemblage of species that interact with polyploids. The question is whether data from naturally occurring populations support this view that polyploids experience different community contexts than their diploid parents. In this section, I summarize the scant community-level data on how the interaction landscape changes from the perspective of a polyploid plant, acknowledging that there exists a much larger literature on specific pairwise interactions (reviewed in Segraves & Anneberg, 2016).

Although below-ground species interactions are key in determining above-ground productivity and diversity (Wardle *et al.*, 2004), they have been largely ignored in the study of WGD. To date, only three studies have compared below-ground species composition of diploids and polyploids, and the results show a diversity of outcomes. First, Thébault *et al.* (2010) used a pot experiment to show that soil bacterial species differed between pots containing diploid and allotetraploid *Centaurea maculosa*; however, they found no effect of allopolyploidy on soil bacteria of pots containing *Senecio inaequidens*. Second, comparisons of natural mycorrhizal guilds of diploid and autotetraploid *Gymnadenia conopsea* orchids showed a strong shift in species composition, particularly when the cytotypes were growing in sympatric field sites (Těšitelová *et al.*, 2013). Not only did diploids and autotetraploids have significantly different mycorrhizal guilds, but all except one mycorrhizal species was exclusively associated with a specific cytotype (Těšitelová *et al.*, 2013). Lastly, Stutz *et al.* (2016) showed that the root herbivores of diploid and allotetraploid *Leucanthemum* consisted of the same species and had similar attack rates, but that the species evenness of the communities differed. For example, two root-feeding weevils were more common on diploids, while a root-galling fly attacked allotetraploids more frequently. Together, these studies show us the full range of possible outcomes from no effect in *Senecio* to changes in the dominance hierarchy to strong shifts in community composition in *Gymnadenia*. It remains unclear whether these effects are a direct outcome of WGD or of alternative factors such as local adaptation. As allopolyploids were examined in three of the four study systems, hybridization may also play a major role in dictating the results. Interestingly, the below-ground system in which the most change was observed was of an autopolyploid.

Not surprisingly, there has been more work on above-ground interactions, although efforts have only focused on guilds of herbivores and pollinators/flower visitors of autopolyploids. For plant–herbivore interactions, studies show that the herbivores associated with diploids and autopolyploids are often the same species, but that species evenness and attack rates can drastically change between diploids and autopolyploids (e.g. Nuismer & Thompson, 2001; Halverson *et al.*, 2008a; Richardson & Hanks, 2011; Münzbergová *et al.*, 2015). Similarly, comparisons of diploids and autopolyploids show shifts in the dominance of particular pollinator species (Thompson & Merg, 2008) or flower visitor species (Segraves & Thompson, 1999; Borges *et al.*, 2012). In rare instances, there can be unique sets of floral visitors, such as those observed in autopolyploid *Erythronium* lilies (Roccaforte *et al.*, 2015). By contrast, floral visitors can also exhibit no differentiation between diploids and autopolyploids; however, their visitation frequency may show differential preference for one cytotype (Husband, 2000; Kennedy *et al.*, 2006; Castro *et al.*, 2011; Nghiem *et al.*, 2011). It seems the most common effect is for shifts in the dominance hierarchy of species rather than a change in guild membership *per se*, but as observed below-ground, above-ground interactions can also exhibit a range of outcomes from no change to strong species turnover. Since all of the above-ground work has been done with autopolyploids, the variability among studies cannot be attributed to hybridization, pointing to other factors that may drive these patterns.

Taken together, the limited data on above- and below-ground interactions suggest that WGD can impact community context, yet we lack a clear view of how these effects are mediated or whether the outcomes are predictable. As there are many potential factors that could contribute to how a polyploid plant interacts with other members of its community, perhaps the breadth of observed outcomes is expected. Not only are we comparing different types of studies from field observations to glasshouse experiments, but we are also comparing different plant lineages that vary with respect to phenotypic divergence, niche divergence, evolutionary divergence, and whether hybridization was involved during WGD. The results of these pioneering studies emphasize the multivariate nature of the problem and indicate that as we move forward, the key is to isolate how the effects of WGD contribute to shaping community context. This will allow us to build a predictive framework for how WGD mediates changes in species interactions.

III. Predicted mechanisms by which WGD could affect community context

Determining the pathways by which WGD can impact community context is the first step in forming the foundation of our predictive framework. Although we know that WGD-induced phenotypic change is the connection that ties WGD to community context, we are sorely lacking tests that examine how often these changes arise and whether phenotypic shifts in polyploids translate into changes at the community level. An array of phenotypic changes following WGD have been shown in many species (e.g. Otto & Whitton, 2000; Levin, 2002; Ramsey & Schemske, 2002;

Suda *et al.*, 2015), yet this may represent a biased sample, as many polyploid species may be morphologically cryptic and thus difficult to identify (Soltis *et al.*, 2007). This may be especially true for autopolyploids that can very closely resemble their diploid progenitors (e.g. Judd *et al.*, 2007). Consequently, in order to appreciate the impact of WGD on community context, we must evaluate whether polyploidy results in phenotypic change and, when differentiation arises, if these changes instigate alterations in the community of organisms interacting with polyploids. In this section, I outline a set of predictions that illustrate a diversity of potential mechanisms that connect WGD and community context (Table 1). This list is not intended to be exhaustive, but to serve as a starting point for future work.

1. Increase in DNA content

Perhaps the most obvious and universal feature of polyploidy is the increase in DNA content of cells. This physical change has direct consequences for cell size that can impact the speed of cellular processes (Muntzing, 1936; Stebbins, 1971). For instance,

there is a positive relationship between nuclear DNA C-value and cell division time (e.g. Cavalier-Smith, 1978; Bennett, 1987; Bennett & Leitch, 2005) that can also correlate with changes in relative growth rate and generation times (e.g. Knight *et al.*, 2005; Herben *et al.*, 2012). In addition, changes in plant growth rates have also been correlated with WGD (Garbutt & Bazzaz, 1983). If WGD alters growth rates, this can change patterns of phenology, potentially delaying or accelerating the timing of flowering, shortening or extending the flowering season, or altering the timing of leaf unfurling (e.g. Garbutt & Bazzaz, 1983; Bretagnolle & Thompson, 1996; Segraves & Thompson, 1999; Knight *et al.*, 2005; Oswald & Nuismer, 2011; Laport *et al.*, 2016). I predict that such shifts in phenology will have direct consequences for interactions with a wide range of community members. We know, for instance, that changes in flowering phenology and leaf emergence can affect the guilds of pollinators, florivores, and herbivores that use flower and leaf resources, altering the abundance and composition of species that visit (e.g. Yang & Rudolf, 2010; Rafferty & Ives, 2011). Furthermore, changes in the timing of flowering can also change the timing of

Table 1 Predicted mechanisms for the effects of whole-genome duplication (WGD) on community context

Cause	Effect	Potential outcome(s) of effect	Predicted consequences for community context	
Increased DNA content	Decreased growth rate	Flower later, leaf out later, prolonged flowering	Pollinator, herbivore, pathogen species composition shift to late-season species; increased diversity of these species	
	Increased growth rate	Flower earlier, leaf out earlier	Species composition shifts to early-season pollinators, herbivores, pathogens	
	Gigas effect	Larger flowers, fruit, seeds, pollen, leaves, stems, overall plant size	Species composition shifts to those that prefer larger organs or have ability to handle larger organs; increased competitive ability	
	Physiological changes	Increased root exudation	Increased root exudation	Stimulates soil microbe growth, species turnover, diversity
		Increased stress tolerance	Increased stress tolerance	Increases competitive ability
Genetic phenomena	Changes in genotype	Improved water relations	Increased competitive ability in dry habitats	
		Ecological niche shifts	Encounter new species; lose some of the former associations	
	Translocations	Decreased photosynthetic rate	Mycorrhizal species composition shifts to those that require less carbon (C)	
		Changes in stoichiometry	Increased requirement for nitrogen (N)	Decreased competitive ability; loss of mycorrhizal species with high N requirements or decreased benefits conferred to host; herbivores consume more tissue or species composition shifts to herbivores with decreased N requirements
			Increased requirement for phosphorus (P)	Decreased competitive ability; increased association with mycorrhizal species that forage for P
Evolutionary processes	Changes in genotype	New allelic combinations, increased heterozygosity	Genotype-specific interactions such as gene-for-gene interactions will be altered; specialists more likely to be affected	
		Transition from sexual monomorphism to dimorphism	Pollinator and florivore species composition shifts to those that favor new sexual systems; altered competition for pollinators	
	Hybridization	Disruption of cytonuclear interactions, change in mating system	Pollinator and florivore species composition shifts to those that favor new sexual system; altered competition for pollinators	
		Divergence in phenotype, niche divergence	Decrease in competitive interactions; divergence in species composition	
	Neofunctionalization	Altered defensive chemistry	Altered defensive chemistry	Reduction in herbivory, pathogen attack; increased frequency of specialists with counterdefenses
Altered flower color, scent			Pollinator and florivore species composition shifts to those favoring new color or scent	
Natural selection		Divergence in phenotype, niche divergence	Decrease in competitive interactions; divergence in species composition	
Recurrent formation	Divergence in phenotype across independent origins	Geographic mosaic of species interactions		

fruit maturation, impacting interactions with the community of seed dispersers and seed predators (e.g. Elzinga *et al.*, 2007). Although studies have shown that there can be modest differences in flowering phenology between polyploids and their diploid progenitors (e.g. Segraves & Thompson, 1999; Husband & Schemske, 2000; Gross & Schiestl, 2015; Roccaforte *et al.*, 2015), we are still determining how these changes come about (e.g. Mayfield *et al.*, 2011) and the role they play in shaping community context.

Another common phenotypic change in polyploid plants is the gigas effect where polyploids have larger features than their diploid progenitors (Stebbins, 1971). The gigas effect is often attributed to a larger volume of nuclear DNA causing increased cell size that results in an overall increase in organ size; thus, polyploid plants often have larger flowers, leaves, pollen, seeds, and fruit, as well as more robust stems and an overall increase in plant size (e.g. Levin, 2002; Ramsey & Schemske, 2002). Changes in these traits could impact interactions ranging from mutualism to antagonism. For example, there is strong evidence demonstrating that flower size and shape dictate the pollinator species that visit flowers and can also alter the per-visit efficacy of pollinators (e.g. Galen, 1999; Policha *et al.*, 2016). Thus, pollinator and floral visitor guilds are predicted to change when WGD alters flower size, shape, or other floral traits, favoring attraction of species that prefer larger flowers and that can successfully reach the floral rewards within the larger flowers of polyploids. Moreover, these effects on the community may, in turn, extend to the next trophic level, for example, by altering the interactions between pollinators and their predators (Segraves & Anneberg, 2016). Similar predictions would also be made for herbivores. For instance, we know that some insect herbivores preferentially oviposit on larger shoots and leaves and that this may also affect subsequent offspring survival (e.g. Fritz *et al.*, 2000). WGD-induced changes in organ size, then, could alter herbivore guilds or attack rates, and we would expect to see an increase in the species that prefer the larger stems and leaves of polyploid plants. Increases in fruit and seed size could also cause significant changes in the guilds of seed dispersers or predators. For example, changes in seed or fruit size can impact seed dispersal distances or alter attractiveness to specific disperser species (e.g. Benítez-Malvido *et al.*, 2014); thus, we would expect to see an increase in interactions with species that are able to process larger fruit or prefer larger seeds. A similar outcome would be predicted for seed predators where we may see a reduction in the number of species able to access the seeds. Seed predation by soapberry bugs, for instance, is limited by the size of the fruit, with larger fruit requiring longer mouthparts in order for the bugs to gain access to the seeds (Carroll & Boyd, 1992). Finally, competitive ability is mediated in part by the overall size of the plant, and so large polyploid plants may have an advantage over their diploid parents.

Increased cell size can also lead to physiological changes in polyploids, affecting a broad array of traits such as the ability to withstand drought, salt tolerance, and photosynthetic activity (e.g. Levin, 2002; te Beest *et al.*, 2012; Ramsey & Ramsey, 2014). Shifts in physiology could have important consequences for the ecological

interactions of a polyploid plant. For example, we know that WGD can increase root exudation (Tal & Gardi, 1976). An increase in root exudation also increases carbon (C) input into the soil, stimulating microbial activity (Hamilton & Frank, 2001) and potentially altering diversity (Wardle, 2006; Dennis *et al.*, 2010; Steinauer *et al.*, 2016). Thus, changes in root exudation caused by WGD could be an important pathway for modification of soil microbial communities. Along with this, we should also expect to observe changes in community context if the physiological shifts that occur in polyploids move them into new niches. Although not a universal feature of polyploids (e.g. Glennon *et al.*, 2014), niche divergence is often linked to WGD (e.g. Jakob *et al.*, 2007; Raabová *et al.*, 2008; Manzaneda *et al.*, 2012; McIntyre, 2012) and could play a key role in determining the community of organisms that interact with polyploids.

Increased DNA content may also influence the ecological stoichiometry of the plant. If DNA content per cell doubles and cell number remains constant, polyploids should experience an increased need for limiting nutrients such as nitrogen (N) and phosphorus (P) (Leitch & Bennett, 2004; Leitch & Leitch, 2008; Hesse *et al.*, 2010; Guignard *et al.*, 2016). The reason for this change in nutrient requirements is that the additional DNA content of polyploid cells will theoretically increase the need for N and P during DNA replication and translation. Although this idea remains untested, there is evidence that polyploidy/DNA content of cells is positively correlated with nutrient limitation (Neiman *et al.*, 2009; Šmarda *et al.*, 2013; Guignard *et al.*, 2016). If this is the case, plant stoichiometric changes could alter competitive interactions. For example, WGD could reduce competitive ability of polyploid plants if they are more strongly limited by their nutritional requirements. If so, we would expect to see changes in community composition where polyploids are restricted to environments with more available nutrients. There is some evidence for this in long-term nutrient addition experiments where plant community composition in plots with low N and P shifted towards species with predominantly lower nuclear DNA content (Šmarda *et al.*, 2013; Guignard *et al.*, 2016). Experiments comparing diploid and polyploid competitive ability should reveal a disadvantage of polyploids if stoichiometry and nutrient demands change following WGD. Moreover, herbivory could be impacted if the nutritional quality of forage decreases as a result of a change in stoichiometry. We know, for instance, that herbivores increase the volume of plant tissue consumed and that the species composition of herbivores changes as forage quality decreases (e.g. Mattson, 1980; Awmack & Leather, 2002); thus, I predict that polyploid plants will host herbivore species that are tolerant to consuming low-quality forage and that damage on these plants will be increased as compared with diploids. In addition, WGD-induced nutrient limitation could also impact the communities of below-ground mutualists. For instance, arbuscular mycorrhizal fungi (AMF) on diploids and polyploids are predicted to differ if polyploidy causes P limitation. I predict that polyploids will selectively form associations with AMF species that have enhanced ability to acquire P for their host plants. Furthermore, we may also see divergence in the guilds of mycorrhizal associates between diploids and polyploids growing in sympatry. This latter pattern was observed in sympatric

diploid and autotetraploid *Gymnadenia* orchids and may be a mechanism that reduces competition between the cytotypes (Těšitelová *et al.*, 2013).

2. Genetic phenomena

Increased DNA content clearly has a number of direct consequences for the phenotype of polyploid plants, but the process of WGD also confers genetic differences that could similarly alter phenotype. Extensive research in this area has revealed that there are many genetic effects of WGD (e.g. Birchler, 2012; Soltis *et al.*, 2014a; Yoo *et al.*, 2014; Wendel *et al.*, 2016), but several stand out as being particularly relevant for explaining how WGD could shape interacting communities. Genotypic changes, for instance, could have a tremendous impact on community context (e.g. Crutsinger *et al.*, 2006; Johnson *et al.*, 2006; Abdala-Roberts & Mooney, 2013; Barbour *et al.*, 2016), especially as WGD can increase heterozygosity and bring together allelic combinations that are impossible in diploids. As a consequence, I predict that allelic changes following WGD will impact interactions that are dependent on host-plant genotype. AMF and fungal pathogens are good examples of organisms that have been shown to be directly impacted by plant genotype (e.g. Hartnett *et al.*, 1993; Pánková *et al.*, 2008; Lamit *et al.*, 2014), and are strong candidates for future work on the ecological effects of genotypic change in polyploids. Moreover, I also predict that highly specialized interactions are more likely to be altered by WGD-induced changes in plant genotype. We know that specialization can be extreme; for example, some scale insects may have evolved to feed on a single host plant genotype (Edmunds & Alstad, 1978). Although this degree of specialization is not required to observe changes in the composition and abundance of organisms interacting with a polyploid, it does illustrate the potential for genotypic changes to alter community context. Similarly, we could also imagine how gene-for-gene or genotype \times genotype types of interactions, such as those between plants and pathogens or nitrogen-fixing symbioses, could be directly affected by the genotypic changes conferred by polyploidy (Oswald & Nuismer, 2007; Powell & Doyle, 2015), and models of gene-for-gene interactions have shown that polyploids are predicted to have increased resistance to pathogens as a result of the genotypic effects of WGD (Oswald & Nuismer, 2007). Although we have evidence indicating that genotypic effects can be important in defining interactions with diploid plants, this remains to be tested in polyploids.

Changes in the genotype, however, are only one type of genetic change that occurs with WGD. Genomic rearrangements, for instance, have also been tied to critical changes in phenotype. A noteworthy example is the proposed connection between genomic translocations and shifts in mating system. Translocations that occur with WGD have been proposed as one mechanism that can cause transitions from sexual monomorphism to dimorphism in polyploids (Miller & Venable, 2000; Ashman *et al.*, 2013; Glick *et al.*, 2016; Miller *et al.*, 2016). Because changes in mating system can alter floral traits that can influence visitation patterns of both pollinators and florivores (e.g. Dart & Eckert, 2015), a prediction is that WGD-induced changes in mating system will alter the guilds

of organisms that visit flowers. Furthermore, changes in mating system can also alter plant competition for pollinators (e.g. Runquist *et al.*, 2016); thus, it would be interesting to determine whether WGD frequently impacts pollinator guilds and/or competitive interactions between diploids and polyploids via this mechanism.

Interestingly, shifts in the mating system can also occur through interspecific hybridization, a common mode of polyploid formation that can have many effects on phenotype. WGD involving hybridization (allopolyploidy) could induce changes in mating system via disruption of cytonuclear pathways (Glick *et al.*, 2016). Because shifts in mating system have been attributed to interactions between nuclear genes and cytoplasmic male sterility genes (e.g. Dudle *et al.*, 2001), and hybridization can disrupt these interactions (Bock *et al.*, 2014), WGD has strong potential to lead to changes in mating system in allopolyploids. Moreover, hybridization coupled with WGD is also known to cause a range of phenotypic effects, creating plants that are similar to one parent, intermediate, or that have extreme phenotypes exceeding the values of either parent (e.g. McCarthy *et al.*, 2016); thus, we could observe greater phenotypic variance in allopolyploids because of phenotypic changes generated by polyploidy or hybridization, or an interaction of these two processes. As a consequence of the effects of hybridization, I predict that we will see greater variability in the community context of allopolyploids vs autopolyploids, simply because trait variation is expected to be higher in allopolyploids, especially as genetic divergence between the diploid parents increases. These effects could extend to a number of different members of a community. Thus far, there are too few studies to make formal comparisons, as all of the above-ground studies to date have focused on autopolyploids and all but one below-ground study has focused on allopolyploids.

3. Evolutionary processes

So far, this discussion has focused on mechanisms in which WGD immediately affects phenotype as an outcome of the increase in chromosome sets; however, we should also keep in mind that there are other forms of phenotypic change driven by evolutionary processes. For example, another mechanism by which WGD could affect community context is neofunctionalization. This genomic recycling can create novel gene products or gene expression patterns that could alter phenotype in a number of ways. One particularly intriguing pathway for phenotypic evolution is through neofunctionalization which leads to diversification of biochemical pathways that produce plant secondary chemicals. We know, for instance, that WGD can strengthen the chemical defensive machinery of a plant that may allow it to escape herbivory (Edger *et al.*, 2015; Münzbergová *et al.*, 2015; van den Bergh *et al.*, 2016; Meyerson *et al.*, 2016) or confer resistance to pathogens. I would predict, then, in situations in which WGD causes heightened defenses, that polyploids will have reduced diversity of herbivore or pathogen species attacking them or that they will be attacked by a larger proportion of specialist species that harbor counterdefenses to the defensive chemistry. Alternatively, neofunctionalization coupled with changes in gene expression can create novel floral

scent bouquets (e.g. Jersáková *et al.*, 2010; Gross & Schiestl, 2015) or alter flower color (e.g. Borges *et al.*, 2012; Gross & Schiestl, 2015; McCarthy *et al.*, 2015). These modifications could impact a range of species that interact with flowers, particularly affecting those species that are attracted via floral signals.

Even in the absence of neofunctionalization, natural selection could create divergence between diploids and polyploids that can strongly impact community context. WGD causes instantaneous speciation, offering the opportunity for these new lineages to follow independent evolutionary trajectories from their diploid parents (Rieseberg & Willis, 2007). As a case in point, selection is predicted to favor polyploids with divergent phenotypes because of the reproductive disadvantage experienced by newly formed polyploids. Levin (1975) modeled the establishment of a newly formed polyploid (neopolyploid) in an existing diploid population and showed that because neopolyploids will be the minority cytotype, they will be at a disadvantage finding suitable mates. For this reason, natural selection should push polyploids into new niches or phenotypic spaces that favor assortative mating. An excellent example of this is the work conducted on *Chamerion angustifolium* where significant phenotypic divergence has been observed between diploids and naturally occurring autotetraploids (Husband *et al.*, 2016). This divergence creates substantial prezygotic isolation of the cytotypes, favoring assortative mating via several mechanisms, including shifts in plant–pollinator interactions. Comparisons of phenotypic divergence and prezygotic isolation of diploids and newly formed autotetraploids, however, indicated that while there are instantaneous changes in neopolyploid phenotypes, they are much reduced compared with those observed in evolved autotetraploids (Husband *et al.*, 2016). Moreover, prezygotic isolation was substantially reduced in neopolyploids, indicating that selection has favored traits promoting reproductive isolation (Husband *et al.*, 2016). Thus, evolutionary change will play a key role in shaping the phenotype of polyploids through time.

IV. Moving towards a predictive framework

There are clearly many ways in which WGD could directly or indirectly change the phenotype, suggesting a number of possible avenues for alterations of the network of interactions associated with polyploids. Although characterizing phenotypic change in polyploids is an excellent starting point for understanding the ecological effects of WGD, gaining a deeper appreciation of these patterns will require bridging several gaps in our knowledge. First, we need tests of whether the observed effects are caused by WGD. Studies that exclusively examine established polyploid populations are confounded by evolutionary history because selection will have shaped these populations, potentially obscuring the original effects of WGD (Ramsey & Ramsey, 2014; Husband *et al.*, 2016). A good example of this is the evolution of flowering phenology in *Heuchera grossulariifolia*. At a sympatric diploid–autotetraploid site along the Salmon River in Idaho, established autotetraploids of *H. grossulariifolia* flower earlier than their diploid progenitors (Segraves & Thompson, 1999); however, first-generation synthetic

autotetraploids flower later than diploids even when derived from parental Salmon River diploids (Oswald & Nuismer, 2011). These differences between synthetic and established polyploids are probably driven by selection favoring early flowering in natural populations of autotetraploids (Nuismer & Cunningham, 2005), showing how selection could blur the effects of WGD and give misleading results. Thus, we need to conduct experiments that include synthesized and/or natural early-generation polyploids, established polyploids, and their diploid parents. Experiments using these groups could then tease apart the contribution of WGD to phenotype, as well as testing whether there is an unintended effect of synthesizing polyploids (e.g. Husband *et al.*, 2016). In addition to evolutionary change, we must also consider whether observed differences between diploids and polyploids are potentially confounded by hybridization, as about 50% of extant polyploids are of hybrid origin (Barker *et al.*, 2016). As hybridization will confer genetic and phenotypic effects independent of WGD, sorting out these contributions is essential. The best approach would compare synthesized allopolyploids with synthesized homoploid (diploid) hybrids and the diploid parental species to assess the relative effects of hybridization and WGD. Resolving the effects of hybridization and natural selection could be challenging, as it may be difficult or impossible to synthesize homoploid hybrids or polyploids in some species. As a consequence, development of model systems that are amenable to these manipulations would be very useful.

Second, our predictive framework will be incomplete without experiments that also determine how WGD causes a specific community-level effect. Although we have volumes of information on the phenotypic effects of WGD, we have yet to pin down how these changes impact species interactions. This information would allow us to directly link WGD to community context, providing a framework for us to predict when and where WGD effects are likely to occur. Having said that, making these connections will require labor-intensive, controlled experiments that use diploids and their derived (synthetic and established) polyploids in an ecologically realistic setting. Ideally, we would use manipulative field experiments to alter phenotypic traits to test how one or more members of a community are affected. Although these types of experiments can be technically difficult, there are great examples of how the effect of traits can be isolated through elegant manipulations (e.g. Policha *et al.*, 2016).

Third, in addition to drawing connections that enable us to determine the mechanisms of WGD effects on the community, we also need to understand how interactions between the community members affect community context. Unfortunately, we cannot naïvely assume that WGD is the source of all alterations in the community. Studies on community context have shown a multitude of ways in which changes in biotic context can affect other interactions. For example, we know that the presence of AMF can alter plant resistance to root pathogens, with specific AMF species assemblages conferring enhanced resistance (Sikes *et al.*, 2009; Sikes, 2010). AMF can also affect above-ground interactions by altering plant resistance to above-ground herbivores and/or their predators (Borowicz, 1997; Gange *et al.*, 2003; Hempel *et al.*, 2009; Koricheva *et al.*, 2009; Vannette & Hunter, 2011; Jung

et al., 2012; Barber *et al.*, 2013; Del Fabbro & Prati, 2014), altering plant attractiveness to pollinators (Gange & Smith, 2005; Wolfe *et al.*, 2005; Barber *et al.*, 2013; Barber & Soper Gordon, 2014), and causing changes in the composition of the surrounding plant community (van der Heijden *et al.*, 1998a,b). Moreover, these interactions are mediated by the identity of the AMF species (van der Heijden *et al.*, 1998a; Varga & Kytöviita, 2010; Barber *et al.*, 2013). These indirect effects also extend beyond plant–AMF interactions, with studies showing, for example, that interactions with competitors can influence interactions with pollinators and herbivores, or that above-ground herbivores can also impact pollinators, and soil microbes can affect the outcome of competitive interactions between plants (e.g. Sotomayor & Lortie, 2015). Observing patterns such as these can be difficult to interpret without appreciating the extent to which WGD has direct effects. We know that WGD can directly impact interactions such as resistance to root herbivores (e.g. Hannweg *et al.*, 2015), and so the challenge is to design experiments that allow us to understand the community-level effects driven by WGD vs the effects caused by other species interactions.

Finally, we need to keep in mind that community context will also change with the abiotic environment. For instance, a plant's response to AMF inoculation is largely dependent on the context of the soil characteristics, specifically whether the plants are limited by P (Hoeksema *et al.*, 2010). Some evidence for the role of the abiotic environment in altering community context has also been suggested by studies comparing herbivory in diploids and autopolyploids. Previous work suggests that the local habitat can influence patterns of herbivory (Münzbergová, 2006; Richardson & Hanks, 2011; König *et al.*, 2014; Münzbergová *et al.*, 2015). For example, Richardson & Hanks (2011) showed that *Solidago* cytotypes in natural populations experienced differential attack by some herbivore species, but when the plants were placed together in a common garden, the attack rates were the same. The differences observed between garden and field experiments suggest that the local environment might also mediate changes in community context. Thus, interpretations of the role of WGD in structuring the community will require both the abiotic and biotic environments to be considered.

V. Recurrent formation, geographic mosaics, and community context

We face many challenges in resolving how and when WGD will have community-level effects, and one factor we have yet to consider is recurrent polyploid formation. Multiple origins of polyploidy are common, with a majority of polyploid taxa having evolved replicate lineages (e.g. Soltis & Soltis, 1999). For instance, *Tragopogon miscellus* allotetraploids have evolved c. 20 times in <100 yr (Symonds *et al.*, 2010), polyploidy in *Draba norvegica* has evolved 13 times (Brochmann *et al.*, 1992), and tetraploid *Galax urceolata* has at least 46 independent origins (Servick *et al.*, 2015). The presence of multiple, independent polyploid lineages could play a key role in shaping the community of organisms that interact with polyploids. Because independently formed origins can derive

from different parental genotypes, recurrent formation can create enhanced genetic diversity of the polyploid gene pool. Gene flow between polyploids of independent origin could also create unique allelic combinations that may give polyploids an evolutionary advantage (Soltis & Soltis, 1999; Soltis *et al.*, 2010), creating novel phenotypes that can alter their interactions with other species.

Another possibility is that recurrent formation sets the stage for a geographic mosaic of interactions (Thompson *et al.*, 2004). When independent origins form in different populations, they will come from populations with different genetic backgrounds and live in different biotic and abiotic contexts. Together, these factors can lead to local adaptation, creating divergence in traits and species interactions across origins. If this is the case, then we would expect to see strong variability in species interactions across origins, suggesting that studies of single populations could present misleading results. Alternatively, we could observe consistent patterns among origins if those patterns are being driven by a universal effect of polyploidy itself. A good example of this would be changes induced by the physical effects of increasing nuclear DNA content such as increased organ size. These effects would be consistently observed across independent origins irrespective of genotype, and so communities across origins might converge. I am aware of only two study systems that have incorporated knowledge of multiple origins into their analyses of species interactions. *Heuchera grossulariifolia* has at least five origins of tetraploids that occur across its geographic range (Segraves *et al.*, 1999) and includes several sympatric sites where diploids and autotetraploids grow in close proximity (Thompson *et al.*, 1997). Studies of the herbivore and pollinator guilds of this plant suggest a surprising consistency across origins. The pollinating seed-feeding parasite *Greya politella* prefers autotetraploid *H. grossulariifolia* across origins (Thompson *et al.*, 1997) and the pollinator guilds of autotetraploids are consistent in comparisons of two independent origins that occur sympatrically with diploids (Thompson & Merg, 2008). Similarly, *Solidago altissima* has multiple origins of polyploidy (Halverson *et al.*, 2008b) and comparisons of herbivore guilds show that the galling insect *Eurosta* was more frequently found on autotetraploids across sites/origins (Halverson *et al.*, 2008a). It would be interesting to know if we generally observe replicate assembly of the same communities across origins or whether these examples present a special case.

VI. Alternative perspectives – impact of the appearance of polyploid plants in a community

Thus far in our discussion we have considered how community context changes from the perspective of a plant lineage that has undergone WGD; yet the introduction of a new polyploid species may also alter species interactions of other members of a plant community. As has been found in other studies of community context, there should be both direct and indirect effects of the appearance of polyploids in a plant community (Fig. 2), and the strength of these effects will be determined by the natural history and population growth parameters of the plant species involved.

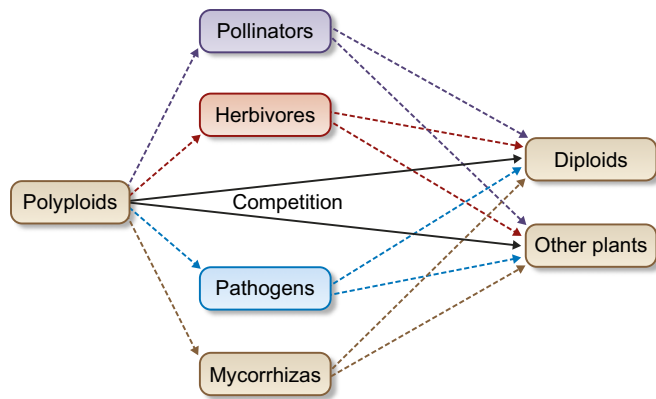


Fig. 2 Direct and indirect effects of whole-genome duplication (WGD) on the diploid parents and other plants within a community. Solid arrows indicate direct effects of competition on other plant species. Dashed arrows indicate the indirect effects on other plants mediated through members of the community.

Because direct and indirect effects will occur with the introduction of any new plant species to a community, the ultimate question is whether adding a polyploid is profoundly different.

In the case where polyploids arise elsewhere and migrate into a new plant community, there are no *a priori* reasons to predict that they would elicit an exceptional community-level response. As a polyploid becomes established in a new population, it would fill the role of a new plant in a community, and this process should be the same irrespective of whether a plant has undergone WGD. That is, a polyploid entering a population should have the same effect as a diploid. Having said that, there is a known relationship between polyploidy and invasiveness, suggesting that the many changes induced by WGD confer polyploids with an advantage in a novel range (e.g. Pandit *et al.*, 2011; te Beest *et al.*, 2012; Suda *et al.*, 2015). Invasive species often cause remarkable changes in community context (Simberloff *et al.*, 2013), yet it is unclear whether an invasive polyploid would have a dramatically different impact than an invasive diploid.

By contrast, as WGD is arguably the most common form of instantaneous, sympatric speciation in plants (Rieseberg & Willis, 2007), polyploids that arise *de novo* within populations might be uniquely situated to have direct effects on the community context of their diploid parents. Direct effects will be mediated through competitive interactions (Fig. 2), and because newly formed polyploids are very close relatives, they could have exceedingly similar requirements to those of their diploid progenitors. If so, I predict that diploid parents will experience an increase in competition and that this increase will be greater than that of the addition of a random, more distantly related plant species in the community. However, we also know that WGD can cause immediate phenotypic changes that could reduce the strength of competition between diploid progenitors and polyploids, and that the greater the divergence in these traits, the less likely it is that the cytotypes would have overlapping resource requirements and would compete. In fact, this scenario may be common as we know that polyploid establishment is tied to niche divergence (Levin,

1975) and that many polyploid lineages perish following their formation (Mayrose *et al.*, 2011), suggesting that ecological constraints could dictate which lineages persist. We have evidence that diploids and polyploids compete with one another (Maceira *et al.*, 1993; Baack & Stanton, 2005; Fialová *et al.*, 2014; Thompson *et al.*, 2015), but we do not know if the strength of this competition is greater than that expected when a random plant species invades a community.

Another factor that could determine whether WGD plays a special role in altering the community context of the parental diploids is the mode of formation of the polyploids. Allopolyploids, for instance, might express strong shifts in phenotype that reduce competition with one or both parental species. By contrast, autopolyploids can closely resemble their parents (Soltis *et al.*, 2007), increasing the likelihood of competition. For example, we know that a number of sympatric diploid and autopolyploid species have overlapping pollinator communities (e.g. Kennedy *et al.*, 2006; Thompson & Merg, 2008) and this pollinator sharing can set up competitive interactions which can lead to the competitive exclusion of the minority cytotype (Levin, 1975; Fowler & Levin, 2016). There is also some evidence that sympatric diploids and autopolyploids might compete for mycorrhizal species that acquire critical plant nutrients for their hosts, as evidenced by strong changes in species composition of the mycorrhizal root communities in sympatric diploid and polyploid *Gymnadenia* orchids (Těšitelová *et al.*, 2013). Consequently, it would be interesting to make comparisons between auto- and allopolyploids to assess the overlap in resource requirements with their diploid parents and whether this creates strong competitive interactions. Testing these ideas would shed light on how and when we would expect to observe far-reaching effects of WGD within plant communities.

This discussion has focused on the direct effects of competitive interactions, but indirect effects could also be altered by WGD through the same mechanisms (Fig. 2). Indirect effects are effects that are mediated through another species and they could have a positive or negative impact on the focal species. For example, the presence of polyploid plants in a community might alter the presence and abundance of herbivore species. These changes in the herbivore community caused by WGD could, in turn, indirectly affect the amount of damage experienced by the parental diploids or other members of the plant community, potentially increasing or decreasing damage. Similar scenarios could be envisioned for WGD-induced changes in pathogen, pollinator, AMF, and other types of organism, creating a vast number of possible indirect effects that could be mediated by WGD. As with direct interactions, the introduction of a polyploid to a community could have substantially different effects from those of a randomly added plant species. For example, allopolyploids could act as a bridge between parental diploid species, facilitating host shifts of herbivores or pathogens and increasing the diversity of herbivores feeding on diploids. Alternatively, allopolyploids may act as a sink that reduces attack. Both of these patterns have been observed in diploid hybrid systems (e.g. Whitham, 1989; Whitham *et al.*, 1999), but are yet to be shown in polyploids. The question remains as to whether WGD creates a fundamentally different effect on indirect interactions within a community.

VII. Sand, pebbles, and boulders

The recent, albeit modest, upswing of research on the ecology of WGD is leading us towards a better understanding about how far the effects of polyploidy extend through natural communities. We are now faced with the challenge of disentangling how and when WGD has played a major role in shaping the ecological interactions within a community. A central question in this regard is to determine the circumstances in which we expect to observe small vs large changes in the community context. For example, the placement of polyploids within an interaction network may dictate the magnitude of the observed effect of WGD. Large changes would be predicted when WGD changes the interaction network structure such that polyploids become highly connected within the network. If a polyploid occupies a central, well-connected node within an ecological interaction network, the loss of that species could have large effects on the community. Studies of mutualistic networks, for instance, have shown that the removal of highly linked species is more likely to cause declines in overall species diversity (e.g. Memmott *et al.*, 2004; Saavedra *et al.*, 2011). Whether WGD can change the interaction structure remains to be tested, but indirect evidence suggests a tie between genetic changes and interaction diversity. For example, hybrid plants and their backcrosses can harbor higher interaction diversity than their parents (e.g. Whitham *et al.*, 1999), suggesting that the position of allopolyploids within an interaction network may be different from that of the diploid parents. Sorting out the confounding effects of hybridization in allopolyploids, however, would be an essential aspect of testing this idea.

Another situation that could promote large changes in community context is when there are strong feedbacks between different types of interaction. For example, we know that above-ground interactions can influence the outcome of below-ground interactions such as when above-ground herbivores cause exudation of C from roots that can stimulate the growth of soil microbes (Wardle *et al.*, 2004). These indirect effects can also generate feedback loops where, for instance, increased microbial activity may in turn increase N availability for the plant and surrounding plant community (Wardle *et al.*, 2004). Thus, the stronger the feedbacks between different types of interaction, the more likely it is that indirect effects will cascade throughout the community. In this case, even subtle changes in one type of interaction could have large overall effects.

Although large effects are possible, the multitude of ways in which WGD can affect species interactions probably means that we will observe a range of community-level effects and that these may be species-specific. Yet, even in the cases where we find subtle effects, we should still pursue whether WGD matters, because small changes in community context could result in significant changes in fitness. As a consequence, if we observe changes in community context, it is important to determine whether the observed differences cause fitness-related effects or alter ecosystem functioning in some way. Otherwise, jumping to conclusions about the overall impact could lead us astray if changes in community context have unpredictable effects on fitness. Ideally, at the end of the day we would like to draw conclusions about how WGD functions in a community context.

We may not find general predictions that govern the role of WGD in community ecology, but we are bound to reveal exciting new data on how plant species become established and evolve in native communities.

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