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Ecological studies of polyploidy in the 100 years following its discovery

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Polyploidy is a mutation with profound phenotypic consequences and thus hypothesized to have transformative effects in plant ecology. This is most often considered in the context of geographical and environmental distributions—as achieved from divergence of physiological and life-history traits—but may also include species interactions and biological invasion. This paper presents a historical overview of hypotheses and empirical data regarding the ecology of polyploids. Early researchers of polyploidy (1910s–1930s) were geneticists by training but nonetheless savvy to its phenotypic effects, and speculated on the importance of genome duplication to adaptation and crop improvement. Cytogenetic studies in the 1930s–1950s indicated that polyploids are larger (sturdier foliage, thicker stems and taller stature) than diploids while cytogeographic surveys suggested that polyploids and diploids have allopatric or parapatric distributions. Although autopolyploidy was initially regarded as common, influential writings by North American botanists in the 1940s and 1950s argued for the principle role of allopolyploidy; according to this view, genome duplication was significant for providing a broader canvas for hybridization rather than for its phenotypic effects *per se*. The emphasis on allopolyploidy had a chilling effect on nascent ecological work, in part due to taxonomic challenges posed by interspecific hybridization. Nonetheless, biosystematic efforts over the next few decades (1950s–1970s) laid the foundation for ecological research by documenting cytotype distributions and identifying phenotypic correlates of polyploidy. Rigorous investigation of polyploid ecology was achieved in the 1980s and 1990s by population biologists who leveraged flow cytometry for comparative work in autopolyploid complexes. These efforts revealed multi-faceted ecological and phenotypic differences, some of which may be direct consequences of genome duplication. Several classical hypotheses about the ecology of polyploids remain untested, however, and allopolyploidy—regarded by most botanists as the primary mode of genome duplication—is largely unstudied in an ecological context.

1. Introduction

Polyploidy—whole genome duplication—is common in flowering plants [1–4]. First described almost a century ago, polyploidy was well studied in the cytogenetics era as well as more recently in the context of molecular genetics and genome evolution [5–8]. While polyploidy has historically garnered the greatest attention from geneticists and evolutionary biologists, the presence of ploidy variation within plant genera—and in some cases, among populations of single species—raises major ecological questions [9–14]. How do new polyploid populations establish themselves demographically? Does polyploidy directly or indirectly mediate environmental adaptation? What are the consequences of genome duplication for interactions with other species? Such questions were raised by early students of polyploidy, some of whom showed remarkable foresight in their writings [1,15–19]. Moreover, data produced by plant breeders, geneticists and taxonomists in subsequent years offered insights to the biological attributes of polyploids that are clearly relevant to their ecology [20–26]. It would be many decades, however, before the ecology of polyploids received dedicated study. Even in the early 1990s, Ernst Mayr [27] was astonished by the absence of ecological data about polyploids as he applied

alternate species concepts to a regional flora. How can so much be known about polyploidy, and yet so little?

In an attempt to answer this question—and more generally, to report on the state of the field and avenues for future study—this paper takes a historical approach to describe hypotheses and empirical data about the ecology of polyploids. Several caveats are acknowledged at the outset. First and foremost, summarizing a century of polyploid research in a short paper requires some degree of simplification, in particular regarding the types of research activities that were conducted at different times. We have tried to identify noteworthy exceptions as well as examples of particularly influential and pioneering efforts in the text. Second, there are many research efforts and findings that are glossed over or excluded altogether for space reasons. We want to acknowledge the many students of polyploidy, past and present, whose hard work has contributed to botanists' understanding of chromosome evolution.

In this paper, we use the term autopolyploid to indicate polyploids arising within or between populations of single species, and allopolyploid to denote polyploids derived from interspecific hybridization, where species are defined by the biological species concept [5,6,16]. The term neopolyploid refers to an early generation polyploid mutant—either arising spontaneously or induced by chemical or environmental treatment—while established polyploids occur in natural populations, and thus have been subject to conventional evolutionary processes like natural selection and genetic drift for an unknown number of generations [5,6,10,14,28–31].

2. Early conceptions by geneticists who first described polyploidy (1910s–1930s)

Polyploidy was regarded as a potent agent of phenotypic change from its earliest descriptions by geneticists—in fact, the vast majority of spontaneous and induced polyploids were originally recognized on the basis of distinctive outward characteristics rather than karyotype or meiotic behaviour [32–38]. For example, Hugo DeVries [32] identified autotetraploid mutants of *Oenothera biennis* (evening primrose) based on the size and shape of flower buds and inflorescences, as well as foliage colour and pubescence. Similarly, in the F_2 generation of *Digitalis purpurea* × *Digitalis ambigua*, tetraploid plants ('*D. mertonensis*') were recognized based on their morphological constancy (e.g. no segregation for parental leaf or floral traits) and large size (e.g. linear measurements on floral structures approx. 25% greater compared with diploid F_1s) [35,38]. The broader significance of such phenotypic manifestations was not lost on early workers, and geneticists speculated on their potential role in ecological adaptation, evolutionary diversification and crop improvement. In his description of a spontaneous autotetraploid plant of *Datura stramonium* (jimson weed), Albert Blakeslee [33] wrote that he suspected polyploidy was 'one of the principle methods in the evolution of plants . . . its occurrence would establish the barrier between a new species and its parental form that Darwin sought, and it would give a reason for the prevalence of even numbers in the counts of chromosome pairs' (p. 264). With such encouragement, many geneticists initiated studies of polyploids through the 1920s and 1930s.

Several works from this time period showed particular foresight, providing a framework for studying the ecology of polyploids that would stand for many years. Foremost among these is Øjvind Winge's description of allopolyploids as 'constant species hybrids' that exhibit intermediacy to diploid progenitors in their phenotypic traits, environmental tolerances and geographical distributions [16,39–41]. Because chromosomes contributed by different species (homeologous chromosomes) rarely or never interact during meiosis (allosyndesis), Winge suggested that allopolyploids are locked into a state of permanent hybridity that has the 'quality of pure species'—in contrast to diploid hybrids, which if fertile segregate for parental traits in F_2 and backcross generations. Chromosome pairing in autopolyploids was thought to involve random interactions among three or more homologous chromosomes (autosyndesis) contributed by individuals of a single species (and typically, a single population). Thus, trait differences between diploid progenitors of autopolyploids would be very small compared with trait differences between diploid progenitors of allopolyploids, and lost over time to segregation and independent assortment [5,6]. Winge's ideas strongly influenced expectations about the phenotypic characteristics and ecology of auto- and allopolyploids, as discussed later in this paper.

Another influential work from this era was Arne Müntzing's 'The evolutionary significance of autopolyploidy' [1]. A Swedish geneticist, Müntzing researched polyploidy in *Dactylis glomerata* (orchard grass), *Secale cereale* (rye) and *Galeopsis* spp. (hemp-nettle) while following developments in other taxa [1,20,21,37,42–44]. Müntzing [1] summarized available information about 'intraspecific polyploids' (i.e. autopolyploids but also allopolyploids derived from hybridization of cryptic diploid species) in natural species and 'experimental autopolyploids' (i.e. neopolyploids) in model systems with an exhaustive, 116-page paper published in the journal *Hereditas* in 1936. Müntzing argued that diploids and autopolyploids exhibit quantitative differences in growth and morphology, maintain distinct spatial and environmental distributions that are suggestive of ecological divergence and are reproductively isolated to a degree that seems comparable to that of good diploid species. Data presented by Müntzing [1] were based on limited sampling and basic measurements, and in some cases, were simply impressions of plant breeders and taxonomists. Moreover, Müntzing's broad definition of autopolyploidy—which did not invoke specific cytogenetic criteria, like chromosome pairing and patterns of inheritance—would be criticized by G. Ledyard Stebbins and others during the Modern Synthesis [2,45]. Nonetheless, the sheer volume of information presented by Müntzing and the repeated findings across plant genera made a compelling case for transformative effects of genome duplication.

3. The cytogenetics era (1930s–1960s)

Following early descriptions of polyploidy, there was an explosion of genetic and cytological studies of experimental polyploids in model systems. At the time, polyploidy represented an unusually tangible genetic feature that could be directly observed and manipulated—it thus attracted interest, not only from plant breeders but also from a broad spectrum of empirical and theoretical geneticists. For example, pioneers of the field like Albert Blakeslee and Barbara McClintock dabbled with polyploidy in their respective studies of jimson weed and maize [46–48], while Sewell Wright, R. A. Fisher

and J. B. S. Haldane adapted formulae to consider multisomic populations [49–52]. Much was learned about the biology of polyploids in a short period of time, and many of these findings would influence botanists' views of polyploid ecology.

The phenotype characteristics of experimental polyploids are well described in other papers [5,6,11,12,53] so will be summarized briefly here. Arguably, the most widespread and conspicuous features of neopolyploids are increased cell size, slowed cell division and tissue development, and increased organ size at maturity—a suite of characters sometimes called *gigas* effects, in reference to Hugo de Vries tetraploid mutant of evening primose ('*Oenothera gigas*'). Both auto- and allopolyploids were found to have reduced fertility compared with diploid progenitors (attributed to complex chromosome pairing at the tetraploid level) and a breakdown of gametophytic self-incompatibility (attributed to allele interactions in diploid pollen) [1,20,42,54,55]. Crosses between diploids and experimental polyploids yielded progeny of low viability (the so-called triploid block) and fertility [43,47,56]. An image of neopolyploids thus emerged—robust plants, usually large in stature and vigorous in growth, if less fecund than diploids and more prone to self-fertilization [5,6]. Because polyploids achieved reproductive isolation and a substantial degree of phenotypic divergence from diploid progenitors in a single generation, polyploidy was viewed as a macromutation and mechanism of sympatric speciation [1,15,16,37,42,48].

Increasingly sophisticated cytogenetic studies revealed that expectations about the meiotic behaviour of polyploids described in the 1920s and 1930s were, at least in some cases, simplistic or incorrect. For example, experimental autopolyploids were found to exhibit much less than the maximum possible number of pairings between homologous chromosomes during meiosis; many autopolyploids have random bivalent pairing, thus achieving multisomic inheritance without multivalents [25,57]. Moreover, chromosome pairing in both auto- and allopolyploids was found to evolve rapidly in the face of fertility selection, suggesting that meiotic behaviour is not an indelible feature of polyploids determined at the time of formation [58,59]. Finally, Winge's notion of allopolyploids as constant hybrids was found to break down in many cases, due to pairing of homeologous chromosomes during meiosis [60–62]. For example, in *Nicotiana glauca* × *Nicotiana landsdorfii*, allotetraploid F_2 plants exhibit occasional multivalent pairing and subsequent generations (F_3–F_5) segregate for leaf and floral characters that distinguished the parental diploid species [63]. Based on these experiments with wild tobaccos, Russian geneticist Dontcho Kostoff [63] concluded, 'it seems that the constancy of amphidiploids is very questionable . . . the process of meiosis in the majority of amphidiploids recorded by various authors suggests that they should not be constant' (pp. 197–198).

In the wake of cytogenetic investigations of model systems in the 1930s and 1940s, studies of polyploidy in wild species became mainstream. The disciplines of cytogeography and cytotaxonomy were particularly important for insights into the spatial distributions of polyploids. For example, floristic comparisons suggested that the incidence of polyploidy varied by latitude, altitude and habitat [19,64–68]. In an analysis of Scandinavian plant communities, Åke Gustafsson [19] concluded that polyploids were common in arctic, shore and weed floras—in part due to the abundance of perennials with means of vegetative reproduction, which are often polyploid—but sparse in haline and alpine floras. Perhaps the most famous claim about the geographical incidence of polyploidy regarded latitude [2,69]. Several authors reported increased frequencies of polyploids in arctic and boreal areas compared with temperate and Mediterranean regions, but these datasets were confounded by latitudinal differences in the occurrence of genera and families, plant life-forms and environmental disturbance. Attempts were made to account for these factors, which are interesting in their own right [2,68–72]. Most botanists today acknowledge latitudinal variation in the incidence of polyploidy but it seems an area ripe for additional study [3,73]. For example, latitudinal analyses of polyploidy are biased towards floras of Europe and North America; much less cytogeographical work has been done in the tropics or in temperate regions of the Southern Hemisphere [69]. Building on knowledge of species distributions and evolutionary relationships among genera and families, more explicit testing of the incidence of polyploids is now possible [73–76]. For example, a phylogenetically explicit analysis of the genus *Clarkia* found that polyploids on average have fivefold greater range sizes (area in km^2) than diploids [75]. On the other hand, a broad-scale analysis of the North American flora revealed differences in the size and latitude of species' ranges based on phylogenetic history but not ploidy [76]. Among arctic plants with restricted distributions, polyploids are much more common in the 'Atlantic region' (which was heavily glaciated during the Pleistocene) than in the 'Beringian region' (which was much less glaciated during the Pleistocene), but this result was not evident for widespread species groups [73].

Much less contentious than the aforementioned floristic comparisons were analyses of closely related diploids and polyploids. Within genera and taxonomic species, cytogeographic studies in the 1930s and 1940s revealed cytotypes to have allopatric or parapatric distributions in the wild, with infrequent co-occurrence within local populations [15–17,64,65,77–81]. For example, Giles [17] found diploid *Cuthbertia graminea* (=*Callisia graminea*, grass-leaved roseling) in the arid sandhill environments of North Carolina while autotetraploids occupied a wider area of the coastal plain, including Georgia and Florida. In studies of plants with broad environmental distributions, Clausen *et al.* [15] often discovered geographically structured variation in ploidy level within taxonomic species or among closely related species. Together with chromosomal rearrangements, polyploidy was therefore viewed as a principle stage in plant evolution that facilitated ecological adaptation and speciation [15,16,82,83]. It should be noted that early cytotaxonomic work was based on limited field sampling (in terms of number of sites and total number of individuals) and inferred climatic or edaphic associations without quantitative data. These projects nonetheless made a strong case for the spatial structuring of polyploid populations and species; the emphasis that population biologists would later place on environmental adaptation and competitive exclusion can be traced to classical cytogeographic findings [3,9,11].

4. Framing of polyploidy by the Modern Evolutionary Synthesis

The architects of the Modern Synthesis downplayed sympatric speciation and saltational change in their respective

works, but polyploidy was nonetheless featured prominently as a counterpoint to how evolution usually worked. By the 1940s, polyploidy was known to be a common and recurrent form of genetic variation in plants, and implicated as a factor in ecological adaptation and speciation, as well as in plant breeding [1,15,16,20,33,48]. Thus, G. Ledyard Stebbins devoted two chapters of *Variation and Evolution in Plants* [2] to polyploidy, while Theodosius Dobzhansky had one chapter in *Genetics and the Origin of Species* [84]. Even zoologist Ernst Mayr mentioned polyploidy routinely in his writings, including *Systematics and the Origin of Species* [85].

While the focus of the Modern Synthesis was on evolutionary biology, these works had direct and indirect implications for ecological studies of polyploids. In particular, the argument that allopolyploidy is much more common in nature than autopolyploidy—advocated most vociferously and influentially by G. Ledyard Stebbins [2]—would discourage ecologists from studying genome duplication for many years. As it was articulated by Stebbins and other North American botanists, including Verne Grant and Jens Clausen, allopolyploidy presented three major problems to nascent ecological work [2,3,16,45,69]. First, allopolyploid systems posed taxonomic challenges; historical relationships were complex and reticulate, and it was difficult to precisely identify diploid progenitors for comparison to an allopolyploid species. Second, the phenotypic attributes of allopolyploids reflected not only ploidy *per se* but also genomic composition achieved during polyploidization in the F_1/F_2 generation or thereafter via introgressive hybridization. Thus, many genetic factors could contribute independently and in combination to the ecology of allopolyploids. Third, new classification schemes for evaluating allopolyploid origins were convoluted, as they incorporated cytogenetic criteria that were less intuitive than mode-of-origin models that had been used in the past. In the 1930s and early 1940s, polyploidy was envisioned as a chromosome polymorphism that—at least for a first pass—could be studied in an ecological context by comparing closely related diploid and polyploid populations [1,20,67]. By the mid-1950s, polyploidy was a hot mess of interspecific hybridization, nebulous taxonomic boundaries and cytogenetic complexities that, while fascinating from an evolutionary perspective, was not inviting to ecological research.

In hindsight, the emphasis placed on allopolyploidy during the Modern Synthesis is curious given widespread recognition of autopolyploidy just a few years prior [1,17, 18,20,54,64,65,77–79,81]. In part, this represents sleight-of-hand on the part of Stebbins, who in 1947 introduced a new classification system [45]. The term segmental allopolyploid was intended for leaky allopolyploids with occasional pairing of homeologous chromosomes; in practice, it often included autopolyploids that either (i) were derived by crosses among populations or subspecies; or (ii) exhibited cytogenetic features that were 'unexpected' for non-hybrids (regular bivalent pairing, high fertility, structural divergence among homologous chromosomes, etc.). Thus, polyploids that prior (and many current-day) researchers would describe as autopolyploids were re-typed as segmental allopolyploids in Stebbins' classification scheme [2,5,6,45,69,86,87].

Looking beyond semantics, Stebbins [2,69,88] was influenced by findings of plant breeders that allopolyploids generated from wide crosses tend to be vigorous and highly fertile, and moreover that hybridization among autopolyploids induced in different varieties or subspecies could

sometimes improve agricultural performance [21,89,90]. Although Stebbins downplayed the importance of mutation rate in his writings, he may have been impressed by much more frequent formation of polyploids by F_1 interspecific hybrids compared with pure species populations [36,91,92]. In the F_2 generation of *Layia pentachaeta* × *Layia platyglossa*, for example, Clausen *et al.* [16] found that more than 80% of plants were triploid or tetraploid. Results from artificial crossing experiments indeed highlight the potential role of hybridization in polyploid formation and establishment. It may be argued, however, that application to natural systems should be tempered by the low occurrence of interspecific hybridization in the wild compared with what is routinely achieved in the greenhouse or experimental garden [5,6].

Related to the strong emphasis on allopolyploidy, writings of the Modern Synthesis discussed potential advantages of polyploidy principally in terms of genetic phenomenon, like hybrid vigour, rather than discrete phenotypic traits (physiology, life-history, phenology, etc.) that could practically be investigated using the tools of ecology [2,3,16,45,69]. In this context, it is interesting to compare the writings of Arne Müntzing versus G. Ledyard Stebbins. While himself a student of crop improvement in polyploid grasses, including the role of heterosis and use of intervarietal crosses to improve yield, Müntzing also highlighted the effects of polyploidization *per se* in evolution—increased size and stature that could affect competition, altered anatomical and biochemical features that could affect environmental tolerances, delayed flowering times that could affect reproductive isolation and the timing of events in the life-cycle, and so forth [1,20,21,42,44]. By contrast, Stebbins focused on advantages afforded by increased hybrid vigour, allelic diversity and epistatic gene interactions, as well as the increased number of hybrid combinations possible at the polyploid level [2,69,88,93]. Thus, polyploidy was a neutral factor or detriment to evolutionary progress, except in providing a wider canvas for hybridization.

In fairness to Stebbins, he was not the only North American botanist who advocated for the importance of allopolyploidy in this time period; Verne Grant and Jens Clausen suggested that allopolyploidy was more common and evolutionarily significant than autopolyploidy, while acknowledging autopolyploidy may be important in some genera [3,15,16]. Grants' thinking reflected his empirical studies in the Polemoniaceae, including elegant work with neopolyploids produced in crosses of closely related species of *Gilia* [23,92,94,95]. In *Plant Speciation* [3], Grant wrote 'my view, coloured by my personal experience with several groups . . . in both nature and the experimental garden, is that [allopolyploids] often exhibit superior vigour, homeostatic buffering, and adaptability compared with their diploid relatives' (p. 316). Grant suggested that naturally occurring polyploids rarely exhibit cytogenetic characteristics of autopolyploidy (multivalent pairing, sterility, multisomic inheritance, etc.) and that such plants are in any case unlikely to have the advantages of allopolyploids. Grant concluded that 'the available evidence in the vascular plants is that [allopolyploidy] is far more common and widespread than autopolyploidy' (p. 306).

Jens Clausen's thinking is more difficult to parse and, to our reading, more centrist on the roles of auto- versus allopolyploidy than would later be interpreted by Stebbins and Grant [2,3,22,69,93]. On the one hand, Clausen was fascinated by allopolyploidy and studied it extensively in California tarweeds and North American violets [15,16,82,96]. Clausen, Keck and

Hiesey's 1945 monograph on allopolyploid speciation in the Madiinae [16] was an especially influential work that investigated cytogenetic origins of allopolyploids as well as their morphological features. The monograph also critically reviewed instances of polyploidy known at the time of publication; the heavy emphasis on allopolyploidy, both in the empirical work presented by the volume and in its literature review, would later be cited as evidence of the role of interspecific hybridization during and following genome duplication [2,3,69]. On the other hand, Clausen et al. [15,97] for many years worked with plant systems that were understood in the context of autopolyploidy. For example, the North American members of the *Achillea millefolium* complex (=*Achillea borealis*, wild yarrow)—the focus of Clausen, Keck and Hiesey's 1948 monograph about climatic adaptation, and subject of research from the 1930s through to the 1960s—exhibit biogeographic and cytogenetic features that by the Carnegie Group's own description appear characteristic of autopolyploidy. Crosses among ecological races of wild yarrow at the hexaploid level segregate widely for parental phenotypes in a manner that is consistent with polysomic inheritance, while crosses between tetraploids and hexaploids yield semi-fertile F_1 pentaploids with seemingly random chromosome pairing and viable F_2/F_3 generations [15,97–99].

Careful reading of the literature review in the 1945 monograph makes it seem less damning of autopolyploidy than has sometimes been assumed [16]. The lion's share of the review focuses on experimental polyploids generated by interspecific crosses—some 18 enumerated examples, as well as another dozen briefly summarized cases—that are directly comparable to the empirical work on tarweeds contained in the volume. Clausen in this section acknowledged that 'discussion of the many known cases of autoploidy falls somewhat outside the scope of this review' (p. 73). Later in the monograph, Clausen et al. [16] considered 10 examples each of natural autopolyploids and allopolyploids. While highlighting shortcomings of available data on wild polyploids, their respective classification was nonetheless accepted pending future study. In the case of putative autopolyploid complexes, the principle concern was whether multiple cryptic diploid species may exist within the group, such that a hybrid origin of polyploids would be undetected—a reasonable concern given the state of plant taxonomy before the biosystematics era [1,15,16,20]. The monograph concluded that 'simple doubling of the chromosomes, with all their included genes, clearly is a process that may alter the physiologic balance of a plant, so that it can occupy an ecologic niche to which its progenitor was not adapted' (p. 148). This sentiment is echoed in Clausen's later writings—which acknowledged autopolyploidy as an evolutionary mechanism in plants, albeit less common than allopolyploidy [82,83]—and contrasts with conclusions reached by Grant and Stebbins [2,3,22,69,88].

In summary, the emphasis on allopolyploidy that emerged from the Modern Synthesis reflected multiple factors—empirical data from crossing experiments that had recently been published, the particular plant systems that had been selected for investigation by researchers, and probably most importantly, evolving terminology that focused on cytogenetic criteria rather than mode-of-origin. The emphasis may also have been an overreaction to work in the 1930s and early 1940s that was quick to assign the moniker of autopolyploidy on the basis of morphological similarity, rather than detailed consideration of parentage and cytogenetic issues [1,15–17,20,77–79]. It is interesting that European researchers, including Arne Müntzing, C. D. Darlington and Áskell Löve, maintained that auto- and allopolyploidy were both common and important in plants [21,44,100,101] yet proved less influential than Stebbins in the emerging biosystematics era. By the mid-1950s, views on polyploid origins had profoundly changed from that of the previous 30 years, and the dominant role of allopolyploidy would remain largely unquestioned until nearly the end of the twentieth century.

5. Polyploidy in plant taxonomy

(a) The biosystematics era (1950s–1970s)

In the years following World War II, a multidisciplinary form of plant taxonomy rose to prominence in North America and Europe. Biosystematics integrated analyses of geographical and ecological distributions, crossing barriers, chromosome behaviour of parental species and F_1 hybrids, morphology and anatomy, and breeding systems. Polyploid groups were a common subject of biosystematic analysis, owing both to their frequent occurrence in north temperate floras (where most biosystematic work was performed) and evolutionary complexities that had stymied traditional morphological classification; some standout examples include monographs of the genus *Camissonia* [102], *Clarkia* [24], *Lasthenia* [103] and *Microseris* [104], as well as more concise published works on *Achlys* [105], *Claytonia* [106], *Gilia* [94,95] and *Viola* [96]; Grant's *Plant Speciation* [3] and Lewis' 1980 paper ('Polyploidy in species populations') [9] provide reviews of polyploidy work during the biosystematics era. Nearly every polyploid that would be subject to ecological investigation at the end of the twentieth century had a preceding biosystematic study conducted between 1940 and 1980—biosystematics efforts were thus influential and framed many research questions that would be studied by population biologists.

In general, biosystematic work corroborated earlier cytogeographic and cytotaxonomic research, for example, by demonstrating contrasting spatial distributions for related diploid and polyploid cytotypes [9]. By the 1970s, plant taxonomists were sampling across large geographical areas and performing chromosome counts on 100s or 1000s of individuals—providing more rigorous sampling than previously had been done in natural species, and in some cases rivalling contemporary work that leverages flow cytometry [106–108]. Crossing experiments revealed reproductive barriers between ploidy levels (hybrid inviability caused by triploid block, hybrid sterility caused by production of aneuploid gametes by triploids) as expected from work by cytogeneticists in model systems [23,26,95,103,104,109]. In some cases, biosystematists anticipated results from molecular work in the 1980s and 1990s. For example, multiple origins of polyploid taxa are well known today based on analyses of DNA sequence data and molecular markers (isozymes, restriction fragment length polymorphisms, microsatellites, etc.), but during the biosystematics era were inferred on the basis of disjunct geographical or ecological distributions [110,111], morphological or karyotypic divergence among polyploid populations [112–114], and the occurrence of unreduced gametes in wild populations [108,115].

With a handful of exceptions [26,107,116], biosystematists were reluctant to apply the label of autopolyploidy to naturally occurring polyploid populations and species, even in cases

where cytogenetic features corresponded to those expected for autopolyploidy (e.g. multivalent chromosome pairing) and there were no signs of interspecific hybridization (e.g. polyploids in morphologically well-defined or monotypic species and genera). By contrast, allopolyploids were routinely identified—sometimes on the basis of limited empirical evidence, other times following meticulous study—and more often than not named as Linnean taxa [94–96,102,104]. Thus, Lewis & Lewis [24] recognized *Clarkia delicata* ($2n = 4x = 36$) as an allopolyploid formed by hybridization between *Clarkia epilobioides* ($2n = 2x = 18$) and *Clarkia unguiculata* ($2n = 2x = 18$), while *Clarkia prostata* ($2n = 6x = 54$) was an allopolyploid derived from *Clarkia speciosa* ($2n = 2x = 18$) and *Clarkia davyi* ($2n = 4x = 34$). The concepts of 'intraspecific polyploidy' and 'chromosome race' were applied by some authors to polyploids appearing to arise within a diploid species, where species boundaries are defined on the basis of morphological variation (taxonomic species concept, *sensu* Arthur Cronquist [117]) [26,108,109,113,118]. The most probable explanation for intraspecific polyploids is autopolyploidy, but such instances could represent allopolyploidy involving (i) sibling species that lack clear morphological boundaries, and thus are not taxonomically recognized; or (ii) morphologically divergent species with structural chromosomal similarities, so that allopolyploids segregate for parental traits and come to resemble one progenitor species more than the other [101,103,119,120]. Intraspecific polyploidy and chromosome race are neutral concepts that speak primarily to the appearance of polyploids and to their taxonomic treatment, hence avoiding the minefields associated with formal cytogenetic classification [9].

A dichotomy thus developed in the taxonomic treatment of polyploids [26,101,109,119,120]. Allopolyploids were thought to be common in nature and evolutionarily successful, and moreover to possess a phenotypic intermediacy to diploid progenitors that facilitated practical identification in the field. Allopolyploids were named as species and treated as *de facto* taxonomic units for the purposes of ecological study and conservation [24,95,96,102,104]. By contrast, autopolyploids were regarded as rare and evolutionarily much less significant. Because of the morphological similarities between diploids and autopolyploids—and potential for gene flow via triploid F_1 hybrids and unreduced gametes—there was general disinterest in naming autopolyploids, even among the few biosystematists who thought they existed frequently in nature [99,111–113,116]. Thus, Harlan Lewis [26] (who investigated autopolyploidy in *Delphinium* and allopolyploidy in *Clarkia*) wrote 'on no grounds . . . can one consider an autotetraploid population and its diploid progenitor as biological species or sibling species' (p. 269), while Walter Lewis [9] (who studied chromosome races in *Claytonia* and *Houstonia*) warned 'anyone planning wholesale naming of cytotypes ought to reconsider this approach before flooding the taxonomic literature with impractical names' (p. 135). One dissenting voice was Askell Löve [101], who argued for recognition of both auto- and allopolyploids on what he saw as a reasonable application of the biological species concept.

Looking beyond their contributions to cytogeography and cytotaxonomy, biosystematists described phenotypic and environmental correlates of polyploidy and thus contributed to hypotheses about its broader ecological significance. As early as the 1930s, botanists had noted variability in the incidence of polyploidy across genera and identified attributes that may be associated with polyploidization—either as cause (i.e. factors that promote the formation and establishment of polyploidy in diploid lineages) or effect (i.e. features that appear in polyploid lineages following establishment because of their particular genetic and phenotypic characteristics) [1,2]. Reputed correlates of polyploidy from this early period included life-history and physiological characteristics (annual versus perennial life-cycles, cold tolerance), reproductive traits (mating systems, self-compatibility) and habitat associations (latitude, elevation and disturbance) [1,19,64,67,68,121–123].

Leveraging the accumulating database of chromosome counts and inferred ploidy series within genera, biosystematists refined these correlates of polyploidy and reported new ones [3,22,69–73,88,100,124–127]; the most widely recognized and compelling of these correlations include the following. First, polyploidy occurs more commonly in perennial taxa with means of vegetative propagation than among annuals or monocarpic perennials. Second, polyploidy more commonly occurs in self-fertilizing than outcrossing groups, in particular among short-lived plants that lack vegetative reproduction. Third, polyploidy is more common in plant groups that reside in recently glaciated regions than in areas less affected by Pleistocene climate changes. Fourth, polyploids generally occupy larger geographical ranges than related diploids. There are counterexamples to these trends. For example, polyploidy occurs in some groups of primarily or obligately outcrossing plants—including annuals and perennials without vegetative reproduction [96,102,103,106,108]—and some polyploids have small geographical ranges or scattered distributions [26,73,110,111,128]. To our reading, however, correlates of polyploidy reported by biosystematics seem believable and worthy of further investigation.

Issues of cause versus effect and correlation versus causation loom over the aforementioned patterns and seem like particularly fruitful avenues for comparative and theoretical work. For example, Grant [3,22,92] viewed associations between polyploidy, life-history traits and mating systems principally in terms of polyploid formation (i.e. perennials have a longer life-cycle in which to experience somatic doubling, while self-fertilizing annuals have a higher probably of uniting unreduced gametes produced by F_1 interspecific hybrids); on the other hand, associations between polyploidy and historical disturbance were viewed by Grant in terms of establishment and persistence (i.e. neopolyploids may escape competition with diploid progenitors in disturbed habitats). Alternate interpretations, however, were proposed by other researchers during the biosystematics era. Thus, associations between polyploidy, life-history traits and mating systems could reflect (i) phenotypic manifestations of genome duplication (e.g. slowed growth and larger plant size leading to the perennial habit, breakdown of gametophytic self-incompatibility leading to self-fertilization); (ii) the dynamics of establishment (e.g. vegetative propagation and self-fertilization ensuring that neopolyploids reproduce even if there are few compatible mates in the vicinity); or (iii) indirect environmental correlations (e.g. polyploidy is favoured at high latitudes, and plants inhabiting these regions tend to be perennial and self-fertilizing) [1,2,19,55,69,100,129]. Similarly, associations between polyploidy and environmental disturbance could reflect polyploid formation rather than establishment (e.g. recently glaciated areas may experience temperature extremes that stimulate unreduced gamete production or may be occupied by multiple congeners that hybridize in unique combinations) [2,15,64,65,69,126,130].

(b) The molecular era (1980s–2000s)

Although polyploids pose special challenges to molecular systematics, the tools of modern genetics were increasingly applied to polyploid species complexes in the 1970s, 1980s and 1990s. This was a major development that is described in detail by other reviews [7,8,131,132] so will be covered briefly here. Paralleling efforts in diploid plants, molecular studies of polyploids focused first on isozymes, then the chloroplast genome, and finally low-copy nuclear genes. Les Gottlieb—the prolific evolutionary biologist to whom this volume is dedicated—was a pioneer in applying each of these approaches to polyploid plants, including projects in the genus *Clarkia*, *Stephanomeria* and *Tragopogon*; other major contributors include Douglas and Pamela Soltis as well as Jeffrey Doyle.

Isozyme electrophoresis is ostensibly the most problematic molecular method to apply to polyploids because of the complex heterodimeric banding patterns that can be produced in some enzyme systems. Nonetheless, isozymes have had a profound influence on polyploid research because, as co-dominant marker systems, they could address issues of polysomic versus disomic inheritance and fixed heterozygosity [7,131]. Renewed interest in autopolyploidy owes a lot to allozyme studies of *Tolmeia menziesii* and other plants for which polysomic inheritance was inferred [133,134]. Analysis of chloroplast restriction fragment length polymorphisms and DNA sequences would prove useful in resolving phylogeographic patterns and historical relationships in polyploid complexes [135–137], while sidestepping complexities of paralogy and orthology that sequencing of low-copy nuclear genes would face head-on in the late 1990s and 2000s [138–140].

Three findings from molecular studies of polyploid complexes are of particular relevance to ecological research. First, molecular approaches have resolved previously intractable problems regarding historical relationships within polyploid species complexes as well as the status of species as auto-versus allopolyploid [133,140,141]. Although biosystematists were resourceful in using diverse criteria (morphology, cytogenetics and biogeography) to study polyploid groups [3,9], molecular data provides much more confidence regarding phylogeny in particular. Ecological studies of polyploids are by their nature comparative—evaluating features of a tetraploid compared to its progenitor diploids, for example—so the resolution of historical relationships may be important for data interpretation [14,142–144]. Second, phylogeographic analyses provide insights into the ecological history of polyploid complexes (geographical distributions, demographic characteristics, gene flow within and between cytotype populations, etc.) and thus provide context for studies of modern-day populations [132,144–147]. Third, molecular data have confirmed independent origins of polyploidy within plant genera or even single taxonomic species [137,139,145,148,149]. As discussed in more depth at the end of this paper, polyphyly of polyploid taxa may be a useful feature for ecological analysis and hypothesis testing [150,151].

6. The modern era

(a) An influx of population biologists (1980s–2000s)

From the initial discovery of genome duplication, much speculation was made regarding the ecology of polyploids—about competition with progenitor diploids, contributions of ploidy to environmental adaptation, intrinsic and extrinsic factors that could favour the demographic establishment of polyploid populations, and the broader significance that ploidy variation may have for species interactions and community structure [1,2,15,16,19,20,22,64–66,97,121]. It is remarkable, then, that little empirical work was focused explicitly on these issues prior to the 1980s. There are some noteworthy exceptions. As a graduate student at the University of Michigan in the 1940s, Harriet Smith [18] compared the growth, architecture and physiology of *Sedum pulchellum* cytotypes ($2x$, $4x$ and $6x$) that had been collected across the eastern US by her advisor, J. T. Baldwin [79]. This comprehensive project demonstrated *gigas* phenotypes on autopolyploid plants as well as physiological attributes (e.g. tolerance of soil water deficit) that made sense of their geographical and climatic distributions [18]. Similarly, as a researcher at Kew Gardens during World War II, Polish cytogeneticist Marie Skalińska studied the ecological distribution and phenotypic characteristics of *Valeriana officinalis* cytotypes ($4x$ and $8x$) in the UK [81]. This work revealed latitudinal segregation of cytotypes, and in an area of co-occurrence in central England, that tetraploids were restricted to upland habitats on calcareous soils. Neither of the aforementioned systems was developed in the latter part of the twentieth century. (Smith passed away shortly after completing her dissertation and her advisor Baldwin left Michigan for a position at the College of William & Mary; Skalińska returned to Poland after the war.)

Between the 1940s and 1970s, some well-known researchers dabbled in the ecology of polyploids as part of larger projects focused on taxonomy, evolutionary biology or plant breeding. For example, Jens Clausen and colleagues studied polyploid speciation in several genera and climatic adaptation in some widespread taxonomic species, including polyploid complexes [15,16,97,99]. Noteworthy datasets included measurements on the growth and phenological characteristics of an autopolyploid mutant of *Artemisia ludoviciana* (silver wormwood) [15] that had fortuitously been included in transplant gardens (p. 336) as well as more comprehensive measurements on tetraploid and hexaploid populations of *A. borealis* sampled along an elevational transect through California [15,97,99]. The Carnegie Group also evaluated morphological characteristics of spontaneous allopolyploids generated by interspecific crosses in the genus *Layia* [16] and later would measure photosynthetic rates of an allotetraploid *Mimulus* (monkeyflower) that formed spontaneously in experimental cultures [152]. Similarly, during studies of polyploid speciation in the genus *Gilia*, Verne Grant and co-workers [23,92,94,95] measured foliage and reproductive traits of allopolyploids generated by experimental crosses. Japanese botanist Taro Jinno [153] compared shoot phenology and flowering times of diploid versus polyploid species in *Rubus* (blackberry). Plant ecologists Harold Mooney and Albert Johnson evaluated growth and photosynthetic rates of autotriploid *Thalictrum alpinum* (meadow rue) discovered in a broader comparison of arctic and alpine populations [154]. Welsh agronomist Martin Borrill investigated environmental distributions of diploid and autotetraploid *D. glomerata* in the wild, as well as the potential for inter-cytotype hybridization [155,156]. Last, but not least, Stebbins [88,157] performed field plantings of neopolyploid *Ehrharta erecta* (veldt grass) developed as part of cytogenetic studies of forage grasses and followed demographic characteristics of

these populations over time. The aforementioned activities yielded important findings about polyploidy but either (i) were focused primarily on evolution and genetics rather than ecology *per se*, or (ii) were side projects that never received the full attention of investigators.

The emergence of dedicated ecological projects in the 1980s was achieved by an influx of population biologists—many of whom came from an ecological background rather than that of plant genetics or taxonomy—into polyploidy research. Because of their training, population biologists brought a more mechanistic, trait-based approach to polyploidy and used more statistical methods in their work; they were also explicitly interested in ecological questions. The increased attention given to polyploid ecology was precipitated by several key events. First, acceptance of the role of autopolyploidy in plant evolution had progressed to a point that researchers were no longer so discouraged from studying it [9,11,13,158]. In the late 1960s and early 1970s, a small contingent of plant biosystematists challenged the party line about the roles of allopolyploidy versus autopolyploidy. This group of botanists—which included James Estes, Harlan Lewis, Walter Lewis and Theodore Mosquin, among others—argued that the incidence of autopolyploidy was underestimated because of reliance on questionable cytogenetic criteria (e.g. expectations of multivalent pairing in autopolyploids) and sampling biases (e.g. lack of chromosome counts in widespread taxonomic species that were monotypic or exhibited clinal variation) [26,107–109,113,116,118–120,156]. Articles like 'Cytocatalytic evolution in plants' [120] and 'The taxonomic significance of autopolyploidy' [26] drew attention to autopolyploidy as an evolutionary mechanism, even if they failed to dissuade the majority of biosystematists about the dominant role of allopolyploidy [3,69,88,93]. It is noteworthy that essentially all ecological studies of polyploidy from the 1980s to 2000s were performed in autopolyploid complexes. Because of the genetic complexity of allopolyploids and inherent challenges of resolving historical relationships in allopolyploid groups, autopolyploids (often referenced as intraspecific polyploids or chromosome races) were a seemingly simpler and more inviting platform for ecological research [9,11,129,156].

Another stimulating factor was the publication of work that showcased polyploidy as a phenomenon that could be studied with the tools of population biology. In the mid-1970s, Walter Lewis *et al.* [159–161] investigated the spring ephemeral *Claytonia virginica* for local ploidy variation, which was found to associate with flowering time in the field. Work by Donald Levin was also very influential. Levin's 1975 paper considered reproductive competition in mixed cytotype populations [129]. While the concept had been studied earlier—including experiments with diploid and autotetraploid crops in the 1940s and 1950s [21,162,163]—Levin generalized the problem, derived mathematical formulae that predicted its outcome, and coined a term (minority cytotype exclusion) to describe the phenomenon. Later, in 1983, Levin published a landmark paper, 'Polyploidy and novelty in flowering plants'. Like Müntzing's [1] paper a half-century before it, Levin [11] summarized qualitative and quantitative findings about the phenotypic characteristics and spatial distributions of polyploids and made a compelling case for the transformative effects of genome duplication *per se*, including both autopolyploidy and allopolyploidy.

The final event that stimulated empirical work in the 1980s and 1990s was the emergence of techniques that could be used to reliably cytotype plants on the basis of DNA content rather than chromosome counts; by using flow cytometry, for example, researchers could achieve larger sample sizes with less destructive sampling than they had in the past [164–166]. Such was the power of these new approaches that within a period of only 10 years, polyploidy research transitioned from complete reliance on traditional microscopy to heavy integration of other methods. Notable research efforts from this transitional period include Kathleen Keeler's studies of the North American prairie grass *Andropogon gerardii* (big bluestem) [165,167,168]; Rosalyn Lumaret and colleagues' work on natural populations of *D. glomerata* [169–174]; A. J. Davy's studies of *Deschampsia cespitosa* (tussock grass) in the UK [175]; van Dijk and van Delden's investigations of European *Plantago media* (hoary plantain) [176,177]; Christian Brochmann's work on arctic *Draba* [178,179]; Kik and Bijlsma's experiments with the clonal European grass *Agrostis stolonifera* (creeping bentgrass) [180,181]; and Macdonald and Chinnappa's research on the North American *Stellaria longipes* polyploid complex [182–184]. The aforementioned projects focused on geographical and environmental distributions of cytotypes in the wild, but also included some experimental manipulations. For example, garden experiments were used to compare shoot phenology and growth plasticity of diploid and autotetraploid *D. glomerata* [173,174], while greenhouse grow-outs were used to investigate trait divergence (plant architecture, size and phenology) among cytotypes in the *S. longipes* complex [182–183]. While not explicitly investigating polyploidy and relying on Fuelgen staining rather than flow cytometry, Grime's studies of DNA content and shoot phenology [185,186] were also noteworthy efforts from this time period that drew attention to the ecological significance of genome size.

Activities by population biologists accelerated in the 1990s, and by the early 2000s there were published ecological studies on autopolyploids in *Epilobium angustifolium* (= *Chamerion angustifolium*, fireweed) [187–189], *Arrhenatherum elatius* (button-grass) [190,191] and *Heuchera grossulariifolia* (alumroot) [192–194], among other systems. By the early 2010s, the floodgates had opened and ecological studies were published about polyploid complexes in more than a dozen other genera. For the most part, the emphasis of recent projects is on classical questions in polyploid ecology, but the diversity of topics and methodological approaches is impressive—the work encompasses analyses of spatial and environmental distributions of cytotypes, including niche modelling [75,147,195–206]; gene flow and reproductive barriers, including ecologically mediated components of isolation [151,207–211]; detailed phenotypic and fitness measurements of plants in natural habitats [212–219]; phenotypic attributes of plants cultured in controlled greenhouse or garden conditions [29–31,143,150,220–226]; and field transplant experiments [14,227–230]. In addition to empirical projects focused on specific autopolyploid systems, recent work by population biologists has spawned theoretical models about the establishment of polyploids [231–234] as well as large-scale floristic analyses of the spatial distributions and invasive tendencies of polyploids [73,76,235–238].

It is beyond the scope of this paper to catalogue specific findings from recent ecological projects, unfortunately, so a general summary will be provided here. First and foremost,

it is apparent that multi-faceted phenotypic, distributional and/or environmental differences exist between diploid and autopolyploid populations in almost all systems studied to date. Not every comparison is statistically significant, even for characteristics that would biologically 'make sense' to differ between cytotypes. For example, diploid and hexaploid populations of *Aster amellus* are allopatric and occur in habitats that on average differ in degree of competition intensity, but in a common garden experiment there was no relationship between ploidy level and performance under competition [222]. Similarly, ecological niche modelling failed to identify climatic differences between populations of diploid and autotetraploid *Heuchera cylindrica* despite their spatial segregation across the US Pacific Northwest [206]. Among comparisons that are statistically significant, cytotype differences tend to more often be quantitative than qualitative, as recognized by Müntzing [1] many years ago. In sympatric occurrences of diploid and autotetraploid *C. angustifolium*, for example, inflorescence heights and dates-of-flowering differ in aggregate between cytotypes but overlapped for some individuals [188]. Despite examples of statistical non-significance and numerous instances of trait overlap between cytotypes, the vast majority of ecological studies in the past 30 years report divergence between diploids and autopolyploids for phenological and life-history traits in particular, as well as spatial and environmental distributions of cytotypes in the field. This trend is perhaps unsurprising given findings from traditional cytogeographic efforts as well as speculations of early students of polyploidy. It bears emphasis, however, that recent investigations are based on much more intense sampling and statistical rigour than efforts performed from the 1930s–1960s. Population biologists have in effect modernized classical work on polyploidy, bringing it up to speed with standards of modern science and providing foundations for new research directions.

Another major trend from recent ecological projects is for phenotypic characteristics of wild autopolyploids to mirror, at least in general terms, those reported for spontaneous and induced neopolyploids in crop plants and model systems. Thus, established polyploids tend to be taller than diploids, to have larger and sturdier (but less numerous) leaves and reproductive structures, and to initiate flowering later than diploids. There are some exceptions as well as instances where phenotypic differences between diploids and established polyploids are so slight that they are of uncertain functional significance. In the grass *A. stolonifera*, for example, sympatric occurrences of tetraploids and hexaploids showed only trivial differences for size-related morphological traits (leaves and stolons) and growth attributes (vegetative biomass and number of stolons) despite divergence of these characteristics across populations [180,181]. Because the vast majority of ecological studies report similarities between wild autopolyploids and the neopolyploids described in the cytogenetics literature, it nonetheless seems reasonable to posit that genome duplication *per se* contributes to the divergence of diploids versus polyploids in many cases. The goals in studying the ecology of polyploids have arguably changed—the question confronting us is not so much if autopolyploids differ from diploids, but rather how cytotypes are divergent (i.e. what traits are involved, and what is their functional significance?) and why (i.e. does ploidy *per se* underlie major trait

differences, and in what context?). The latter questions will be a major focus of the final section of this paper.

(b) Broadening horizons (2000s to present)

In studying the ecology of polyploids, botanists have focused on growth, phenological and life-history traits as well as the spatial distributions of cytotypes in relation to environmental factors like altitude and latitude. This reflects the strong tradition of plant cytogeography as well as the widespread belief that polyploidy mediates ecological adaptation. Work by population biologists in the 1990s and 2000s expanded the breadth of ecological comparisons made in polyploid complexes, most notably to include analyses of plant/animal interactions and biological invasion. The logic behind the latter is that—in altering patterns of plant growth, secondary chemistry production and habitat distribution—polyploidization may influence interactions with animals, especially specialist herbivores and pollinators [9,11,12,159]. Explicit research efforts on these possibilities emerged in the late 1990s and 2000s [151,188,189, 192–194,209,212,214–216]. For example, John N. Thompson and colleagues examined insect floral visitors on diploid versus autotetraploid *H. grossulariifolia* and found substantial differences between the cytotypes—especially for moths in the genus *Greya* and *Eupithecia* [151,192–194]. Similarly, Halverson *et al.* [214] found ploidy to be one of several factors influencing attack by gall-forming insects on *Solidago altissima*. Other forms of species interactions—such as between plants and arbuscular mycorrhizae—have also been studied recently [224,225].

Plant/animal interactions have a lot of potential for integrative research between ecology and genetics, especially in the context of plant mating systems and the evolution of reproductive isolation; both may be mediated by behavioural responses of pollinators to plant polyploidization. For example, polyploids are generally expected to exhibit more self-fertilization than diploids, owing to potential loss of gametophytic self-incompatibility, masking of the genetic load (reduced expression of deleterious recessive alleles and thus inbreeding depression) and the dynamics of cytotype establishment (polyploids are more likely to be demographically successful in populations and species that exhibit self-fertilization) [29,187,239–245]. Polyploidy is also associated with the transition to asexual reproduction via apomixis, which in some widespread species has evolved multiple times [246,247]. On the other hand, morphological and phenological changes associated with genome duplication—potentially including increased flower size, altered nectar and pollen rewards, and delayed flowering—may influence flower visitation rates and geitonogamy, and hence outcrossing rates [188,244]. The phenotypic effects of polyploidization may also lead to specialization of pollinator species to particular cytotypes, or constancy of pollinator visitation to particular cytotypes during foraging bouts, and thus pre-zygotic reproductive isolation in sympatry [151,188,194,209–211].

For its part, the correlation between polyploidy and invasion has interested botanists since the early part of the twentieth century, when Müntzing [1] and Gustafsson [19] noted the very common occurrence of polyploidy among perennial weeds with means of vegetative reproduction; Gustafsson [19] concluded that 'man's society apparently favors polyploidy' (p. 21). Associations of polyploids with recently glaciated regions were also sometimes interpreted in the context of invasion [2,66,68,69,124–126]. In an explicit analysis of

chromosome numbers in the weeds of California, biosystematist Charles Heiser reported a complicated result [123]. Polyploidy is no more common in weedy than non-weedy species, but weeds of the California flora are most often annuals that show low base incidences of polyploidy; accounting for variation in life history within the two most abundant families of the flora (Poaceae and Asteraceae), polyploidy is more common among weeds than it is on average in these families as a whole [123]. A later analysis of the California weed flora by Stebbins [69,70] focused on 17 species groups native to western North America: among those species groups comprised of both diploids and polyploids, the latter cytotype have more often become invaders. Floristic evaluations of polyploidy and invasion returned to fashion in the 1990s and 2000s, as botanists leveraged electronic databases cataloguing 2C DNA content estimates and chromosome numbers [236,237,248,249]. Floristic analyses based on the latter are complicated by phylogenetic and functional constraints on genome size evolution—as well as the phenomenon of 'genome downsizing' (reduction in DNA content without numerical loss of chromosomes) in polyploid lineages—and have reached different conclusions depending on the taxonomic group and geographical region under consideration [250]. By contrast, recent floristic analyses based on chromosome numbers appear to corroborate the association between polyploidy and biological invasion [236–238]. For example, in a worldwide survey of 81 invasive species and their 2356 congeners, Pandit et al. [237] reported that polyploids are 20% more likely to be invasive than related diploids.

Although the association between polyploidy and biological invasion has support from floristic surveys, the underlying causes are still nebulous. Early explanations emphasized the connection between polyploidy and growth form: polyploidy is more likely to establish in perennial plants with means of vegetative propagation—or may itself underlie the transition from the annual life cycle—and perennials are well represented in weedy floras of temperate and far northern regions [1,19]. Stebbins suggested that new habitats create opportunities for interspecific hybridization and formation of allopolyploids, which in turn may be well suited to reside in these environments because of their genetic attributes [2,69,70,88,125,126]. As ecologists have thought more about genome duplication in the modern era, hypotheses about the association between polyploidy and invasion have become more sophisticated and generally fall into three non-exclusive types: (i) the suite of phenotypes associated with polyploidy (perennial habit, increased plant size, loss of gametophytic self-incompatibility, altered allocation patterns and physiological traits, etc.) may coincidentally be advantageous to weeds in many environments; (ii) genetic attributes of polyploids (increased or fixed heterozygosity, complex epistatic interactions, multisomic inheritance, etc.) may facilitate population establishment and persistence in a new geographical region; and (iii) rapid phenotypic changes in polyploid lineages (as achieved by epigenetic processes, inter-genomic recombination, improved responses to selection, etc.) may enable polyploids to adapt to new habitats [143,218,223,250]. Invasion by triploids is a special case that reflects not only genetic and phenotypic characteristics of these cytotypes, but also asexual reproduction as achieved by vegetative growth or apomixis [154,251,252].

Recent empirical work on invasion—which focuses on specific study systems, in which closely related diploid and autopolyploid plants may be studied in the native and introduced ranges—has aimed to test the association between genome duplication and invasion as well as to clarify factors that may be responsible for it [143,195,198,199,218,223,226]. In Centaurea maculosa (spotted knapweed), populations in the native range comprise both diploids and tetraploids, while naturalized populations are almost exclusively tetraploid [218]. Tetraploid plants occur in somewhat drier habitats than diploid plants and are more often polycarpic, suggesting that the phenotypic characteristics of tetraploid knapweeds may pre-adapt them to be successful invaders [218,226]. By contrast, diploid Hedera helix and tetraploid Hedera hibernica (English ivy) are found in similar proportions in their native and introduced ranges, but appear to be ecologically segregated (maritime versus continental climates) in both cases; thus, polyploidy may broaden environmental distributions of English ivy but does not appear intrinsically favoured in the introduced range [142,143]. Like plant/animal interactions, biological invasion seems like a promising avenue for integrative ecological and genetic research [250].

The diversification of ecological studies has not yet extended to allopolyploidy—a great irony to the history of polyploidy research, given that autopolyploidy was for a long period of the twentieth century thought to be of minor significance in nature [11–13,132,158]. Some pioneering investigations of allopolyploids were done in the 1970s on wild relatives of the cultivated strawberry, including the octoploids Fragaria chiloensis and Fragaria virginiana (allopolyploid species that are sometimes considered conspecific) and the diploid Fragaria fresca [253–255]. On the Pacific Coast of North America, F. chiloensis and F. virginiana occur across a wider range of climatic and edaphic conditions than F. fresca. Greenhouse experiments indicate that octoploid populations have achieved substantial divergence in architectural and phenological traits, and that trait variation correlates with climatic and edaphic variables [253,254]. Thus, the broad environmental distributions of these allopolyploids appear to reflect local adaptation rather than a general advantage of heterozygosity and hybrid vigour, as has sometimes been postulated [254,255]. Because historical relationships and cytogenetic traits of plants with agronomic importance are relatively well understood, plant breeders have studied features of polyploidy that historically would have been difficult to investigate in non-model systems. In the case of allopolyploids in strawberry and autopolyploids in several groups—most notably potato, blueberry and orchard grass—natural populations of polyploid cytotypes have been evaluated by agronomists alongside cultivars [156,256–258].

Among the handful of non-model allopolyploids that have been studied in an ecological context, most work has been done on taxa of recent origin (less than 200 years) where parentage can be traced unambiguously—in particular, Senecio cambrensis (allohexaploid formed in the UK by hybridization of the native tetraploid, Senecio vulgaris, and the introduced continental diploid, Senecio squalidus) [259,260]; Spartina anglica (dodecaploid formed in coastal Europe by hybridization of the native hexaploid, Spartina maritima, and introduced North American hexaploid, Spartina alterniflora) [261–263]; and Tragopogon mirus and Tragopogon miscellus (allotetraploids formed in North America by hybridization of the introduced Eurasian diploid species, Tragopogon dubius, Tragopogon pratensis and Tragopogon porrifolius) [264,265]. Even in such seemingly straightforward cases, the vast majority of research effort has focused on resolving taxonomic and genetic problems—number of independent

origins, changes in karyotype and chromosome structure and DNA methylation patterns, inheritance of phenotypic traits from progenitor diploids, and so forth [8,266,267].

Nonetheless, some phenotypic and ecological work has been done recently with the aforementioned allopolyploids and may pave the way for future projects. For example, morphological variability and geographical distributions (including examples of local extinction events) have been assessed in *S. cambrensis* [260,268,269]. In *Spartina*, growth performance and phenotypic plasticity of allopolyploid *S. anglica* plants were evaluated experimentally for plants grown in different environments, though without comparison to its progenitors *S. maritima* and *S. alterniflora* [270,271]. In *Tragopogon*, field surveys of the allopolyploids *T. mirus* and *T. miscellus* were conducted to determine spatial distributions and population sizes 40 years after their initial description in the 1940s and 1950s [265], while isozymes were used to evaluate mating systems of allotetraploid *T. mirus* and one of its diploid progenitors, *T. dubius* [239]. More recently, neopolyploids of *T. mirus* and *T. miscellus* were produced by colchicine treatment, enabling studies of these plants' morphology, cytogenetic behaviour and gene expression immediately following genome duplication [272,273].

7. Long-standing questions about polyploid ecology and their future prospects

Population studies of autopolyploid complexes have expanded greatly since the 1980s and provide critical insights into the potential ecological consequences of genome duplication. There are, nonetheless, significant limitations to the existing body of work. First and more obviously, the majority of research efforts represent field sampling without experimental manipulation: there are relatively few common garden studies, field perturbations or transplant experiments to corroborate observational findings. Field sampling has also tended to be relatively simple—leaf and stem sizes, flowering times, spatial mapping of plants and so forth—and for the most part has not incorporated more sophisticated analyses of physiological attributes, the intensity and direction of selection, demographic characteristics and so forth. The underlying concern about observational data is that contrasting spatial and environmental distributions of cytotypes may not reflect adaptation of polyploids and diploids to alternate conditions, but rather chance colonization events [26]. Because of the phenomenon of minority exclusion, it is unlikely for a population comprised of outcrossing diploids to be invaded by outcrossing tetraploids, even if the latter enjoys a substantial fitness advantage over the former [12,129, 231,232,274]. Thus, experimental methods and plant trait measurements in the field are important to corroborate results inferred from cytotype distributions. It is completely reasonable, of course, that ecological studies would build from basic field sampling—to proceed otherwise in developing a research programme would be folly—and already there is a greater focus on experimental methods than there was 10–15 years ago [14,143,222,223,226,227,229,230,275].

The second and more fundamental limitation is that almost all research efforts have focused on established polyploids sampled in natural populations, despite the historical precedence of studying neopolyploids (formed spontaneously or induced by chemical treatment) in the cytogenetics era [5,6].

Moreover, population biologists have rarely capitalized on multiple origins of polyploidy that have been inferred from molecular data in some study systems. These approaches are important because they enable researchers to tease apart the contributions of ploidy *per se* to ecological phenomenon [14,29–31]. While it is tempting to conclude that observed phenotypic and ecological differences between closely related cytotypes are a direct reflection of genome duplication, established polyploid populations have been sculpted for 100s or 1000s of generations by the forces of natural selection and genetic drift—and thus reflect differences in allele frequencies as well as chromosome number. Setting aside genic differences that may exist, comparison of diploids and polyploids in the wild confounds immediate effects of genome duplication (e.g. differences achieved by changes in cell size and rates of division, developmental processes and gene dosage) with consequences of genome duplication that are played out over longer periods of time (e.g. improved responses to natural selection because of changed trait correlations or increased genetic variability, ecological components of reproductive isolation that evolve via reinforcement or character displacement, etc.) [5,6,10,190,208,235,241,276].

In the handful of cases where ecologists have included neopolyploids in research projects, differences between diploids and established polyploids are of much greater magnitude than those between diploids and neopolyploids—and sometimes, the direction of trait divergence is altered as well [14,29–31,172,220]. In *A. borealis*, for example, Justin Ramsey [14] found that tetraploids and hexaploids on the north coast of California reside in mesic grasslands and xeric dune environments, with associated differences in flowering phenology and very rare co-occurrence within populations. Field transplant experiments in dune habitat revealed that established hexaploids exhibit a fivefold survivorship advantage over tetraploids, whereas neohexaploids (identified from the progeny of unreduced gamete-producing plants) on average have a 70% survivorship advantage over sibling tetraploids [14,275]. In greenhouse studies of *Heuchera grossularifolia*, Scott Nuismer and colleagues found colchicine-induced neotetraploid plants to have delayed reproduction, larger (but numerically fewer) flowers and fewer stems than related diploid plants [31]. By contrast, field investigations of wild populations revealed that tetraploids reproduce earlier and have more flowers than diploids [208]. Field and garden studies both point to greater phenotypic divergence of established diploid and tetraploid populations of *H. grossularifolia* than was discovered from comparisons using neopolyploids [150,151,208]. In *C. angustifolium*, diploids in general reside in more northerly and higher elevation sites than autotetraploids, though mixed populations occur frequently in zones of cytotype contact in the Rocky Mountains of the US and Canada [116,189,209]. Field transplant experiments by Brian Husband and colleagues suggest that established diploid and tetraploid populations are adapted to the elevations inhabited by the cytotypes [230]. In greenhouse studies, colchicine-induced neotetraploids exhibited higher xylem hydraulic conductivity and longer times-to-wilt than diploids—expected physiological attributes for plants adapted to warmer and drier low-elevation environments—but trait values were much more similar for diploids and neotetraploids than for diploids and established tetraploids [29,30,230].

Neopolyploids are a powerful tool for testing the role of genome duplication *per se* in environmental adaptation, species

interactions and other ecological phenomenon—but they are not a panacea for all of the challenges confronting polyploid research, for several reasons [5,6,10,14,29,172]. First, it is not feasible to identify original populations from which wild polyploids arose, so neopolyploids cannot precisely recreate historical speciation events; they simply provide a window on the nature of polyploids at their earliest and most critical stage of evolution. Second, neopolyploids are usually discovered or somatically induced by researchers in randomly selected diploid populations and maternal families [30,31, 172,275]. Because demographically successful polyploids may tend to arise in particular genetic backgrounds or by specific cytogenetic mechanisms (e.g. heterozygous unreduced gametes produced by first division restitution), studies of 'average' neopolyploids may underestimate the potential effects of genome duplication on plant phenotypes and performance [277,278]. Finally, studies of neopolyploids do not reveal consequences of genome duplication that appear after establishment, in the context of reinforcement or as a result of their peculiar genetic characteristics [190,235,276].

An alternative approach that addresses some of these shortcomings is the analysis of polyploid lineages that have evolved repeatedly within a taxonomic species or genus. While such lineages have been subject to the force of natural selection as well as random allele changes from genetic drift, they presumably will have done so independently. Thus, phenotypic traits and ecological features that are shared across polyploid lineages are likely to reflect intrinsic effects of genome duplication. Polyploids in some study systems do not appear to have had multiple historical origins—or have insufficient genetic variation for multiple origins to be inferred from molecular markers—but independently derived polyploid lineages have been documented in other cases [137,139,145,148,149]. To our knowledge, the only examples that have been leveraged for ecological research are in *H. grossulariifolia*, where John N. Thompson and colleagues have studied river canyons inhabited by autotetraploids of different historical origins inferred from cpDNA and morphology [150,151,192,193]. The combination of field comparisons across independently derived lineages and experimental studies of neopolyploids would seem a particularly powerful approach for testing the ecological consequences of genome duplication. In study systems where multiple origins of polyploidy have not or cannot be inferred, analysis of multiple cytotype contact zones seems advisable—independently derived polyploids may occur across the study regions unbeknownst to the researcher, and at the very least, the contact zones will have different geological histories and environmental contexts.

With the aforementioned methodological considerations in mind, we here outline major questions about the ecology of polyploids and their prospects as we enter the second century of investigations about genome duplication in plants.

(a) Are closely related diploids and polyploids intrinsically adapted to alternate environmental conditions, and if so, what phenotypic traits are involved and why did they diverge?

There is strong circumstantial evidence for polyploidy as a mechanism of adaptive evolution and ecological transformation [1,6,9–12,15,16,20]. Neopolyploids have distinctive characteristics that are reflected at least to some degree in established polyploid populations. The incidence of polyploidy varies across geographical regions and along environmental clines, and closely related diploids and polyploids are usually allopatrically or parapatrically distributed. Finally, field studies over the past 30 years have demonstrated multifaceted phenotypic and ecological differences between cytotypes in most systems. There have been few attempts, however, to 'connect the dots' within study systems—to demonstrate experimentally, for example, that polyploids have higher fitness in environments they inhabit and that known adaptations trace to polyploidization *per se* [14,30,172,222,227–230].

Perhaps more than is the case for other evolutionary mechanisms, there are reasons to be concerned about unconnected datasets in polyploid research. The emergence of ploidy variation in plant genera may in theory be explained by a ratcheting process (increases in ploidy level occur frequently while decreases in ploidy level are rare), even in the absence of ecological advantages [233]. Because of minority cytotype exclusion, chance colonization events may have profound influence on the geographical and environmental distributions of polyploids [26,129,274]. Comparisons of diploids and polyploids from wild populations appear to overestimate the contributions of polyploidization *per se*, because of divergence of cytotype populations over time via natural selection and genetic drift [14,30,31,172]. There are instances of statistical non-significance in comparisons of diploids and polyploids, and these may garner less attention than comparisons that happen to be significant; moreover, choices of phenotypic traits or ecological phenomenon for investigation are in all likelihood motivated by cytotype differences noted by casual field observation or pilot studies.

The good news is that many of the aforementioned concerns are being addressed in a natural way as population biologists ask increasingly integrative questions about the ecology of polyploids. For example, is there functional significance to the phenological and life-history differences that are commonly observed between diploid and polyploid populations? Are the immediate phenotypic consequences of genome duplication favoured in environments where polyploids naturally occur? Do the genetic attributes of polyploids increase mean population fitness or the response to natural selection? Could polyploidy set the stage for adaptive evolution via reinforcement (divergence in flowering times or other traits that reduce production of low-fitness hybrids) or simply by preventing gene flow between populations residing in different habitats? Answers to these questions will require experiments with neopolyploids and/or independently derived polyploid populations and may be impractical in some taxa. Findings from even a few systems, however, would help across the board with interpreting observational field data in a wider range of species.

(b) Is the ecology of autopolyploids fundamentally different from the ecology of allopolyploids?

Hypotheses about the ecology of allopolyploids have historically focused on two major ideas [2,3,15,16,40,69,70,88]. First, allopolyploids were thought to have 'intermediate' phenotypic and ecological characteristics compared with their diploid progenitors, because genome duplication may isolate homeologous chromosomes from pairing during meiosis. Second, allopolyploids were expected to achieve broader geographical and environmental distributions than diploids, owing to

hybrid vigour and homeostatic buffering. Findings from the cytogenetics era cast doubt on the first hypothesis in particular, as many allopolyploids were found to segregate for parental traits—in a few generations, an allopolyploid population may much more closely resemble one diploid progenitor than the other [60,62,63]. Molecular studies confirm the dynamic nature of polyploid genomes, including rapid epigenetic changes and inter-genomic recombination events in recently formed lineages [7,8,131]. It is still uncertain whether allopolyploids enjoy a general fitness advantage over diploids, though the handful of published experimental studies suggest divergence of allopolyploid populations to local environmental conditions [254,255,270,271]. For these reasons, it seems that hypotheses about allopolyploids are due for an overhaul, which is not unexpected given their development in the early days of polyploid research.

What is surprising, however, is that there are so few empirical datasets about the phenotypic characteristics, geographical and environmental distributions, and species interactions of allopolyploids in the wild—especially since allopolyploidy was for many years thought to be the primary form of genome duplication that was successful in nature [3,120,158]. Ecological work was stimulated in the 1980s and 1990s by the growing acceptance of autopolyploidy, as it gave population biologists an opportunity to develop their methods in simpler taxonomic systems [11,159,165,169]. But the time seems right for increased research focus on allopolyploid complexes, even if there is uncertainty about phylogenic relationships and introgression hybridization in these systems that cannot be fully resolved by the tools of molecular systematics. Questions about historical relationships confront many autopolyploid complexes as well [143,144,148] and may be mitigated by combining experimental studies of neopolyploids with observations of wild populations. Given the frequent production of polyploids by F_1 interspecific hybrids, it may be easier to develop experimental research with allopolyploids than in autopolyploid systems, where the rate of neopolyploid formation is much lower [5,6,275].

(c) Do ecological and phenotypic correlates with polyploidy represent cause, effect or something else altogether?

Botanists recognized variation in the incidence of polyploidy shortly after its initial discovery, and over the years have reported many statistical associations with genome duplication—life-form, mating systems, geographical and environmental distributions, climatic tolerances, occurrence in naturally or anthropogenically disturbed habitats, taxonomic affinities and so forth [2,3,73,122–124,126,127]. In many cases, these associations have been interpreted both in terms of cause and effect; for example, polyploidy may be more likely to establish in perennial populations (vegetative reproduction may ameliorate minority cytotype exclusion) but in principle polyploidy could also underlie the phenotypic transition from an annual to perennial life-cycle [1,19]. It is also anticipated that the correlates of polyploidy reflect indirect relationships among variables. For example, the high incidence of polyploidy in arctic regions is thought to reflect the abundance of the plant families Poaceae and Rosaceae in these floras, as well as the physical environment—which itself may be broken down into temperature and precipitation, length of the growing season, historical disturbance from glaciation and other factors [2,68,69,71–73,88].

It may never be possible to fully untangle the functional, historical, phylogenetic and environmental factors that were associated with polyploidy by classical botanical research, but much more comprehensive efforts may now be attempted. Phylogenetic relationships within polyploid species complexes provide the foundation for these efforts, coupled with improved knowledge about cytotype spatial distributions and biological characteristics [73–76,237,250]. Arguably the biggest limitation to recent studies is the focus on small numbers of factors—geographical range size being the most popular choice for analysis—which makes it difficult to tease apart direct and indirect relationships among variables. Theoretical models may complement large-scale floristic analyses by providing insights into dynamics of polyploid establishment, and thus issues of cause versus effect. For example, it has been suggested that the frequent occurrence of polyploids in recently glaciated regions reflects increased rates of polyploid formation—owing to cytogenetic aberrations and unreduced gamete production being stimulated by temperature extremes or interspecific hybridization—but it is unclear whether mutation rate is a limiting factor in polyploid establishment under conditions of minority cytotype exclusion [5,6,29,232]. Finally, we note that it may be insightful to test correlates of polyploidy in animals where it sometimes occurs, such as fish and amphibians, as a comparison to plants [279,280].

(d) Do ecological differences between diploids and polyploids contribute to reproductive isolation, and hence incipient speciation?

Because of the inviability and sterility of triploids, polyploidy creates 'instantaneous' post-zygotic reproductive isolation in sympatry with a progenitor cytotype [1,5,6,20]. Polyploidy is sometimes described as an archetypal form of non-ecological speciation, especially in attempts to classify mechanisms of speciation [281–283]. For example, Schluter [281] writes that '[polyploidy] is unambiguously non-ecological because reproductive isolation between diploid parent and tetraploid descendant populations does not build by divergent natural selection . . . reproductive isolation arises automatically via the low fertility of the triploid hybrids. For these reasons, instances of polyploid speciation may be useful as a barometer of non-ecological speciation' (p. 198). Crossing barriers have profound impacts on the fate of neopolyploid mutants, and it is understandable that polyploid speciation is viewed principally in the context of post-zygotic reproductive barriers. On the other hand, established polyploids appear to be reproductively isolated from their diploid progenitors by multiple components of pre- and post-zygotic mechanisms, including environmentally mediated barriers like habitat isolation, flowering phenology and pollinator behaviour [150,151,170,188,208,210,211]. It is unclear to what extent these reproductive barriers are achieved immediately following genome duplication; arguably this is the critical issue for evaluating polyploidy as an agent of ecological versus non-ecological speciation. Studies in *A. borealis*, *C. angustifolium*, *D. glomerata* and *H. grossularifolia* suggest that neopolyploids enjoy a modest degree of habitat and/or phenological isolation from their progenitors [14,29–31,172]. Much more work is needed to quantify the actual strength of these

reproductive barriers, however, and there is no comparable information available for allopolyploid species complexes.

Related to the aforementioned issues is the application of taxonomic nomenclature to polyploid complexes: genome duplication presents special challenges to each of the major forms of species concepts [3,9,158]. For example, application of the morphological species concept (*sensu* Arthur Cronquist [117]) is complicated by the overall phenotypic similarity of cytotypes, especially for diploids and autopolyploids [103,105,108,109,116,119]. Phylogenetic species concepts are also problematic, because recently derived polyploid lineages may lack fixed genetic differences with their diploid progenitors while long-established polyploids often have had multiple origins and are thus polyphyletic [113,137,142,144, 148,149]. While the biological species concept would seem straightforward to apply in polyploid groups, the occurrence of unreduced gametes, de novo polyploid formation and semi-fertile F_1 hybrids suggest the existence of non-trivial levels of inter-cytotype gene flow [26,99,172,258,275,284].

Although squabbles about the taxonomic nomenclature of polyploid complexes reflect philosophical beliefs about the nature of species, these issues have wide-reaching implications for plant ecology and conservation biology [9,13,26,120,158]. Taxonomic recognition of autopolyploids—which at the present time are in most cases treated informally as chromosome races without naming at the specific or subspecific level—would increase species richness estimates of flowering plants worldwide. Because polyploidy is ostensibly more common in arctic and north temperate floras than in the tropics [2,3,69,88], recognition of chromosome races may alter latitudinal and geographical patterns of plant biodiversity. Finally, there are many instances of rare cytotypes (geographically restricted or sparsely distributed) in polyploid complexes that are otherwise common [15,26,106,110,111,128,285]. Recognition of these cytotypes at the specific or subspecific level may influence formal protection under the law and is probably warranted given their biological attributes [158,286].

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