

## ON THE NATURE OF THINGS: ESSAYS

*New Ideas and Directions in Botany*

# Out of one, many: The biodiversity considerations of polyploidy<sup>1</sup>

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The history of species concepts is fraught with confusion and heated exchanges. This is no less true for how best to treat polyploid plant taxa. Polyploidy—whole-genome duplication—is an important source of vascular plant diversification (Wood et al., 2009). Following the discovery of polyploidy just over a century ago, interest in genome duplication and the revelation that ploidy variation is more than an infrequent and curious phenomenon generated support for recognizing ploidy races as units of biological diversity (Ramsey and Ramsey, 2014). Nevertheless, chromosome number variation continues to challenge studies of plant ecology and evolution because of persistent uncertainties over polyploid phenotypic diversity and reproductive interactions with their diploid progenitors. Plant systematists have struggled with the classification of polyploid complexes because, in contrast to diploid populations where phenotypic differences are often evident and concomitant, polyploid complexes can exhibit phenotypic differences ranging from subtle to strikingly distinct, despite usually strong reproductive incompatibilities (Fig. 1). This disagreement over how genetic differentiation without corresponding morphological differences should be interpreted in the context of speciation has resulted in relatively few polyploids being widely recognized as taxonomic entities (Soltis et al., 2007). As a result, polyploids have been left stranded in a taxonomic no-man's land where polyploidization is simultaneously considered a major mechanism of plant speciation and biodiversity, yet insufficient for species recognition (Mayr, 1992).

Although arguments over the tacit or formal recognition of polyploids as taxonomic species are likely to continue, more widely recognizing polyploids as functional units of biological diversity in ecological studies would acknowledge the contemporary importance of genome duplication to ecological and population dynamics, and align with the recognition of its importance to plant evolution. For example, the inclusion of ploidy variation in ecological analyses will likely challenge our understanding of interspecific

interactions and biodiversity across spatial and phylogenetic scales, and have significant consequences for ecological applications such as conservation efforts (Severns and Liston, 2008) and the management of invasive species (te Beest et al., 2012). Moving forward, polyploids meeting minimum criteria for species delimitation (de Queiroz, 2007) should be explicitly treated as units of biodiversity in ecological studies similar to diploid groups, perhaps relying on functional designations such as varieties or cryptic species. To do so, integrative approaches combining evolutionary genetics and ecological analyses should be extended to identify and evaluate polyploid populations for ecological novelty. Otherwise, the continued reluctance to recognize some polyploids in ecological studies will ignore an important source of phenotypic novelty and mask the influence of genome-scale mutations on the origins of new biodiversity.

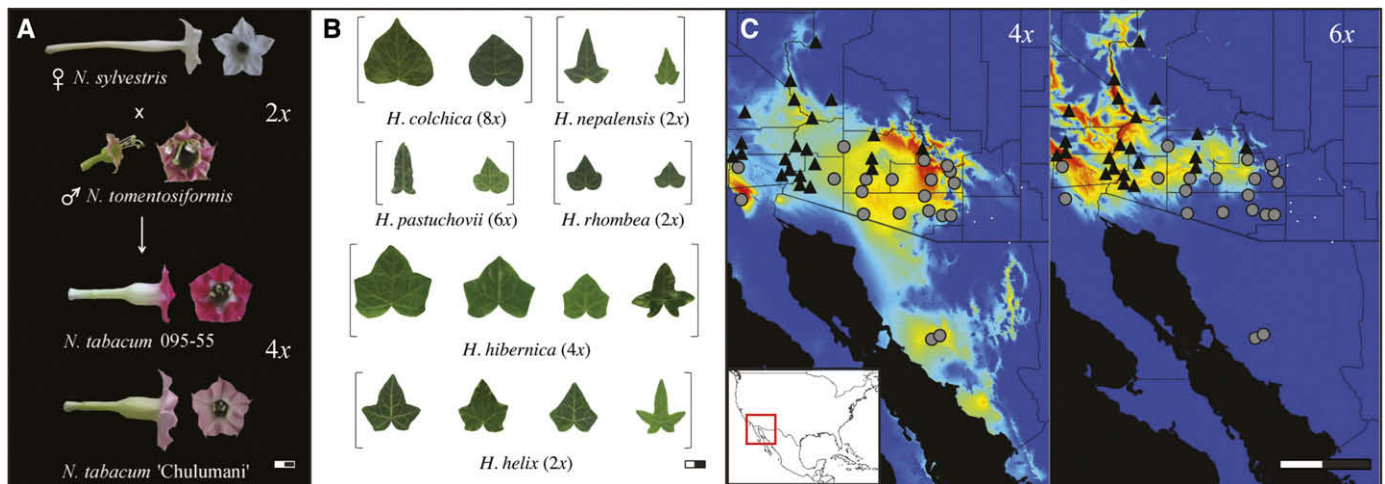
## THE POLYPLOID “PROBLEM”

The confusing relationships between polyploids and their diploid progenitors (e.g., hybridization, recurrent formation) have justifiably fostered a conservative stance by evolutionary biologists and systematists when dealing with polyploid complexes. Polyploids often exhibit low rates of intercytotype gene flow via semifertile F1 hybrids (i.e., triploids, pentaploids, etc.) or unilateral sexual polyploidization (i.e., unions of reduced and unreduced gametes), especially among higher ploidies (e.g., tetraploids, hexaploids, etc.). Yet, intercytotype reproductive isolation is typically as strong as that between diverging diploid species (Husband et al., 2016), such that polyploids meet species criteria under the Biological Species Concept. However, ploidy remains a difficult phenotypic/genetic trait to identify in the field or herbarium, and despite the evolutionary implications of polyploidy, taxonomists have largely argued that it is impractical to broadly apply Linnean classification to populations differing in ploidy without corresponding morphological differences. Taxonomic decisions can therefore be biased by a polyploid lineage's mode of origin: allopolyploids (those formed via hybridization between closely related populations) often exhibit phenotypic and molecular intermediacy, or even transgressive

<sup>1</sup> Manuscript received 19 May 2017; revision accepted 19 June 2017.

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**FIGURE 1** Whole-genome duplication can produce an array of ecologically relevant phenotypic differences. (A) Natural interspecific crosses between diploid *Nicotiana sylvestris* and *N. tomentosiformis* produce allotetraploid *N. tabacum*, which is distinct in floral morphology and transgressive in floral pigmentation and coloration from the perspective of their pollinators (McCarthy et al., 2017). (B) Closely related European and Asian *Hedera* species (Green et al., 2011) exhibit staggering leaf variation at multiple ploidal levels, including diploid *H. helix* and its autotetraploid *H. hibernica*, which are invasive in North America. (C) The geographic distributions of diploid, autotetraploid, and autohexaploid *Larrea tridentata* in the southwestern United States and northern Mexico are mostly non-overlapping, but in areas where they do co-occur, environmental niche predictions (warmer colors indicate higher suitability), here shown for tetraploids (gray circles) and hexaploids (black triangles), suggest the cytotypes exhibit some degree of ecological niche differentiation (Laport et al., 2013). Scale bars: (A, B) = 1 cm, (C) = 200 km. Images provided by Elizabeth McCarthy (A) and by Adam Green, Justin Ramsey, and Tara Ramsey (B).

phenotypes (differentiated from both parents), making them easier to identify in the field or with molecular markers than autopolyploids (those formed from genome duplication within a lineage), where morphological differences are often ambiguous or absent (Soltis et al., 2007).

The current genomics revolution, however, is drastically altering the way we understand species and necessitates a re-evaluation of polyploid biodiversity. For example, molecular tools are being leveraged to identify cryptic species, and whole-genome sequencing has revealed that both plant and animal species hybridize much more commonly than previously appreciated. Therefore, while a conservative approach to polyploid taxonomy may remain prudent in light of disagreements over species concepts, simply decrying the complexity of diploid–polyploid relationships as a reason for not recognizing populations differing in ploidy as units of biodiversity is not. Failing to account for the phenotypic novelty that can accompany genome duplication in ecological studies obscures the fact that an increasing number of studies show that allo- and autopolyploid cytotypes often have unique responses to the abiotic environment and novel interspecific interactions (Segraves and Anneberg, 2016). Thus, it seems appropriate that there be judicious functional recognition of currently intraspecific polyploids (e.g., as varieties or cryptic species), just as has become common practice for diploid species where significant geographical or ecological structuring, genetic or phenotypic differentiation, and/or reproductive isolation is evident.

## THE INFLUENCE OF POLYPOIDS ON PATTERNS OF BIODIVERSITY

Many studies clearly show that ecological and phenotypic differences associated with ploidy shifts are common and sometimes

profound. These ploidy-specific changes have the potential to influence patterns of biodiversity across varying scales. For example, recent work has demonstrated that populations differing in ploidy can exhibit climatic niche differences (Laport et al., 2013), distinct physiological strategies for water use (Maherali et al., 2009), unique mycorrhizal associations (Těšitelová et al., 2013), shifts in pollinator visitation (Thompson and Merg, 2008), increased competitive or colonization potential (te Beest et al., 2012), and differences in secondary chemistry resulting in altered flower coloration (McCarthy et al., 2017). These ploidy-specific changes have the potential to influence patterns of biodiversity across varying scales, and including ploidal diversity in ecological studies will ensure that we are not misunderstanding the fundamental ecological processes influencing patterns of biodiversity. For example, given the frequent occurrence of polyploidy in herbaceous taxa of temperate and arctic regions, measures of diversity in these areas (e.g., phenotypic, phylogenetic, or species diversity) that do not account for intraspecific ploidal variation risk misrepresenting the diversity of regional floras. Furthermore, predicting the impact of climate change on species distributions may hinge upon whether a species' range comprises ecologically and geographically differentiated cytotypes (e.g., Hersch-Green, 2012; Laport et al., 2016).

The ecological consequences of genome duplication on biotic interactions is perhaps most consequential at the community level. Given the potential for ploidy-specific phenotypes and ecological differences, ploidy information could be crucial in studies of community ecology when identifying the processes underlying why particular populations and species co-occur (e.g., niche partitioning, invasiveness), and for informing restoration or management strategies (e.g., community responses to human-caused disturbance or changing environments). Interpretations of species co-occurrence or invasion naïve to ploidal variation run the risk of misrepresenting biotic interactions within a community if, for example, they fail

to recognize cytotype-specific pollinator visitation (e.g., Thompson and Merg, 2008). Shifts in flowering phenology associated with genome duplication could result in an extended flowering period where two cytotypes co-occur, relative to communities comprising a single ploidy. Such differences could have cascading ecological and evolutionary effects on the pollinators and co-occurring plant species, such as providing additional opportunities for pollinator resource collection or promoting cytotype-specific specialization. Thus, whether recognition of polyploids is formalized or not, recognizing polyploids as functional units of biodiversity has the potential to offer novel insights into ecological processes and patterns at both community-level and broader spatial scales.

## OUTLOOK

Polyploidy continues to challenge our understanding of speciation and patterns of biodiversity. However, significant headway in understanding the evolutionary and ecological aspects of genome duplication has been made, especially over the last ~20 years. Technological advancements are facilitating the detection and characterization of previously unrecognized ploidal variation. For example, software-aided morphometric or phenotypic analyses, ecological niche models, and phylogenetic models incorporating chromosome numbers have streamlined studies of polyploids in the wild (e.g., Mandáková and Münzbergová, 2008; Glick and Mayrose, 2014). High-throughput flow cytometry screens for DNA content have especially aided in identifying the frequency of polyploids, as well as their phenotypic and geographical distributions, and should be leveraged more widely to better document polyploid complexes (Kron et al., 2007). Moreover, online repositories of chromosome information (e.g., Chromosome Counts Database, Index to Plant Chromosome Numbers) are providing a handy way to document cytogeographic information. Our clearer understanding of the importance of polyploidy in plant evolution, combined with the advent of such tools, suggests the time is right for ecological studies to treat (at least some) intraspecific ploidy variation as independent units of biodiversity to help address major ecological and evolutionary questions. For example, it would be illuminating to identify the frequency and ways genome duplication affects community structure and biotic interactions. Do ploidy changes typically result in novel species interactions? Are polyploids more likely to invade a community? How do polyploid-associated phenotypes influence range shifts and responses to climate change? By explicitly considering ploidy variation, we can only expand our understanding of how such a rampant, radical genomic mutation, which has played such an important role in plant evolution, also affects biodiversity over ecological timescales.

## ACKNOWLEDGEMENTS

The authors thank Justin Ramsey, Tara Ramsey, Brian Husband, Pamela Diggle, and three anonymous reviewers for comments that improved this manuscript. Elizabeth McCarthy, Adam Green, Justin Ramsey, and Tara Ramsey graciously provided images. The ideas presented in this paper were inspired by research funded by National Science Foundation grants NSF-EF 1550813 and NSF-DEB 1556371.

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