INVITED REVIEW

The more the better? The role of polyploidy in facilitating plant invasions

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• *Background* Biological invasions are a major ecological and socio-economic problem in many parts of the world. Despite an explosion of research in recent decades, much remains to be understood about why some species become invasive whereas others do not. Recently, polyploidy (whole genome duplication) has been proposed as an important determinant of invasiveness in plants. Genome duplication has played a major role in plant evolution and can drastically alter a plant's genetic make-up, morphology, physiology and ecology within only one or a few generations. This may allow some polyploids to succeed in strongly fluctuating environments and/or effectively colonize new habitats and, thus, increase their potential to be invasive.
• *Scope* We synthesize current knowledge on the importance of polyploidy for the invasion (i.e. spread) of introduced plants. We first aim to elucidate general mechanisms that are involved in the success of polyploid plants and translate this to that of plant invaders. Secondly, we provide an overview of ploidal levels in selected invasive alien plants and explain how ploidy might have contributed to their success.
• *Conclusions* Polyploidy can be an important factor in species invasion success through a combination of (1) 'pre-adaptation', whereby polyploid lineages are predisposed to conditions in the new range and, therefore, have higher survival rates and fitness in the earliest establishment phase; and (2) the possibility for subsequent adaptation due to a larger genetic diversity that may assist the 'evolution of invasiveness'. Alternatively, polyploidization may play an important role by (3) restoring sexual reproduction following hybridization or, conversely, (4) asexual reproduction in the absence of suitable mates. We, therefore, encourage invasion biologists to incorporate assessments of ploidy in their studies of invasive alien species.

Key words: Biological invasions, genome size, invasiveness, invasion ecology, polyploidy, whole genome duplication.

INTRODUCTION

Plant species originate, expand, differentiate and, eventually, decline (Levin, 2000). In order to succeed, newly formed species need to colonize new habitats and establish reproducing populations away from their location of origin. Factors that affect the capacity of plants to be rapid or efficient colonizers include wide environmental tolerance, high levels of phenotypic plasticity, ability to self-reproduce, effective dispersal, high relative growth rate, high competitive ability and/or avoidance of genetic bottlenecks following founder effects (Baker, 1965; Levin, 2000). The same set of factors determines the fate of plant species that are moved out of their native ranges by humans and must then negotiate novel environments. Like all plants, invasive species need to be good colonizers to succeed in their new habitat. However, most introduced species fail to establish and spread after introduction (Williamson and Fitter, 1996; Richardson and Pyšek, 2006). Recently, plant invasions have been the focus of

substantial and diverse research efforts (see Pyšek *et al.*, 2006; Richardson and Pyšek, 2008, and references therein), and the central question of why certain species become invasive and others not remains at the forefront of many research agendas. The importance of identifying the determinants of invasion success (Rejmánek and Richardson, 1996; Pyšek and Richardson, 2007; Schaefer *et al.*, 2011) is underscored by the recent upsurge in research interest on the impact of invasive species on resident species, communities and ecosystems (Vilà *et al.*, 2010, 2011).

Polyploidy, i.e. the acquisition of more than two sets of chromosomes by means of intraspecific genome duplication (autopolyploidy) or the merging of genomes of distinct species through hybridization and subsequent genome duplication (allopolyploidy), potentially has important ecological and evolutionary consequences for the fate of introduced plant species. Newly formed polyploids often exhibit rapid range expansion (Levin, 1983; Hull-Sanders *et al.*, 2009; Treier *et al.*, 2009) and are over-represented among invasive alien

compared with native species in some regional floras (Verlaque *et al.*, 2002; Pandit *et al.*, 2006) and among invasive alien compared with rare plant species (Pandit, 2006; Pandit *et al.*, 2011). However, empirical data to support this contention are scarce (but see Pandit *et al.*, 2011). This is despite the fact that polyploidy is generally viewed as an important driver of plant evolution in natural populations (Adams and Wendel, 2005*a*) and is believed to be the single most important mechanism of sympatric speciation in land plants (Otto and Whitton, 2000). Moreover, polyploidy has played a crucial role in the domestication of crops, such as wheat, maize and cotton (Dubcovsky and Dvorak, 2007). Polyploidization can alter plant morphology, phenology, physiology and/or ecology within only one or a few generations (Levin, 2002), generating individuals that can cope with fluctuating environments, exploit new niches or outcompete progenitor species (Leitch and Leitch, 2008). Given these arguments, it is highly likely that polyploidy could give introduced species an important advantage in negotiating novel habitats, thereby assisting them in progressing along the introduction–naturalization–invasion continuum (see Richardson *et al.*, 2000).

Research on the mechanisms and effects of polyploidy has advanced recently as new cytogenetic and molecular tools have become available (Ainouche and Jenczewski, 2010; Soltis *et al.*, 2010). For example, plants can now quickly and affordably be screened for ploidy using flow cytometry (Kron *et al.*, 2007; Suda *et al.*, 2007; Suda and Pyšek, 2010; see Box 1), making comparisons among invasive alien, native and non-invasive taxa possible (Pandit *et al.*, 2006, 2011; Kubešová *et al.*, 2010). Similarly, advanced molecular methods for measuring, for example, altered gene regulation and expression and epigenetic structure, have resulted in new insights into the genomic and genetic consequences of polyploidy (Paun *et al.*, 2010, 2011). In allopolyploids, polyploidization and hybridization go hand in hand, resulting in quick divergence of the neopolyploid as well as reproductive isolation between the parent plants and the neopolyploid. Furthermore, allopolyploidy might act as a genetic stabilizing mechanism to prevent hybrid sterility (Ellstrand and Schierenbeck, 2000), although it appears that most allopolyploids form from unreduced gametes and never go through a 'diploid' phase. Though not as drastic as in allopolyploids, autopolyploids also experience genomic changes and increased genetic diversity (Parisod *et al.*, 2010), potentially resulting in altered morphology, physiology and ecology. The increased interest in polyploidy combined with the advances in methodology have led to increased recognition that autopolyploidy is more prevalent in natural populations

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Box 1. *Methods for determining ploidal levels*

The first logical step in comparative studies involving plants with ploidy heterogeneity is the determination of chromosome number or ploidal level, for which counting the number of somatic chromosomes in meristematic cells remains the most straightforward method. The approx. 130 years of karyological research have led to the documentation of chromosome numbers for approx. 25 % of the world's flora (Stace, 2000). These are listed in a number of chromosomal catalogues, the most comprehensive of which is the series *Index to plant chromosome numbers* (Goldblatt and Johnson, 1979 onwards). However, direct chromosome counts can be tedious and time consuming, often require an experienced researcher with cytological skills and in some species are difficult to perform due to the high number, small size and/or faint staining of chromosomes. Consequently, most conventional studies are based on a limited number of karyologically verified plants, which makes their conclusions less robust and precludes any generalization.

Attempts to analyse larger sample sizes resulted in the development of several indirect methods of ploidy estimation, which exploit relationships between the genome copy number and the size/volume of cells or organs. The most commonly used proxies for ploidy are the length of stomatal guard cells, stomatal frequency, chloroplast number in guard cells or pollen diameter (Mishra, 1997). While these characteristics have been successfully applied as a rapid ploidy indicator in several polyploid plant complexes, they still suffer from a number of disadvantages, including environmental sensitivity, necessity for calibration or overlapping ranges between different ploidy classes, which can cause uncertainties and difficulties in application to non-model plant species. Much more reliable for ploidy estimation are cytogenetic methods based on the quantification of the amount of nuclear DNA. Whereas densitometric techniques such as Feulgen densitometry or image cytometry have several sub-optimal features that hinder their more widespread use in plant sciences, this field has been conquered by flow cytometry (e.g. Kron *et al.*, 2007; Loureiro *et al.*, 2010; Suda and Pyšek, 2010).

Flow cytometry is a high-throughput method that simultaneously measures and analyses multiple optical properties of single particles (e.g. cells or nuclei) that are usually labelled with fluorescent stains. The recorded values are then used to infer physical and/or chemical characteristics of the particles, including genome size/ploidy. Because flow cytometry quantifies the total amount of nuclear DNA irrespective of the number of chromosomes, the inference of actual ploidal level requires a calibration against the sample with the known number of chromosomes, using conventional karyology (Suda *et al.*, 2006). The major advantages of DNA flow cytometry in plant science are: (*a*) high speed, which allows high throughput and ensures statistical robustness; (*b*) easy and convenient sample preparation; (*c*) versatility – virtually any plant tissue can be analysed, without the need for mitotically active cells; (*d*) non-destructiveness – small tissue quantities are required for cytotyping and can be reused for subsequent analysis; (*e*) high accuracy and resolution; (*f*) the possibility to estimate ploidy in desiccated plant tissue (Suda and Trávníček, 2006); and (*g*) reasonable operating costs. During the last decade, flow cytometry has significantly advanced our understanding of ploidy variation in invasive plant species and transformed the research from an analysis of single individuals to the analysis of large population samples over different temporal and spatial scales (e.g. Mandák *et al.*, 2003; Kubátová *et al.*, 2008; Schlaepfer *et al.*, 2008; Treier *et al.*, 2009).

than previously thought (Soltis *et al.*, 2007). Autopolyploidy might therefore not be an 'evolutionary dead-end' (Stebbins, 1950), but instead an important driver of plant evolution and genetic differentiation (Parisod *et al.*, 2010).

Polyploidy needs to be viewed in a wider context along with other factors known to influence invasiveness, such as (1) taxonomic predisposition (e.g. Daehler, 1998; Pyšek, 1998; Richardson and Rejmánek, 2004) or the absence of closely related species in the native flora (Darwin, 1859; Schaefer *et al.*, 2011); (2) possession of certain life history syndromes, e.g. wide ecological tolerance, high relative growth rate, high reproductive potential, effective dispersal strategies, self-compatibility, short juvenile period and high phenotypic plasticity (e.g. Baker, 1965; Rejmánek and Richardson, 1996; Pyšek and Richardson, 2007); and (3) the crucial role of anthropogenic factors in introducing and disseminating species (Pyšek *et al.*, 2010; Castro-Díez *et al.*, 2011). Polyploidy may also promote invasiveness indirectly by enhancing the 'evolution of invasiveness'. In their seminal paper, Ellstrand and Schierenbeck (2000) posed the question of whether invasives are 'born' (i.e. released from fitness constraints) or 'made' (i.e. evolve invasiveness after colonization). These authors acknowledged that some invasives are born, as indicated by published life history syndromes for invasiveness and pre-adaptation of successful invaders, but convincingly demonstrated that invasiveness can also evolve via hybridization. Results from studies on polyploid invasive species indicate that both pathways to invasiveness may be important. In many cases where more than one cytotype occurs naturally in native ranges, only polyploids are present in the novel invasive ranges (e.g. Lafuma *et al.*, 2003; Mandák *et al.*, 2005; Kubátová *et al.*, 2008; Schlaepfer *et al.*, 2008; Treier *et al.*, 2009), suggesting pre-adaptation of polyploid invaders. However, examples of introduced species that undergo polyploidization in their novel ranges (e.g. *Fallopia* spp.; Mandák *et al.*, 2003, 2004; Suda *et al.*, 2010) indicate that post-colonization processes (evolving invasiveness) might also operate. This is further supported by the long lag phase that many species (both diploids and polyploids) experience before starting to spread (Williamson *et al.*, 2009; Gassó *et al.*, 2010) and that spontaneous polyploidization seems more likely in marginal habitats and under stressful conditions (Veilleux and Lauer, 1981; Bretagnolle and Thompson, 1995; Ramsey and Schemske, 1998). This strategy might allow plants to cope with a changing environment and to maintain their success at the edge of its distributional range. Therefore, it is highly conceivable that polyploidization may play an important role in determining invasion success in plants.

We synthesize knowledge relating to the role of polyploidy in plant invasions. In the first part of the review, we aim to elucidate mechanisms that are involved in the success of polyploid plants and translate this to the success of plant invaders. We also discuss the effect of genome duplication vs. genome size on plant invasions. In the second part, we provide an overview of current knowledge on ploidal levels in invasive alien plants and explain how polyploidy might have contributed to their success. Specifically, we consider whether polyploidy might represent a particularly favourable avenue to evolve invasiveness.

GENETIC, GENOMIC AND EPIGENETIC CONSEQUENCES OF POLYPLOIDY FOR PLANT INVASIONS

Polyploidy (whole genome duplication) has both costs and benefits (Comai, 2005). Although Stebbins (1950) described polyploids as evolutionary dead-ends, their prominence in the evolutionary history of flowering plants (e.g. Fawcett *et al.*, 2009; Van de Peer *et al.*, 2009; Wood *et al.*, 2009) suggests an important role in adaptive evolution of plants in general. While the exact mechanisms involved in polyploidization remain poorly understood (Soltis *et al.*, 2010), the union of unreduced gametes is paramount (Ramsey and Schemske, 1998; Mable, 2004a; Czarnecki and Deng, 2009). The formation of unreduced gametes is under genetic control and heritable, but may also be affected by environmental stress stimuli (Parisod *et al.*, 2010), such as habitat disturbance, nutritional stress, physical stress (e.g. wounding) and climate fluctuations (Veilleux and Lauer, 1981; Bretagnolle and Thompson, 1995; Ramsey and Schemske, 1998). Mechanisms involved in auto- and allopolyploidization have been thoroughly covered in several recent reviews (e.g. Osborn *et al.*, 2003; Adams and Wendel, 2005b; Brysting *et al.*, 2007; Hegarty and Hiscock, 2007; Chen, 2010; Parisod *et al.*, 2010). Despite a suite of potential problems involved in becoming polyploid, e.g. genomic shock (see below), the prevailing assumption is nevertheless that polyploidy may confer key advantages, which 'double up' for evolutionary success (Hegarty and Hiscock, 2007), such as gene redundancy that shields polyploids from the effects of deleterious recessive mutations and heterosis, or hybrid vigour (Fig. 1).

Masking deleterious alleles

Under the classical model of recessive deleterious alleles/mutations negatively impacting fitness, polyploid lineages should enjoy an immediate benefit by masking these alleles. This may be particularly important in small and isolated populations (Comai, 2005), and important for the initial establishment of founding polyploid populations. While inbreeding depression will initially be lower in polyploids than in the diploid progenitors, deleterious alleles will increase in frequency over time, and fitness advantages may diminish (Otto, 2007). Nevertheless, a 50 % reduction in inbreeding depression has been noted in numerous polyploids when compared with diploid progenitors (Husband and Schemske, 1997; Galloway *et al.*, 2003; Husband *et al.*, 2008). Genetic redundancy may in the longer term facilitate adaptive divergence of duplicated genes and allow the emergence of evolutionary novelties. Only a few such evolutionary novelties or transgressive traits may be needed for a new polyploid to establish via adaptive processes.

Fixed heterozygosity and heterosis

At the gene level, fixed heterozygosity may follow allopolyploidization and has been shown for highly successful allopolyploid invasive species such as *Tragopogon* (Roose and Gottlieb, 1976). In allotetraploid *T. mirus* and *T. miscellus*,
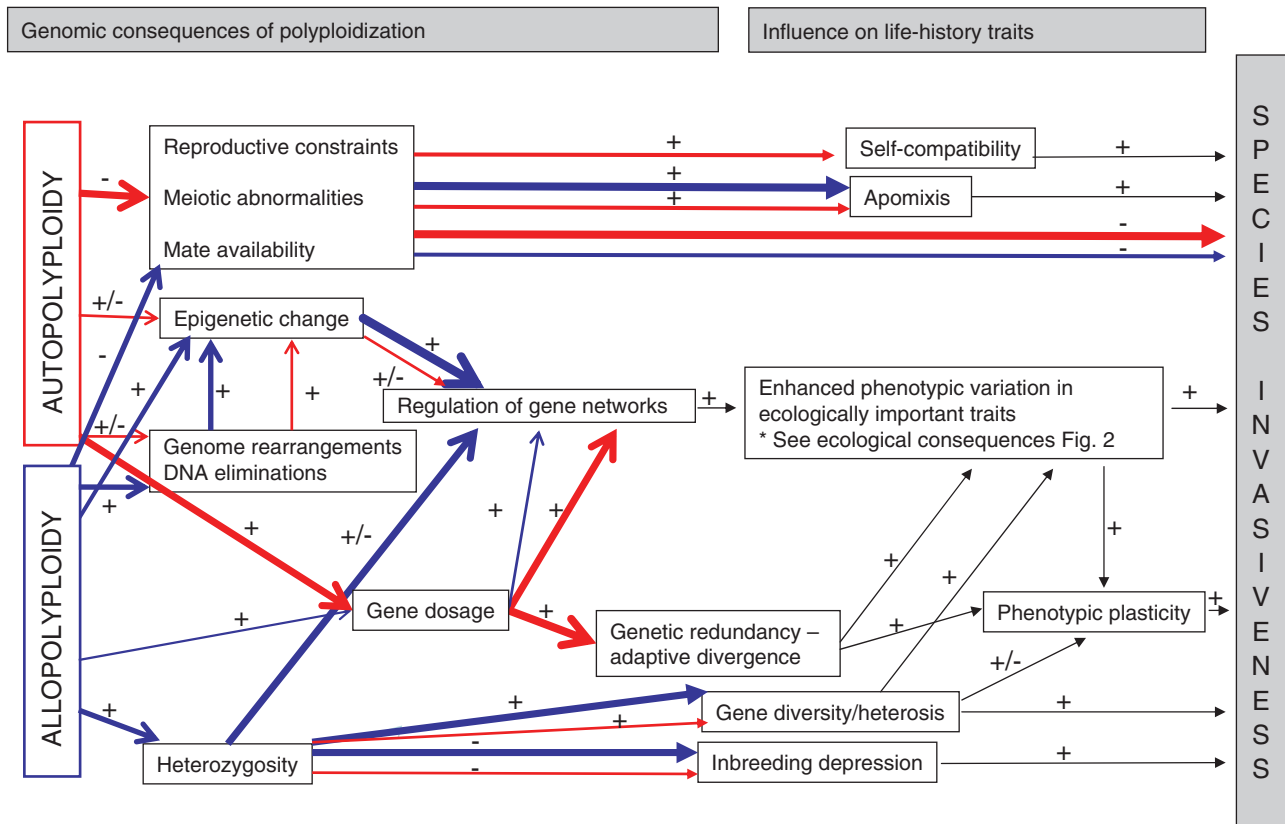
FIG. 1. Genomic consequences of polyploidization and how they may affect species invasiveness. Red arrows refer to autopolyploidy, blue arrows to allopolyploidy and black arrows do not discriminate between modes of polyploidization. The thickness of the arrow indicates the strength of the effect, while the sign gives the direction of the effect.

33 and 43 %, respectively, of analysed loci had different parental alleles. These species represent classic examples of so-called hybrid vigour or heterosis often associated with allopolyploids: an increase in fitness traits such as growth rate, reproductive output and biomass in hybrids, leading to a competitive advantage over the diploid parents (Comai, 2005). Even though fixed heterozygosity is limited to allopolyploid systems, autopolyploids are potentially also characterized by high heterozygosity (and nearly double the effective population size) compared with diploids as a result of polysomic inheritance (Parisod *et al.*, 2010). At the population level, multiple and independent origins of polyploids, which seem to occur frequently in natural populations (Soltis and Soltis, 1999), allow for increased genetic diversity as polyploid offspring from different parents may interbreed.

Gene expression

Another consequence of polyploidization is differential gene expression on a per cell basis, dependent on the dosage of genes as determined by ploidy (Osborn *et al.*, 2003). If levels of gene expression are purely additive, then complete heterozygous individuals should differ markedly from homozygotes, with a range of intermediates corresponding to partial heterozygotes. Alternatively, if gene expression is non-additive, trait values could exceed or fall behind intermediate parental values (Chen, 2007), rendering increased phenotypic variation to

both auto- and allopolyploids. These effects have been particularly well studied in agricultural crop and model systems, including regulation of developmental processes in maize, fruit size in tomatoes and flowering time in *Arabidopsis thaliana* (Osborn *et al.*, 2003, and references therein). For example, it has been shown that up to approx. 90 % of gene expression is additive in synthetic arabidopsis allopolyploids (Wang *et al.*, 2006). However, the same study found only small effects of genome doubling on gene regulation in autotetraploids. Other recent studies have shown similar patterns (for a review, see Adams, 2007), suggesting that the effect of genome doubling *per se* on gene expression may be limited in the short term. Parisod *et al.* (2010) suggested that genetic redundancy in autopolyploids may nevertheless facilitate adaptive variation. In the long run, theory predicts that relaxed selection will operate on copies of duplicated genes, leading to increased gene divergence and, consequently, phenotypic novelty. New expression patterns of duplicated genes can also be a result of tissue specificity, also known as subfunctionalization, a process that has been suggested to operate over long evolutionary time frames (Adams *et al.*, 2003).

Gene expression is dependent on networks of regulators such as transcription factors, epigenetic mechanisms such as DNA methylation (see later) and transposons. While regulatory networks may be severely impacted by the interactions of regulators from divergent contributing genomes in allopolyploids, gene expression will also be significantly impacted in

autopolyploids as regulatory networks are generally dosage dependent (Hegarty and Hiscock, 2007), and duplication of the genome immediately provides one extra dosage. Consequently, modification of regulatory networks, irrespective of the mechanisms involved, must play an important role in heterosis. It is therefore not surprising that polyploid invasive species often possess novel traits and/or higher trait variation intermediate to their parental species (in the case of allopolyploids). It has been proposed that novel and varying phenotypes may predispose polyploid lineages to colonization success in novel environments, i.e pre-adaptation (Buggs and Pannell, 2007), a hypothesis that is supported by evidence from some invasive species. For example, the invasion success of tetraploid spotted knapweed, *Centaurea stoebe* (syn. *C. maculata*), in the USA has been partly attributed to pre-adaptation of native European tetraploids to wider climate ranges, especially drier climates, as compared with diploids. Even though both cytotypes were introduced into the USA, invasive populations are dominated by tetraploids and, following introduction, may have further adapted to arid conditions (Treier *et al.*, 2009; Henery *et al.*, 2010). Similarly, introductions of pre-adapted genotypes from southern Africa have been suggested for highly invasive *Senecio inaequidens* in Europe (Bossdorf *et al.*, 2008; Lachmuth *et al.*, 2010). Separate population genetic (Lachmuth *et al.*, 2010) and cytogenetic (Lafuma *et al.*, 2003) studies have shown that the environmentally pre-adapted tetraploid genotypes occur in highland regions in the native range and are more cold tolerant than lowland diploid populations (Lafuma *et al.*, 2003).

Genomic shock and cell division

Following polyploidization, individuals may experience 'genomic shock' (McClintock, 1984) due to genome incompatibilities (allopolyploids) and genetic redundancy (both auto- and allopolyploids). An immediate disadvantage associated with genomic shock is difficulties associated with the normal completion of mitosis and meiosis (Otto and Whitton, 2000; Otto, 2007). An upset in the geometric relationships among key components involved in segregation of chromosomes during cell division may lead to mitotic instability and somatic aneuploidy, i.e. partial multiplication of chromosomes (Comai, 2005). For example, spindle irregularities have been reported for autotetraploid plants (e.g. Risso-Pascotto *et al.*, 2005), and somatic aneuploidy is common in synthetic and natural arabidopsis allopolyploids (Wright *et al.*, 2009). Aneuploidy may not only represent a form of genetic load and contribute to inbreeding depression in autopolyploid populations (Doyle, 1986), but may also cause epigenetic changes (Comai, 2005). Comai (2005) argued that the deleterious effects of such epigenetic remodelling are greater than the positive effects as they are expected to upset local adaptations in parental species (see later discussion on epigenetic effects).

Meiotic irregularities and a high rate of non-disjunction may also lead to the production of aneuploids. Newly formed auto- and allopolyploids exhibit high meiotic complexity, including multivalent pairing, multisomic inheritance and the production of unbalanced gametes (Ramsey and Schemske, 2002). These complications are more pronounced in autopolyploids than in allopolyploids, but more common in allopolyploids than predicted by theory (Ramsey and Schemske, 2002). Meiotic aberrations and the production of chromosomally and genetically unbalanced gametes may affect and reduce fertility in polyploids. The degree of this may vary considerably between taxa, and evidence suggests that reduced fertility in neopolyploids can be rapidly increased by natural selection (Ramsey and Schemske, 2002). To counterbalance reduced fertility, polyploids often self-fertilize more than diploids (Pannell *et al.*, 2004; Barringer, 2007; Robertson *et al.*, 2010; but see Mable, 2004*b*) and have lower outcrossing rates (Husband *et al.*, 2008).

Genomic shock and DNA elimination

Numerous studies have shown that both synthetic and natural polyploids undergo immediate and rapid structural changes in response to genomic shock (Parisod *et al.*, 2010, and references therein), mostly by reducing nuclear DNA content through the elimination of chromosome- and genome-specific sequences (Chen, 2007). Invasive allopolyploid *Tragopogon* species in the USA have shown a marked reduction in DNA sequence and changes in the transcriptome (Tate *et al.*, 2006). Similarly, Salmon *et al.* (2005) showed that the highly successful allopolyploid *Spartina* underwent DNA sequence elimination following polyploidization. DNA elimination possibly plays a role in the maintenance or establishment of bivalent pairing during meiosis and is therefore more prevalent in allopolyploids than in autopolyploids (Parisod *et al.*, 2010). DNA elimination may also contribute to the loss of duplicated gene expression and function, and has been documented in various plant systems (Chen, 2007, and references therein). DNA elimination represents one mechanism of chromosomal rearrangement that may lead to so-called diploidization of a polyploid genome; others include fusion or fission of chromosomes, and duplication, inversion and translocation of chromosomal segments. Surprisingly, these processes may act swiftly (within a few generations), after which they may remain stable over longer evolutionary periods (e.g. Rieseberg *et al.*, 1996). However, the inability to overcome major genomic constraints on reproduction often leads to rapid development of asexual reproduction in polyploids, a life history trait that has been linked to invasiveness (Rambuda and Johnson, 2004). Nevertheless, while shifts towards apomixis are common in polyploids (Norrmann *et al.*, 1989; Quarin *et al.*, 1998, 2001; Naumova *et al.*, 1999; Krahulcová and Rotreklová, 2010), some polyploid offspring can remain completely sexual (Stebbins, 1950; Hashemi *et al.*, 1989; Ayres *et al.*, 2008).

Genomic shock and epigenetic remodelling

While DNA elimination can explain gene loss over time, structural and functional reorganization of polyploid genomes could also be vastly influenced by changes in epigenetic structure; changes in gene expression due to biochemical modification of DNA rather than changes of the genetic code *per se*. Some of the better understood epigenetic mechanisms in plants include DNA methylation, DNA acetylation and

histone modifications (Chen, 2007). Epigenetic effects include gene expression regulation, changes in imprinting genes, defence against viral infection and the repression of transposable elements (Osborn *et al.*, 2003). Gene silencing in allopolyploids often only impacts one parental genome via the preferential expression of the other parent's protein assembly genes (rRNA), a process known as nucleolar dominance (Pikkard, 2000, 2001). Such gene silencing may also lead to accelerated sequence mutation rates of affected genes.

Even though epigenetic changes may be deleterious when disrupting regulatory and gene expression patterns that are established by selection, they may also contribute to increased diversity, plasticity and heterosis, and provide variation that may in turn allow adaptation to novel conditions (Comai, 2005). The rate and direction of genetic and epigenetic changes in response to genome duplication are greatly influenced by the mode of polyploidization, i.e. auto- or allopolyploidy. Epigenetic reorganization and changes in gene expression have been reported for allopolyploids (Liu and Wendel, 2003; Levy and Feldman, 2004; Paun *et al.*, 2010, 2011), but less so in autopolyploids (see Fig. 1), and it seems likely that hybridization rather than genome doubling *per se* triggers substantial epigenetic remodelling in polyploid genomes (Hegarty *et al.*, 2006; Parisod *et al.*, 2009). Allopolyploids might need major epigenetic modifications to re-establish compatibility between divergent genomes (Rieseberg, 2001). This was elegantly illustrated for invasive *Spartina anglica.* Methylation changes are predominantly associated with hybridization and rarely with genome doubling in this species (Parisod *et al.*, 2009). Changes in genome-wide cytosine methylation affected almost 35 % of allopolyploid *Spartina*'s genome, with little or no genetic change (Salmon *et al.*, 2005). This serves as a powerful example of how invasive behaviour can arise following polyploidization coupled with major modifications in epigenetic regulation of gene expression.

The complexity of genomic, genetic and epigenetic processes associated with polyploidization and how they interact to create phenotypic novelty is just emerging. Whether genome multiplication *per se* (autopolyploidy) actually represents an evolutionary advantage remains an open question. Parisod *et al.* (2010) suggested that the null model for future studies should be to assume that autopolyploidy represents a neutral, racketing process (Meyers and Levin, 2006). Nevertheless, autopolyploids seem to have some immediate advantage of polysomic inheritance, which may be important for establishment in new environments, and increased genome flexibility as a result of gene redundancy for selection to act upon (Parisod *et al.*, 2010).

MORPHOLOGICAL, PHYSIOLOGICAL AND ECOLOGICAL CONSEQUENCES OF POLYPLOIDY FOR PLANT INVASIONS

Compared with genetic and genomic consequences of polyploidy, its effects on the ecology of plants, mediated by altered plant morphology and physiology, remain poorly understood (Soltis *et al.*, 2010). Since the 1950s many hypotheses have been developed and generalizations made to explain the distribution and abundance of polyploids. Most evidence is anecdotal or comes from observational studies, and experimental data are scarce (Soltis *et al.*, 2010). Many of the ecological factors attributed to polyploids, such as higher tolerance of abiotic stress, higher colonization ability and greater ecological tolerance or niche breath, are also associated with invasiveness in novel habitats. Out of these, the two most influential and oldest, however controversial, ideas of the effects of polyploidization on the ecology of plants are that polyploids have (1) broader ecological tolerance and (2) higher colonization ability than diploids (Stebbins, 1950; Grant, 1981). We will discuss these hypotheses in detail and specifically address the ecological consequences of genome duplication pertaining to factors that have been shown to affect plant invasiveness (see Fig. 2).

Morphology

An immediate consequence of becoming polyploid is a change in cell size, with polyploids typically having larger cells than diploids (Müntzing, 1936; Stebbins, 1971). Differential growth of the internal volume vs. the surface area of the nucleus may in turn have implications for cellular architecture and regulatory functions (Comai, 2005). This may potentially slow down metabolism and growth rates in polyploids (Cavalier-Smith, 1978), due to, for example, longer replication times (Bennett and Leitch, 2005; Gregory, 2005). Hessen *et al.* (2009) argued that elemental costs of growth, in the form of nitrogen and phosphorus used to build nucleic acids, may be viewed as direct material cost associated with supporting larger genomes. Correlated with a larger cell size are alterations in plant morphology: polyploids are usually taller and more robust, with larger flowers and seeds (Müntzing, 1936; Garbutt and Bazzaz, 1983; Bretagnolle *et al.*, 1995). However, there is an optimum for chromosome increase beyond which the individual becomes less vigorous, if viable at all (Müntzing, 1936). The seeds of many autotetraploids are larger than those of their diploid conspecifics (Bretagnolle *et al.*, 1995; Levin, 2002). Large seed size often results in more robust and more rapidly growing seedlings compared with diploids, but not necessarily increased germination rates (Bretagnolle *et al.*, 1995). Despite this, polyploid seedling vigour could confer a competitive advantage at the early stages of invasion: a stage often characterized by founder events and resulting in establishment failure. Larger adult size of polyploids might also convey an advantage during invasion. Increased plant size has been suggested as an explanation for invasion success inducing increased competitiveness and vigour (Blossey and Nötzold, 1995; Jakobs *et al.*, 2004; Stastny *et al.*, 2005). Examples include invasive tetraploids of *Solidago gigantea* that grow larger than native diploids but show no increase in plant height and biomass compared with native tetraploids (Schlaepfer *et al.*, 2010), and invasive polyploids of the genus *Fallopia* that are believed to be successful because of their large size, high biomass production and extensive rhizomes (Schnitzler, 1998).

Polyploids generally produce larger flowers than diploids (Garbutt and Bazzaz, 1983) that are also often shaped differently, attracting different suites of floral visitors (Taylor and Smith, 1979; Segraves and Thompson, 1999). Even the type of flowers can be drastically influenced by polyploidization.
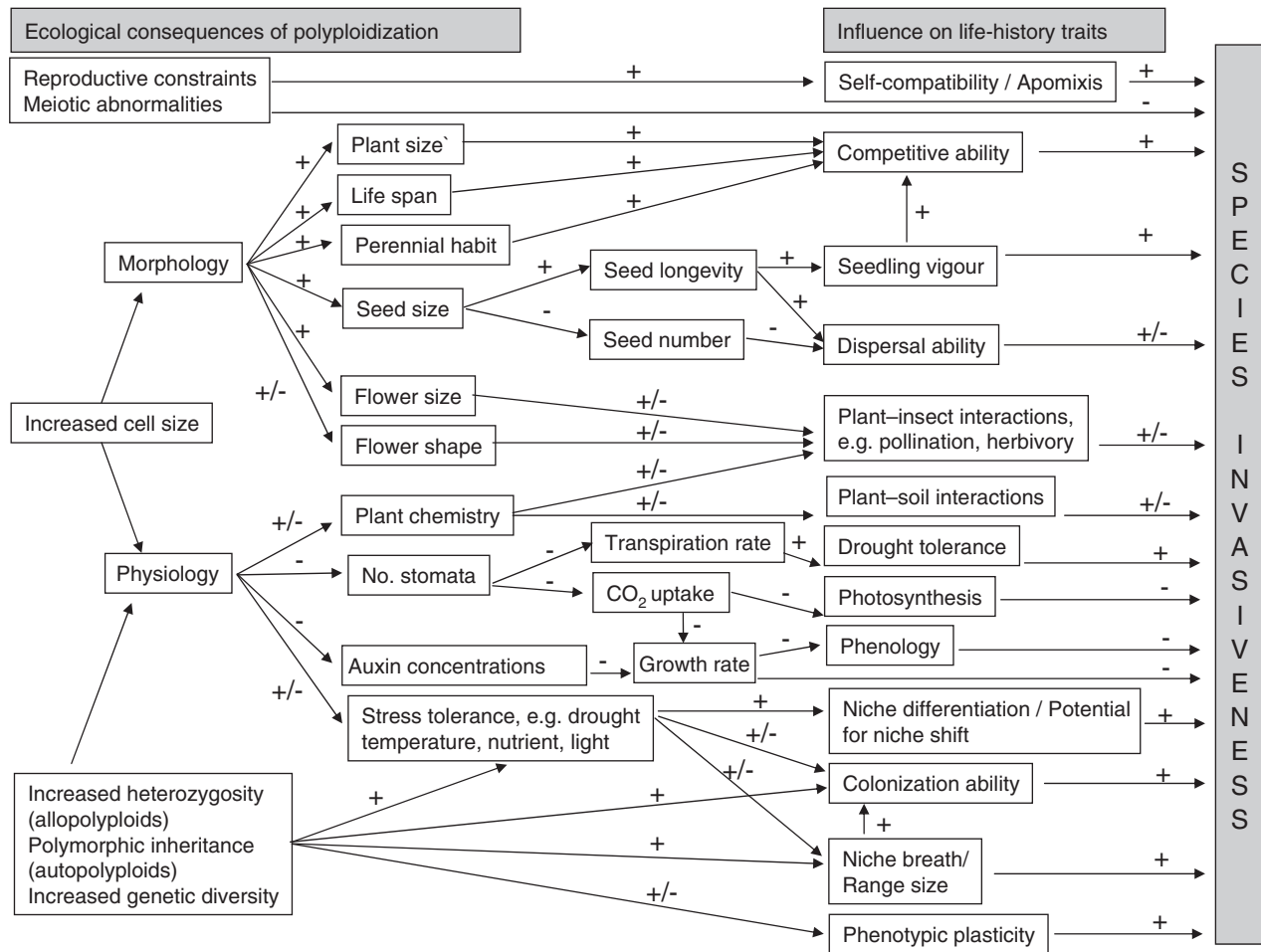
FIG. 2. Ecological consequences of polyploidization and how they may affect species invasiveness. No distinction is made between modes of polyploidization. The sign next to the arrow gives the direction of the effect.

For example, Bernström (1950) found that tetraploid *Lamium amplexicaule* populations had a higher number of cleistogamic (non-opening) flowers than diploid populations, allowing for more efficient self-pollination, which might enhance seed production in unfavourable habitats. In addition to altered flower morphology, many polyploids also show differences in flowering phenology compared with diploids. Petit *et al.* (1997) showed that patterns of flowering phenology in the grass species *Arrhenatherum elatius* were almost fully divergent between parapatric cytotypes. In general, polyploids show prolonged (Bose and Choudhury, 1962) or later onset of flowering (Smith, 1946; Garbutt and Bazzaz, 1983), possibly due to lower growth rates. Changes in phenology may greatly affect invasion success. By shifting or prolonging their period of flowering compared with native species, invaders can escape competition for light, pollinators, etc. (Levin, 2009; Wolkovich and Cleland, 2010) and, notably, early flowering has been shown to facilitate invasiveness (Pyšek and Richardson, 2007; Pyšek *et al.*, 2009).

Another frequently observed shift in polyploids is from annual to perennial habit (Hagerup, 1932; Müntzing, 1936; Sano, 1980), which might be necessary due to the slower metabolism caused by an increased cell size, with the advantage of greater longevity (Frame, 1976; Garbutt and Bazzaz, 1983). Not surprisingly, therefore, the frequency of polyploids differs among growth forms, being more common among perennial herbs and woody plants (Stebbins, 1971; Levin and Wilson, 1976).

Physiology

Associated with the morphological alterations typical of polyploidy and, most importantly, as a result of increased cell size, there are fundamental physiological differences between diploids and polyploids that form the basis for ecological differentiation. Polyploids have been found to differ from related diploids in many ways, such as growth rate, hormone concentrations, content of secondary metabolites, water relations (including drought tolerance), transpiration rate and stomata function, photosynthetic activity and stress tolerance (Smith, 1946; Li *et al.*, 1996; MacArthur and Sanderson, 1999; Levin, 2002; Maherali *et al.*, 2009; Liu *et al.*, 2011). In line with the generally observed lower growth rates (Garbutt and Bazzaz, 1983), lower concentrations of the growth hormone auxin have been reported in, for example, polyploid *Brassica oleracea* var. *capitata* (Avery

and Pottorf, 1945) and *Sedum pulchellum* (Smith, 1946) compared with diploids.

Polyploidization can change the quality and quantity of secondary metabolites. Most research in this area has been focused on pharmaceutical and aromatic plants. For example, in many pharmaceutical plants, e.g. *Datura tatula* (Rudorf and Schwarze, 1951), *Hyoscyamus niger* (Lavania and Srivastava, 1991), *H. muticus* (Lavania, 1986), *Papaver bracteatum* (Milo *et al.*, 1987) and *Solanum khasianum* (Bhatt and Heble, 1978), autopolyploids have increased quantities of alkaloids per unit weight. In several aromatic polyploids, such as *Carum carvi* (Dijkstra and Speckman, 1980), *Ocimum kilimandscharicum* (Bose and Choundhury, 1962), *Mentha arvensis* (Janaki Ammal and Sobti, 1962) and *Vetiveria zizanioides* (Lavania, 1988), increased terpene levels and elevated essential oil concentration have been recorded, although effects may differ greatly between different subspecies (MacArthur and Sanderson, 1999). Changes in the chemical composition of polyploids may lead to changes in interactions with other members of the biotic community, such as insect herbivores, pollinators or soil organisms, and, hence, might have pronounced effects on their success. A recent study comparing native and invasive *Solidago gigantea* showed reduced concentrations of terpenes in invasive cytotypes (diploids and tetraploids) compared with native cytotypes (diploids, tetraploids and hexaploids) (Hull-Sanders *et al.*, 2009). The effect of the continent of origin was generally larger than that of ploidy, although in general tetraploids had higher levels of sesquiterpenes than the other two cytotypes.

Polyploidization can have substantial impact on the water relations of plants. Polyploids typically have fewer but larger stomata, resulting in lower transpiration rates and hence reduced water loss through the leaves, as was shown in penta- and hexaploids of *Betula papyrifera* (Li *et al.*, 1996). A lower transpiration rate compared with diploids has also been found in autotetraploid *Hordeum vulgare* (Chen and Tang, 1945). Tetraploid *Chamerion* (syn. *Epilobium*) *angustifolium* (Maherali *et al.*, 2009) was found to have higher water use efficiency than diploids, and plants took longer to wilt. Garbutt and Bazzaz (1983) grew diploid and polyploid individuals of *Phlox drummondii* on a soil moisture gradient and showed a shift in preference from wet to dry conditions with increase in ploidal level. The contention that polyploids are often better adapted to dry conditions is further supported by numerous cytogeographical studies (e.g. Hagerup, 1932; Stebbins, 1949, 1972; Kay, 1969; Watanabe, 1986), but see Paun *et al.* (2011). Adaptation to dry conditions might influence invasion success, as has been shown for the invasion of tetraploid *Centaurea stoebe* in North America (Treier *et al.*, 2009).

As is the case with lower transpiration rates, CO_2 exchange rates, and therefore photosynthetic ability, are also expected to be lower in polyploids (Levin, 2002). This has been shown in *H. vulgare* (Chen and Tang, 1945), *Galeopsis pubescens* (Ekdahl, 1949) and *Ribes satigrum* (Bjurman, 1959), but no differences in photosynthetic rates between ploidal levels were observed in *Viola adunca* (Mauer *et al.*, 1978). In *Festuca arundinacea* (Byrne *et al.*, 1981) and *Panicum virgatum* (Warner *et al.*, 1987) even a positive correlation between ploidal level and photosynthetic rate per unit leaf area has been observed. However, units play a great role in determining

photosynthetic rates, as shown in *Atriplex confertifolia* (Warner and Edwards, 1989). The number of cells per unit leaf area decreases with increasing ploidal level and, therefore, even if the photosynthetic rate per cell is higher, photosynthetic rates per unit leaf might be equal to or lower than those of diploids. Since photosynthesis is fundamental to plant growth, reduced photosynthetic rates might actually reduce the success of invasive species. However, the study by Hull-Sanders *et al.* (2009) showed that such a generalization is tenuous. They found, contrary to the pattern observed for secondary metabolites (see above), that ploidy is the main factor explaining differences in photosynthesis of *S. gigantea*, with the native hexaploids having the highest photosynthetic rates, but lower specific leaf area and infrutescence mass, which might ultimately result in lower, rather than higher, fitness.

It has long been recognized that polyploidization might increase stress tolerance and thereby form an important factor in polyploid success. Dating back as far as the 1930s, tetraploids of the genera *Dianthus* and *Nicotiana* were shown to perform better on nutrient-poor, calcareous soils than diploids (Rohweder, 1937; Noguti *et al.*, 1940). Recently, the same was found for *S. gigantea* (Schlaepfer *et al.*, 2010). Similarly Liu *et al.* (2011) found evidence for increased cold, drought and salinity but not heat tolerance in artificially induced tetraploids of *Dendranthema nankingense*, while increased salinity tolerance has been found in tetraploid *Brassica rapa* (Meng *et al.*, 2011). Greater tolerance to low nutrient levels or high salinity may arise from higher nutrient uptake efficiency in polyploids. However, a study by Cacco *et al.* (1976) showed that the direction of response is species-specific; nutrient uptake efficiency increased with ploidal level in *Triticum* and *Beta*, but declined in *Solanum*.

The same species-specific response is found for the effect of polyploidization on cold tolerance, although empirical data are scarce. Polyploids show increased (Liu *et al.*, 2011) or reduced (Wit, 1958; Tyler *et al.*, 1978) cold tolerance. Lachmuth *et al.* (2010) found that invasive European populations of tetraploid *Senecio inaequidens* show higher levels of 'pre-adaptation' for cold tolerance compared with native range diploids. In general, cold tolerance is inferred from cytogeographical studies (e.g. Hagerup, 1933; Lewis, 1967; Mosquin, 1967; Schaefer and Miksche, 1977) and linked to the suggestion that polyploids may be more common at higher elevations and latitudes than diploids (Grant, 1981). For example, Tyler *et al.* (1978) showed that tetraploid *Festuca pratensis* var. *apennina* preferred higher elevations, had a cold requirement for germination, but its seedlings were more cold susceptible than diploids. However, in several other cases, a negative correlation was found between polyploidy and elevation, with polyploids occupying the lower elevations, e.g. *Atriplex confertifolia* (Stutz and Sanderson, 1983), *Chamerion angustifolium* (Husband and Schemske, 1998), *Centaurea jacea* (Hardy *et al.*, 2000), *Lotus* spp. (Gauthier *et al.*, 1998) and *Senecio carniolicus* (Schönswetter *et al.*, 2007), but see Tyler *et al.* (1978) and Felber-Girard *et al.* (1996). Stebbins (1971) performed a larger scale study assessing the percentage of polyploids in the flora of the Alps and did not find any elevational pattern. In contrast, a positive correlation of polyploidy with latitude is fairly well supported, e.g. in European and Arctic floras (Soltis, 1984; Brochmann *et al.*, 2004), on the Pacific Coast

of North America (Stebbins, 1984) and in New Zealand (Hair, 1966), but see Martin and Husband (2009). However, it is thought that the high incidence of polyploidy in northern latitudes is not necessarily due to increased cold tolerance (Soltis et al., 2004), but rather a confounding effect with the dominant life form in these regions, namely a perennial habit, in which polyploidy is more frequent (Stebbins, 1971), or due to the degree of previous glaciation, as polyploids seem to be more successful than diploids in colonization after deglaciation (Levin, 2002; Brochmann et al., 2004).

Ecological tolerance

Whether or not polyploids have a broader ecological tolerance than diploids (Stebbins, 1950; Grant, 1981) remains controversial. Discussion in this regard has followed two main tracks. The first deals with stress tolerance and asks whether polyploids have a greater tolerance of extreme ecological or climatological conditions (see previous paragraph). Based on field experiments, Stebbins (1985) rejected the hypothesis that polyploids can tolerate harsher (drier) environments. Nevertheless, the fact that polyploid perennials are the predominant life form in the Arctic (Brochmann et al., 2004) suggests the opposite. The second key area of discussion relates to range size, with the main question being whether polyploids can tolerate a wider range of environmental conditions than their diploid progenitors (translating to larger geographical ranges) (Stebbins, 1950). This is frequently speculated to be the case due to higher levels of heterozygosity and genetic diversity (Lowry and Lester, 2006) and may be more pronounced in allopolyploids, where two parental genomes are combined. Of course a greater stress tolerance might enable a polyploid species to occupy a wider array of habitats, but not necessarily vice versa, and the distinction between these two interpretations is often not made. The empirical evidence for larger range size is conflicting. Stebbins and Dawe (1987) were the first to perform a large-scale comparative study of diploids and polyploids in 75 large European genera. They found no evidence that polyploids were more widely distributed than diploids. Likewise, Petit and Thompson (1999) found no evidence for differences in range size between diploids and polyploids among 451 species of 50 genera in the flora of the Pyrenees. These studies, however, both used sets of unrelated species, allowing for confounding effects of taxonomic identity. Indeed, in a comparison of 144 North American genera, Martin and Husband (2009) showed that most variation in range size is phylogenetically correlated, albeit that no differences existed between polyploid and diploid species pairs, thereby supporting neither interpretation of the ecological tolerance hypothesis. In contrast, a study examining range sizes within the genus *Clarkia* found that polyploids had significantly larger ranges than diploids (Lowry and Lester, 2006). Similar results, where polyploids were more common and widespread than diploids, were found for *Hedyotis purpurea* (Lewis, 1967), *Eupatorium* spp. (Watanabe, 1986), *Plantago media* (Van Dijk and Bakx-Schotman, 1997) and *Aster amellus* (Münzbergová, 2007). Whether or not polyploids have increased ecological amplitude is a pivotal issue when arguing for a strong influence in invasiveness and seems to be species-specific. However, in a recent analysis, Pandit et al. (2011) performed a worldwide comparison of ploidal levels among invasive, widespread plants and rare, localized plants, and indeed showed a positive correlation between polyploidy and invasiveness.

Colonization ability

It is generally believed that increased ecological tolerance will enable polyploids to colonize new habitats with greater ease than their diploid counterparts (Stebbins, 1985). Support for this hypothesis comes from studies on several European and North American plants, where diploids are found to be limited to restricted and disjunct ranges, while polyploids are much more widely distributed (Watanabe, 1986; Novak et al., 1991; Van Dijk and Bakx-Schotman, 1997; Münzbergová, 2007). The glaciation history of these continents might go some way towards explaining this pattern (Watanabe, 1986; Van Dijk and Bakx-Schotman, 1997), which also seems to hold up for contemporary habitat fragmentation. For example, among 'islands' of natural vegetation surrounded by extensive vineyards in southern France, polyploids were found to occupy more different 'islands' than diploids and have an overall wider distribution (Lumaret et al., 1997). Similarly, for European *Dactylis glomerata* the range of diploids has been divided and reduced as a result of deforestation, whereas the range of tetraploids has expanded, as they could invade newly created anthropogenic habitats (Lumaret, 1988). In contrast, the highly successful invasive allopolyploid *Spartina anglica* has a narrow ecological niche despite its ability to completely replace native communities, alter succession, affect food webs, etc. (Thompson, 1991), although new hybrids with high ecological amplitude have been reported between native *S. maritima* and introduced *S. densiflora* in the Iberian Peninsula (Castillo et al., 2010).

Niche differentiation

Apart from the discussion about whether polyploids have wider distributions, given the influence of polyploidy on plant growth, physiology, gene expression, etc., it is likely that niche differentiation readily occurs between different ploidal levels. Cytogeographical studies show that diploids and polyploids often occupy different parts of the landscape and that polyploids typically replace their diploid parents along ecological gradients, such as moisture gradients, with polyploids generally occupying drier habitats than diploids (Hagerup, 1932; Baldwin, 1941; Kay, 1969; Watanabe, 1986; Maherali, 2009; Treier et al., 2009) and gradients of light availability, where polyploids generally prefer more open habitat (Rothera and Davy, 1986; Watanabe, 1986; Lumaret et al., 1987; Brammel and Semple, 1990), but see Fukuda (1967). Some studies, however, have not found evidence of niche differentiation of diploids and polyploids along ecological gradients (Bowden, 1940; Martin and Husband, 2009). For allopolyploids, the level of overlap with the two parental niches gives information on the degree of niche differentiation and shows again that the response is highly species-specific. For example, the niches of the allopolyploids *Erythronium quinaultense* (Allen, 2001) and *Spiranthes diluvialis* (Arft and Ranker, 1998) do not overlap

with those of their diploid parents, while the niches of the allo-tetraploids *Clarkia delicata* (Smith-Huerta, 1986), *Tragopogon miscellus* and *T. mirus* (Novak *et al.*, 1991; Soltis *et al.*, 2004) do. Autopolyploids show a similar species-specific response in niche differentiation between cytotypes. Niche differentiation between diploids and autotetraploids was found in *Dactylis glomerata* (Lumaret *et al.*, 1987; Ståhlberg, 2009), *Senecio carniolicus* (Sonnleitner *et al.*, 2010) and *Anthoxanthum odoratum* (Felber-Girard *et al.*, 1996), but not in *Claytonia virginica*, *Hedyotis purpurea* and *Oldenlandia capensis* (Lewis, 1976).

The conclusive test of whether the observed geographical patterns are indeed due to altered preferences and/or tolerances requires reciprocal transplant experiments. For example, such approaches have shown that niche differentiation was due to local adaptation in polyploid *Anthoxanthum* spp. (Flégrová and Krahulec, 1999), *Aster amellus* (Raabová *et al.*, 2008) and *Achillea borealis* (Ramsey, 2011). Niche differentiation was also observed between tetraploid subspecies of *Dactylis glomerata* (Gauthier *et al.*, 1998) and tetraploid populations of *Arrhenatherum elatius* (Petit *et al.*, 1997). Buggs and Pannell (2007) found support for ecological differentiation between diploid and polyploid populations of *Mercurialis annua*, but since the diploid plants had higher fitness across all sites, the results did not indicate local adaptation. Similarly, Baack and Stanton (2005) did not find a reciprocal advantage in performance between diploid and tetraploid populations of *Ranunculus adoneus*. Reciprocal transplant studies between native and invasive species show similar contrasting results. No evidence for niche differentiation and local adaptation has been found in introduced *Mahonia* spp. in Germany (Ross *et al.*, 2009) and asteraceous forbs in the Swiss Alps (Poll *et al.*, 2009), while local adaptation is suggested in invasive *Bromus tectorum* in North America (Leger *et al.*, 2009) and *Rhododendron ponticum* in Ireland (Erfmeier and Bruelheide, 2010). Evidence of niche differentiation and local adaptations along latitudinal gradients in introduced species comes from common garden and growth chamber experiments (Weber and Schmid, 1998; Sexton *et al.*, 2002; Kollmann and Bañuellos, 2004). Additionally, there is substantial literature showing that niche shifts, whether adaptive or not, readily occur when species are transported to novel environments (Parker *et al.*, 2003; DeWalt *et al.*, 2004; Broennimann *et al.*, 2007; Treier *et al.*, 2009; Alexander and Edwards, 2010; Gallagher *et al.*, 2010). Polyploidy might increase the adaptive potential of invasive species in their novel habitat, but few common garden or reciprocal transplant studies exist actually to test this. Schlaepfer *et al.* (2010) performed one of the few comparisons between native and invasive cytotypes under controlled experimental conditions. They showed that native and invasive tetraploids generally performed better than native diploids, suggesting that the invasion success of tetraploids was not acquired through adaptation after introduction, but due to polyploidization events in the native range (Schlaepfer *et al.*, 2010).

Phenotypic plasticity

Plant performance and invasion success are believed to be enhanced by high phenotypic plasticity (Baker, 1965;

Richards *et al.*, 2006; Davidson *et al.*, 2011), and the same has been suggested for polyploid success. In allopolyploids a higher plasticity may result from higher levels of heterozygosity (Mitton and Grant, 1984) but, conversely, lower plasticity in polyploids is also hypothesized due to greater homeostasis resulting in less variation of fitness-related phenotypic plasticity along environmental gradients (Bretagnolle and Thompson, 2001). However, to date no differences in phenotypic plasticity in either direction have been found between diploids and polyploids (Petit *et al.*, 1996; Petit and Thompson, 1997; Bretagnolle and Thompson, 2001; Münzbergová, 2007), while more and more evidence is pointing towards higher phenotypic plasticity being an important determinant of species invasiveness (Davidson *et al.*, 2011).

Disturbance

Another similarity between theories on polyploid success and success of plant invaders is the role of disturbance. It is generally assumed that polyploids are more successful than their diploid parents in disturbed habitats (Stebbins, 1985; Otto and Whitton, 2000), which is the same for invasive species (Hobbs and Huenneke, 1992). Blackburn *et al.* (2011) argued that disturbance might not be as useful a concept as previously thought, since environmental modification can happen in a variety of ways, both natural and anthropogenic, and colonization of new areas is determined rather by the amount of suitable habitat. Nonetheless, a study by Ehrendorfer (1980) on the flora of lower Austria and the Ivory Coast shows that polyploids are more often found in disturbed or successional habitats, whereas diploids often are found in more stable habitats or climax communities. The same pattern was observed between younger polyploids and older polyploids, where younger polyploids tend to occur more in the disturbed habitats (Ehrendorfer, 1980).

Competition

Ultimately, given the necessary abiotic requirements, interactions between plants and their biotic environment determine their successful establishment and/or spread. Competition constitutes an important part of these biotic interactions. Intuitively, higher competitive ability will facilitate higher colonization ability, although, in time, native communities might adapt to promote coexistence (Leger, 2008; Goergen *et al.*, 2011). It is suggested that polyploids have a greater competitive ability than diploids due to higher seedling growth rates and/or higher seed production coupled with higher germination rates (Bretagnolle *et al.*, 1995). Experimental studies support the higher competitive ability of polyploid *Trifolium pratense* (Anderson, 1971) and *Dactylis glomerata* (Maceira *et al.*, 1993). However, in several crop plants tetraploids were found to be inferior competitors to diploids, e.g. in *Nicotiana tabacum* (Sakai, 1956), *Oryza sativa* (Sakai and Utiyamada, 1957) and *Hordeum vulgare* (Sakai and Suzuki, 1955). Münzbergová (2007) planted diploids and hexaploids of *Aster amellus* together with a common competitor, *Bromus erectus*, and found that although the performance in the presence of competition was equally low in both cytotypes, the hexaploids showed a greater increase in biomass in the

absence of competition, with no response from diploids. Lumaret *et al.* (1997) argues that a higher competitive ability of polyploid perennial herbs may constitute a critical factor responsible for their wider distribution.

In addition to resource competition, newly established polyploids must also compete with their diploid parents for reproductive opportunities. Since the gametes of neopolyploids are lost by union with the more abundant gametes of the diploid through the formation of sterile triploids, the neopolyploids might not be able to persist. This process is known as minority cytotype exclusion (Levin, 1975; Husband, 2004; Baack, 2005*a*). Modelling exercises show that minority cytotype exclusion may be overcome by increased unreduced gamete formation in the diploid population, leading to a higher frequency of polyploids compared with diploids (Fowler and Levin, 1984), by increased fitness of the polyploid (Felber, 1991; Felber and Bever, 1997), by higher self-fertilization rates and lower inbreeding depression in polyploids (Rausch and Morgan, 2005), or by short-distance seed and pollen dispersal of polyploids (Baack, 2005*b*). These mechanisms all lead to the replacement of the diploid by polyploids. Alternatively, coexistence may occur due to slight niche differentiation between diploid and polyploid individuals immediately following the origin of the polyploid (Fowler and Levin, 1984; Rodriguez, 1996).

Biotic interactions

Interactions with other components of the biotic environment, such as insect herbivores, pollinators, soil organisms and/or pathogens, are also of great importance to the success of plants in general, and neopolyploids and invasive species in particular. While this field remains poorly studied, current knowledge suggests that altered biotic interactions can potentially have much larger scale effects on community interactions than previously thought. Polyploidization can affect biotic interactions through, for example, changes in the chemical profile or altered flower morphology. In *Trifolium repens* (Taylor and Smith, 1979) and *Heuchera grossularifolia* (Segraves and Thompson, 1999; Thompson *et al.*, 2004; Thompson and Merg, 2008) tetraploids have longer petals, deeper corolla tubes, fewer flowers per inflorescence and, therefore, attract different assemblages of pollinators compared with diploids. This may in turn provide opportunities for diversification in both plant and insect taxa (Nuismer and Thompson, 2001).

Not only pollination, but also resistance to pathogens and/or insect herbivores may be affected by polyploidization, with polyploids generally enjoying increased pathogen resistance. Mathematical models indicate that neopolyploids might initially be more resistant to pathogens compared with their diploid parents (Oswald and Nuismer, 2007). Changes in disease resistance genes between polyploids and diploids also point towards altered pathogen resistance (Innes *et al.*, 2008), and this is supported by empirical data. For example, comparisons between diploids and tetraploids of several food and ornamental plants all show higher resistance of polyploids to fungal pathogens (Vestad, 1969; Burdon and Marshall, 1981; Kulkarni and Ravindra, 1988) and nematode parasitism (Mehta and Swaminathan, 1957; Busey *et al.*, 1993). Studies on insect herbivory, however, show contrasting results. Thompson *et al.* (1997) proposed that polyploidization may create evolutionary barriers to attack, resulting in lower attack rates than in diploids. However, when testing this idea, they found the opposite: tetraploid *Heuchera grossularifolia* had higher levels of moth attacks than diploids (Thompson *et al.*, 1997; Nuismer and Thompson, 2001; Janz and Thompson, 2002). The same was found in *Aster amellus* where hexaploid populations host more herbivores and suffer higher herbivore damage than do diploid populations, possibly due to higher seed production in hexaploid populations (Münzbergová, 2006). In *Brassica campestris*, however, tetraploids were less affected by aphids than diploids (Choudhury *et al.*, 1968). Altered plant–insect interactions may have many implications for controlling plant invasions with biological control. Accurate matching of biological control agents is essential for effective control, and differences in ploidal level might complicate accurate matching and delay control measures (Müller-Schärer and Schaffner, 2008).

Polyploidization can also affect plant–soil interactions. In a mycorrhiza inoculation experiment of diploid and hexaploid individuals of *Aster amellus*, Sudová *et al.* (2010) showed that ploidy can markedly influence the functioning of the arbuscular mycorrhiza (AM) symbiosis. Diploid plants depend on AM symbiosis, as shown by nearly 100 % mortality in uninoculated treatments. In contrast, the hexaploid cytotypes of *A. amellus* consistently did not respond to inoculation. To explain this result, the authors suggested that because polyploids are already more tolerant to abiotic stresses, the maintenance of AM symbiosis may pose an unnecessary burden. Alternatively, the slower developmental processes, along with higher maintenance costs in polyploids may be inhibited further by the cost of maintaining the AM symbiosis. Finally, diploids of *A. amellus* have less developed root systems, which could make them more dependent on AM symbiosis than polyploids. Sudová *et al.* (2010) found no differences in the mycorrhizal growth response between diploids and polyploids of *Campanula gentilis* and *Pimpinella saxifraga*. Thébault *et al.* (2010) measured soil microbial activity and diversity in native and introduced cytotypes of *Senecio inaequidens* and *Centaurea stoebe* (syn. *C. maculosa*) and showed similar species-specific responses. In *S. inaequidens* the total amount of microbial biomass carbon in the rhizosphere increased in both the native and introduced tetraploids compared with native diploids, while the total rhizosphere DNA content was higher in native diploids than in tetraploids, indicating an effect of polyploidization. In *C. stoebe*, on the other hand, the diversity of the bacterial soil community increased from native diploids, to native tetraploids and introduced tetraploids, indicating effects of both polyploidization and introduction in *C. stoebe*. These studies are among the few (Schlaepfer *et al.*, 2010; Thébault *et al.*, 2010) that compare attributes of native and introduced cytotypes in growth experiments, and many more are needed to shed light on the complex interaction between polyploidization and invasion success.

GENOME SIZE AND INVASIVENESS

Inherently associated with ploidy is the amount of nuclear DNA or genome size. While the holoploid genome size (or C-value)

is used to describe the size of the whole chromosome complement irrespective of the degree of generative ploidy, the term monoploid genome size (or Cx-value) denotes the (averaged) DNA content of the monoploid chromosome set (Greilhuber *et al.*, 2005). Genome sizes vary tremendously in vascular plants, spanning from 0·065 to 152·23 pg/1C (Bennett and Leitch, 2010), and diploid genomes of one species might even be larger than or equal to polyploid genomes of a different species. The ever-growing interest in genome size data has been fuelled by the fact that the amount of nuclear DNA itself can influence several characteristics from subcellular to organismal levels, irrespective of the coded information (the so-called nucleotypic effect; Bennett, 1972; Gregory, 2001). DNA thus plays a dual role in heredity: (1) genic, i.e. holding the precise information about the organism's development and functioning, and (2) nucleotypic, i.e. setting thresholds within which the genes can operate and therefore independently constraining the organism's functional traits. The total DNA amount (C-value) rises with increased ploidy, but the increase is often not proportional, resulting in the decline of Cx-values (i.e. genome downsizing; Leitch and Bennett, 2004). The actual effect of genome size on plant traits then depends on the interplay between ploidy, C- and Cx-values.

Universal nucleotypic effects among most organisms include a positive correlation between genome size and the cell volume and a negative correlation with the cell division rate (Gregory, 2005). Cells must be larger to accommodate larger genomes; larger genomes need more time to replicate, thus constraining the cell growth rate. These nucleotypic correlations further translate into higher levels of biological organization and affect various functional traits (Knight *et al.*, 2005). The value of nucleotypic correlations lies in their broad applicability to all groups of plants as well as in their predictive value. Genome size-constrained traits related to individual growth rates, reproductive success and dispersal, such as the minimum generation time (Bennett, 1972; Leitch and Bennett, 2007), specific leaf area (Morgan and Westoby, 2005; Beaulieu *et al.*, 2007a) and seed mass (Grotkopp *et al.*, 2004; Beaulieu *et al.*, 2007b; Knight and Beaulieu, 2008), may be of particular importance in invasion success. Generally, plants possessing large genomes are constrained in a range of functional traits and, consequently, also in the range of ecological options available to them (see the 'large genome constraint' hypothesis; Knight *et al.*, 2005). For example, whereas small-genome herbaceous species can either be ephemeral, annual or perennial, their counterparts with large genomes are slow-growing obligate perennials. Similarly, large-genome species are generally restricted to the production of large seeds with low dispersal abilities and thus have a lower potential to colonize new habitats. Perhaps not surprisingly, endangered (i.e. typically spatially restricted) species tend to have large genomes (Vinogradov, 2003) whereas the opposite is generally true for weedy angiosperms (Bennett *et al.*, 1998). Linked to seed traits and growth rates, genome size may also co-determine the ecological strategy that the plant adopts (i.e. competitive, stress-tolerant or ruderal) and the type of habitats where it will thrive (Bennett, 1987).

Attempts to incorporate genome size information into models aimed at predicting the invasive behaviour date back to the late 1990s. Rejmánek (1996, 2000) hypothesized that the ultimate determinant of plant invasiveness in disturbed habitats may be short minimum generation time, a genome size-constrained trait. Other ecologically relevant traits associated with small genomes such as small seeds, high growth rate and high specific leaf area may further catalyse the spread of invasive species. For example, Grotkopp *et al.* (2002) reported a negative correlation between the invasiveness and genome size in the genus *Pinus* (particularly in the wind-pollinated species). The same was found in the genus *Artemisia*, where weediness or invasive behaviour was coupled with lower genome sizes (Garcia *et al.*, 2008). Similarly, Chen *et al.* (2010) observed that both C- and Cx-values had significant effects on plant invasiveness in most plant groups, exceptions being trees and the family Fabaceae; Gallagher *et al.* (2011) found no relationship between invasiveness and genome size in Australian *Acacia* species. Chen *et al.* (2010) found that monoploid genome size had a higher predictive value for assessing plant invasiveness than the size of the holoploid genome, and suggested that the high proportion of polyploids among weedy plants can at least partly be explained by genome downsizing. Further insight into the role of genome size in plant invasion was gained by Kubešová *et al.* (2010) who compared genome sizes of nearly 100 alien species naturalized in the Czech Republic with their congeners and confamilials not reported to be naturalized or invasive in any part of the world, and concluded that the former had on average smaller genomes. They showed that invasive species in the Czech flora did not differ in genome size from naturalized but non-invasive species, indicating that small genomes may predispose alien plants to become established in novel environments, but not necessarily to become invasive (Kubešová *et al.*, 2010).

Particularly valuable for the elucidation of the effects of DNA mass on invasive potential in plants are species with both non-invasive and invasive genotypes that show intraspecific variation in genome size. Recently Lavergne *et al.* (2010) showed that invasive genotypes of reed canary grass (*Phalaris arundinacea*) in North America have smaller genomes than their native source populations in Europe. The observed reduction in genome size, which probably occurred over a few generations, was associated with phenotypic changes (e.g. a higher early growth rate) that increased the species' invasive potential. This study shows that the selective changes in the amount of nuclear DNA can be of paramount ecological and evolutionary importance, leading to genetic novelties and possibly to the establishment of pheno-/genotypes with enhanced invasive ability.

PLOIDAL LEVELS IN INVASIVE PLANTS

Invasions are driven by multiple factors, and the role of species traits is context dependent and differs with respect to ecological settings and stage of an invasion (Hamilton *et al.*, 2005; Williamson, 2006; Pyšek and Richardson, 2007; Van Kleunen *et al.*, 2007; Wilson *et al.*, 2007; Gravuer *et al.*, 2008; Küster *et al.*, 2008; Pyšek *et al.*, 2009; Moravcová *et al.*, 2010; Hui *et al.*, 2011). Therefore, the contribution of any biological trait to species' invasion success should be assessed in concert with other factors such as, for example,

propagule pressure, residence time or climatic suitability (Pyšek *et al.*, 2010). Analyses of databases, comparing alien and native floras of large regions, provide opportunities to assess the role of traits in such a context (Pyšek and Richardson, 2007). However, data on ploidal levels are rarely available for the large numbers of species in a complete flora. Consequently, this trait is seldom addressed in multitrait analyses. Of the 18 comparative multispecies studies reviewed by Pyšek and Richardson (2007), none included ploidy as an explanatory variable for invasiveness. However, Pandit *et al.*'s (2011) worldwide comparison of ploidy among invasive and rare plants convincingly showed that polyploidy contributes to invasion success. Pyšek *et al.* (2009) considered the effect of ploidy in concert with other determinants that are traditionally believed to increase the likelihood of a species' invasion success. They showed that, in addition to propagule pressure and climatic pre-adaptation, ploidy is an important factor co-determining the success as a global weed. As with other plant species traits identified as important, the number of ploidal levels only had a significant effect on the probability of a species becoming invasive, but not on the probability of being introduced (Pyšek *et al.*, 2009).

These studies, comparing large data sets of invasive vs. non-invasive species, show that polyploidy might be an important factor in invasion success. However, as mentioned before, a comprehensive overview of ploidal levels across the most invasive plant species worldwide is still lacking; such information is essential for establishing the importance of ploidy in determining invasion success. We therefore collated available data on ploidal levels for 128 of the world's most widespread invasive plant species in natural and semi-natural habitats (Appendix). This list is compiled based on the criterion that a species needs to be listed as invasive in three or more regions of the world, as reported in Weber (2003). The most remarkable feature of this data set is the very high incidence of intraspecific heterogeneity in ploidy. While 71 species are ploidy-uniform, another 55 species (43·7 %) have multiple ploidy races. The

most salient cases of intraspecific ploidy polymorphism concern *Phragmites australis* and *Tradescantia fluminensis*, which are both extremely successful global invaders. Of the 55 ploidy-variable invasive species, 16 of them show one dominant ploidal level (i.e. the minority ploidal level has usually been recorded only once). Even when these cases were excluded, we identified 31 and 17·5 % of the most invasive species as still having at least two and three different ploidy races, respectively. This percentage of ploidy polymorphism is certainly much higher than found in entire floras; for example, only about 13 % of Californian species seem to be ploidy polymorphic (Soltis *et al.*, 2007). It is thus possible that ploidy heterogeneity may predispose species for colonization of large areas with heterogeneous environmental conditions. Alternatively, the higher proportion of species with multiple ploidy races among invasive angiosperms may also be, at least in part, an artefact of considerable research effort applied to this group. In data pooled across families, polyploids are over-represented compared with diploids (55 % vs. 45 %), even if the most conservative approach is adopted (i.e. the lowest known number of chromosomes per genus is always considered as diploid), but with considerable variation among individual families (Fig. 3). However, because high basic chromosome numbers are generally acknowledged as an indication of secondary (ancient) polyploidy, the real proportion of polyploids is most probably higher, approaching about two-thirds. This figure concurs well with the overall proportion of polyploids in extant angiosperms (approx. 70 %) as estimated using stomatal size (Masterson, 1994).

Analysing ploidy in native and introduced ranges reveals two general patterns (Table 1). One set of species shows multiple ploidal levels in the native range, with only one cytotype becoming invasive. This could be the result of pre-adaptation of the polyploid cytotype to environmental conditions in the novel range or caused by strong founder effects after introduction (see Table 1 for examples). A second set of species shows high ploidy heterogeneity in both native and introduced ranges. This may result in shifts in reproductive mode from
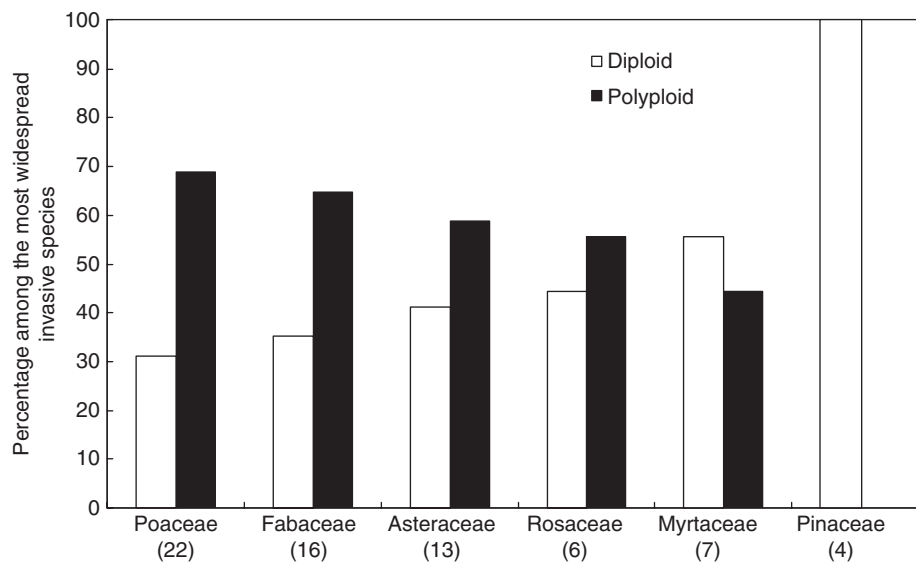
FIG. 3. Proportion of diploids and polyploids among the most widespread invasive plant taxa globally (see text for details) shown for the most represented families (number of species considered is shown in parentheses). Species known to occur as both diploids and polyploids are considered in both categories.

TABLE 1. *Differences in ploidal level of invasive species between native and introduced ranges*

Species	Family	Native range	Introduced range	Reference(s)
Pre-introduction processes and founder effects				
Pre-adaptation of polyploid cytotype				
Centaurea stoebe* (syn. *C. maculosa*)	Asteraceae	Eurasia, **2x**, 4x	North America, 2x, **4x**	Treier *et al.* (2009)
Lythrum salicaria	Lythraceae	Europe/Asia, 2x, (3x), 4x, 6x	North America, 4x	Kubátová *et al.* (2008)
Rubus alceifolius	Rosaceae	Asia, (3x), **4x**	Indian Ocean islands, 4x	Amsellem *et al.* (2001)
Senecio inaequidens	Asteraceae	South Africa, 2x, 4x	Europe, 4x	Lafuma *et al.* (2003)
Solidago gigantea	Asteraceae	North America, 2x, (3x), **4x**, (5x), 6x	Europe/eastern Asia, 2x, **4x**	Schlaepfer *et al.* (2008); Hull-Sanders *et al.* (2009)
Strong founder effects				
Brachypodium distachyon	Poaceae	Eurasia, 2x, 4x	North America, 4x	Bakker *et al.* (2009)
Butomus umbellatus	Butomaceae	Europe, 2x, **3x**	North America, **2x**, 3x	Kliber and Eckart (2005)
Post-introduction processes and 'evolution of invasiveness'				
High ploidy polymorphism coupled with shifts in reproductive mode				
Hieracium pilosella	Asteraceae	Europe, **4x**, 5x, 6x	New Zealand, 4x, **5x**, 6x	Trewick *et al.* (2004)
Oxalis pes-caprae*	Oxalidaceae	South Africa, 2x, **4x**, (5x)	Mediterranean and temperate ecosystems, 4x, **5x**	Castro *et al.* (2007)
Allopolyploidization				
Fallopia japonica*	Polygonaceae	Eastern Asia, 4x, 6x, 8x, 10x	Europe, **8x**	Bailey *et al.* (2007)
F. sachalinensis		Eastern Asia, 4x, 12x	Europe, USA, **4x**, 6x, 8x	
F. × *bohemica*		Eastern Asia, 6x	Europe, 4x, **6x**, 8x	
Phragmites australis	Poaceae	Cosmopolitan, 3x–22x	North America, 3x, **4x**, 6x, 8x	Hansen *et al.* (2007); Saltonstal (2007)
Spartina maritima	Poaceae	Europe, 6x	–	Ainouche *et al.* (2009)
S. alterniflora		Eastern America, 6x	Europe, 6x	
S. × *townsendii*		Europe, 6x	–	
S. anglica*		–	Europe, 12x	

Dominant ploidal levels are presented in bold, and rare ploidal levels in parentheses. Species indicated with an asterisk are discussed in the text.

sexual to asexual, or vice versa, that can enhance invasion success, or it may indicate ongoing hybridization and polyploidization in the introduced range resulting in evolutionary novelty and the evolution of invasiveness. We will elaborate on a few examples of well-studied model systems in each of these categories and detail how polyploidization processes might have enhanced invasion success in these species.

Centaurea stoebe

Centaurea stoebe (spotted knapweed, Asteraceae, syn. *C. maculosa*) is a herbaceous biennial or short-lived perennial tap-rooted forb with a rosette of basal leaves and relatively thick flowering stems (Watson and Renney, 1974; Hook *et al.*, 2004). The native range of *C. stoebe* spans western Asia to western Europe, where diploid and tetraploid cytotypes appear in discrete populations (Broennimann *et al.*, 2007). The species was introduced to the Pacific Northwest of the USA in the late 1800s (Watson and Renney, 1974), from where it expanded rapidly throughout much of North America. It is now widespread in rangelands, pastures and on roadsides, where it often establishes dense monocultures, reduces forage quality and excludes native plant species (Marrs *et al.*, 2008; Broz *et al.*, 2009). Whereas diploids are the dominant cytotype in the native range, tetraploids clearly dominate in introduced ranges, with only a single mixed stand of diploid and tetraploid plants identified in western Canada (Treier *et al.*, 2009). This may suggest that both forms of the weed were introduced, but that only tetraploids became

invasive, or, alternatively, that the original source populations were predominantly tetraploid. Both cytotypes are outcrossing and insect pollinated, but the diploid tends to have a biennial monocarpic life cycle, whereas the tetraploid is mainly a polycarpic perennial, continuing to flower over multiple growing seasons (Broz *et al.*, 2009; Treier *et al.*, 2009). Marrs *et al.* (2008) found relatively high genetic diversity within and among populations in both the native and the introduced range, suggesting multiple separate introductions and little effect of genetic drift resulting from bottlenecks or founder effects on the invasion success of this weed.

The two cytotypes occupy similar ecological niches in their native range (mainly dry meadows and habitats disturbed by human activities) and *C. stoebe* seems to invade similar, albeit drier, habitats in the introduced range (Broennimann *et al.*, 2007; Treier *et al.*, 2009; Thébault *et al.*, 2011). Additionally, tetraploids seem to tolerate broader environmental conditions than diploids. This has been reported for introduced and native populations (Broz *et al.*, 2009; Treier *et al.*, 2009) and suggests that the tetraploid cytotype in Europe was pre-adapted to the ecological conditions in the introduced range through increased tolerance to drier climate. Further adaptation to such conditions through directional selection may have taken place in the introduced range, as indicated by the shift in niche optima and climatic differences between the native and introduced ranges (Broennimann *et al.*, 2007; Treier *et al.*, 2009). The potential for earlier and longer seed production associated with the polycarpic life cycle constitutes an additional factor that, especially

in the absence of specialist herbivores, may have provided tetraploids with a competitive advantage over diploids during the invasion process (Ridenour *et al.*, 2008; Treier *et al.*, 2009; Henery *et al.*, 2010; Thébault *et al.*, 2011).

Centaurea stoebe is an excellent model system for evaluating the role of polyploidy in plant invasions, as it provides the opportunity to compare diploid and tetraploid cytotypes within the native range, as well as tetraploid cytotypes between the native and the introduced range. Several studies have already provided valuable information on this system, using greenhouse experiments (e.g. Ridenour *et al.*, 2008; Thébault *et al.*, 2010, 2011), common garden experiments (e.g. Henery *et al.*, 2010), flow cytometry (e.g. Treier *et al.*, 2009) and molecular analyses (e.g. Marrs *et al.*, 2008; Broz *et al.*, 2009).

Oxalis pes-caprae

Oxalis pes-caprae (Bermuda buttercup, Oxalidaceae) is a winter-growing geophyte indigenous to South Africa with three cytotypes ($2x$, $4x$ and $5x$) (Ornduff, 1987) and two subspecies: diploid subsp. *sericea* and the ploidy-variable subsp. *pes-caprae*. Tetraploid subsp. *pes-caprae* clearly predominates across the species' native range, while diploids are much less common, occurring primarily in the arid Northern Cape province (J. Rauchová *et al.*, unpubl. res.). Pentaploids seem to be rare in South Africa, with only one record near Cape Town (Michael, 1964). Tetraploids are probably of autopolyploid origin, while pentaploids most probably originated by fusion of an unreduced tetraploid gamete with a reduced diploid gamete. Both di- and tetraploid races have well-developed tristylous incompatibility systems, and plants with short-, mid- and long-styled flowers occur in natural populations. Sexual reproduction is only possible after legitimate crosses between floral morphs and compatible ploidal levels. In its native range, the species reproduces both sexually (via seeds) and asexually (via bulbils).

As an ornamental plant, *O. pes-caprae* was introduced across the world, including Europe (in 1757), North America and Australia, and soon became a noxious weed on arable land. Currently, it is one of the most widespread alien species in many Mediterranean-type and other temperate ecosystems. Introduced populations differ markedly both in the mode of reproduction and in the frequency of cytotypes. Pentaploid short-styled morphotypes, which reproduce asexually through the production of a large number of bulbils, clearly predominate in invasive ranges and, indeed, is the only known cytotype in several regions (Castro *et al.*, 2007; J. Rauchová *et al.*, unpubl. res.). Whether pentaploids were introduced once or repeatedly from the Cape or originated in secondary areas *in situ* is unknown, as is the reason for the dramatic difference in their abundance between native and invaded regions. Invasive asexual pentaploids have been subjected to a number of studies aimed at understanding their demography and impact on vegetation (Vilà *et al.*, 2006*a*, *b*), sensitivity to nutrient availability and competition (Sala *et al.*, 2007) or genetic diversity (Rottenberg and Parker, 2004). A recent detailed ploidy and morphotype screening of *O. pes-caprae* in the western Mediterranean revealed the incidence of long-styled plants that were uniformly tetraploid (Castro *et al.*, 2007). The latest observations even found all three floral morphs in both tetra- and pentaploid plants to occur in a single locality in southwestern Portugal (Castro *et al.*, 2009). In these populations, the production of seeds was also observed, for the first time in the invaded distribution range.

Considering these facts, it is possible that *O. pes-caprae* might have undergone several shifts in reproductive behaviour and/or ploidy during its invasion in Europe. First, the initial pentaploid plants spread rapidly over a vast area by clonal propagation as a shift to obligate asexuality allowed them to overcome an evolutionary disadvantage connected with the founder effect and the absence of a suitable mating partner. Subsequently, new morpho- and cytotypes might have originated in (or might have been introduced to) the introduced range that were reproductively compatible and thus able to form viable seeds. Collectively, *O. pes-caprae* represents a unique plant system in which cytotype variation is coupled with a complex incompatibility system and the ability to propagate both sexually and asexually. This offers the opportunity to study how shifts in ploidal levels translate into changes in breeding behaviour and how this affects invasion success.

Fallopia *section* Reynoutria

The section *Reynoutria* of the genus *Fallopia* (knotweeds, Polygonaceae) includes up to 12 herbaceous perennial species characterized by their erect robust stems, thick rhizomes, large leaves and deeply divided styles (Barney *et al.*, 2006). Being of Asian origin (SE Siberia, China, Korea, Japan), some taxa, including two varieties of *F. japonica* (var. *japonica* and var. *compacta*) and *F. sachalinensis*, were introduced into Europe and North America in the 19th century as ornamental and fodder plants (Bailey and Conolly, 2000). They became widely naturalized and now represent some of the worst weeds in these areas, invading mostly ruderal habitats and semi-natural vegetation along rivers (Lambdon *et al.*, 2008; Pyšek, 2009). Due to their high competitive ability, high biomass production and efficient vegetative reproduction (Brock, 1995; Horn and Prach, 1995; Brabec and Pyšek, 2000; Bímová *et al.*, 2003), knotweeds are classified as transformer species (*sensu* Richardson *et al.*, 2000) that negatively affect native wildlife and cause alterations in hydrological processes and displacement of native plant species. The invasion by *Fallopia* taxa exhibits the most severe impact on species richness and diversity among Central-European alien plants, reducing the number of species present prior to invasion by 66–86 %, depending on taxon (Hejda *et al.*, 2009).

Investigations into karyological variation of knotweeds using conventional chromosome counts and, more recently, flow cytometry revealed a large intraspecific ploidy variation (based on $x = 11$) in both native and invaded ranges (reviewed by Mandák *et al.*, 2003). In addition, interspecific hybridization has been found to be a common phenomenon especially in invaded regions (e.g. Gammon *et al.*, 2007; Tiébré *et al.*, 2007). With the exception of tetraploid *F. japonica* var. *compacta*, all other taxa show ploidy heterogeneity and different cytogeographic patterns between species (Mandák *et al.*, 2003; Bailey *et al.*, 2007). The nominate subspecies of *F. japonica* includes $4x$, $6x$, $8x$ and $10x$ cytotypes in eastern

Asia (sometimes in mixed-ploidy populations; Iwatsubo *et al.*, 2004), whereas only octoploids seem to occur in Europe, supporting the idea of a single introduction (Mandák *et al.*, 2005). Native populations of *F. sachalinensis* were found to be tetraploid (in Japan and Sakhalin) or dodecaploid (in Korea), in addition to some other high polyploid somatic counts (approx. 102) from Korea, which are difficult to interpret and probably represent hybrids (Kim and Park, 2000). Tetraploid *F. sachalinensis* also prevails across the invaded area, but the introduction was followed by genome duplication, resulting in the occurrence of hexaploid and octoploid individuals in both Europe and North America but not in the native range (Mandák *et al.*, 2003).

Hybridization between 8*x* *F. japonica* and 4*x* *F. sachalinensis* has led to the origin of 6*x* *F. × bohemica*, which is purely hexaploid in its native Asian range, but minority 4*x* and 8*x* cytotypes have also been recorded in Europe, hence representing an illustrative example of an increased ploidy variation in naturalized areas and rapid karyological evolution after species' introduction. This is further supported by recent experimental evidence, where seedlings resulting from hybridization had a large range of ploidal levels, including ploidal levels that were not observed in the original clones (Saad *et al.*, 2011). Whereas 8*x* *F. japonica* is the most common taxon in the Czech Republic, the 6*x* *F. × bohemica* is the most invasive. Compared with its parental congeners *F. × bohemica* spreads more rapidly (Mandák *et al.*, 2004), possibly because of its regeneration ability from rhizomes (Bímová *et al.*, 2003), and exhibits stronger phytotoxic effects on germination of native species in laboratory conditions than *F. japonica* (Moravcová *et al.*, 2011). The extensive sexual reproduction by hybridization as observed in some *Fallopia* populations can increase their genetic variation and contribute to ongoing evolution of new genotypes with increased invasiveness. Because of its high ploidy heterogeneity and ongoing ploidy differentiation (Saad *et al.*, 2011), *Fallopia* taxa represent a unique model system allowing contrasting of parental species as well as evolutionary consequences of hybridization and polyploidization and its effect on species invasiveness.

Spartina anglica

The genus *Spartina* (Poaceae, subfamily Chloridoideae) contains about 13–15 perennial species, that are often rhizomatous and occur in salt marshes. Most are native to the New World, and until the 19th century *S. maritima* was the only known native species in the Old World, where it grows along the European and African Atlantic coast (Mobberley, 1956; Baumel *et al.*, 2002; Ainouche *et al.*, 2009). Polyploidization has been important in the evolution of the genus, with 4*x*, 6*x*, 7*x* and 12*x* cytotypes present across different species (Marchant, 1968; Fortuné *et al.*, 2008; Ainouche *et al.*, 2009; Renny-Byfield *et al.*, 2010). Several *Spartina* species are highly successful invaders in marshes around the world where they significantly change the physical structure, reduce the biological diversity and affect the ecological function of tidal marshes and mudflats (Thompson, 1991; Ayres *et al.*, 2004; Ainouche *et al.*, 2009). Species introductions resulted from

both natural dispersal and deliberate introductions for marsh restoration purposes (Thompson, 1991; Ainouche *et al.*, 2009).

The allopolyploid *S. anglica* (12*x*) represents a textbook example of hybridization coupled with polyploidization leading to the evolution of a highly invasive species (Thompson, 1991; Ellstrand and Schierenbeck, 2000). The history of *S. anglica* is well documented, starting in the early 19th century with the accidental introduction of 6*x* *S. alterniflora* from the east coast of North America to southern England and western France, where it hybridized with the native 6*x* *S. maritima*, forming the 6*x* hybrid *S. × townsendii*. Genome doubling of *S. × townsendii* resulted in the formation of the fertile and vigorous allopolyploid *S. anglica*, which rapidly colonized British and French salt marshes and estuaries, whereas the parental species have retained a limited distribution (Thompson, 1991; Baumel *et al.*, 2003). *Spartina anglica* is a rhizomatous, perennial grass that spreads by extensive clonal growth. It is strictly confined to salt marshes, but can spread throughout the successional salt marsh gradient. It is considered an ecosystem engineer that expands its habitat by enhancing sediment accretion (Boumat *et al.*, 2005). *Spartina anglica* has deliberately been introduced in several parts of the world, where it rapidly expanded, and is listed as one of the IUCN's 100 worst invasive alien species (Lowe *et al.*, 2000).

Spartina anglica represents an excellent model system for investigating the immediate consequences of hybridization and genome duplication when it comes to ecological success and invasiveness, being of recent origin, with all parental species still extant, and with historical records that track the timing of events. Molecular studies show low genetic diversity in the species, suggesting that *S. anglica* experienced a strong genetic bottleneck at the time of its formation, caused by a single introduction or multiple introductions of similar parental genotypes (Baumel *et al.*, 2001; Ainouche *et al.*, 2004). The genetic diversity of the species relies mainly on the subsequent dynamics of its hybrid genome (Ainouche *et al.*, 2009). Hybridization appears to have triggered both genetic and epigenetic changes in the homoploid hybrid *S. × townsendii* in the form of genomic fragment loss and deviating patterns of transposable element insertions and methylation (Salmon *et al.*, 2005) that were not detected in the young allopolyploid *S. anglica*, for which the genome is nearly additive to the parental ones (Baumel *et al.*, 2001; Salmon *et al.*, 2005; Fortuné *et al.*, 2008; Parisod *et al.*, 2009). This leads to the suggestion that the most important genetic and epigenetic changes in the genome of the *S. anglica* have been triggered by nuclear incompatibilities introduced by hybridization rather than genome duplication (Ainouche *et al.*, 2009; Parisod *et al.*, 2009). However, considerable changes to the transcriptome have also accompanied the formation of both *S. × townsendii* and *S. anglica*, with deviation from parental additivity in *S. anglica* caused by maternal expression dominance following hybridization and, for example, transgressively overexpressed genes following genome duplication (Chelaifa *et al.*, 2010). These changes most probably explain the phenotypic plasticity and other morphological and physiological traits (Thompson, 1991) that characterize *S. anglica* and have made it so successful. The extensive and rapid spread (both through seed production and via vegetative means) of the fertile allopolyploid

S. anglica has not been seen in the sterile hybrid *S. × townsendii*, which may indicate that restoration of fertility by genome duplication may be an important contributory factor to ecological success and invasiveness.

SYNTHESIS

We have described several examples of how intra- and inter-specific genome duplication may enhance the success of introduced plant species and provided a mechanistic explanation of how polyploidy may affect invasiveness (see Figs 1 and 2). On the one hand, the direct effects of polyploidization might predispose species to be better adapted to harsher conditions in novel environments. On the other hand, a versatile genome, with high intraspecific ploidy heterogeneity, might increase potential for evolutionary novelty and/or shifts in reproductive mode. The flexibility in breeding behaviour that is frequently associated with an increase in ploidy might be highly relevant for colonizing species by increasing the ability to reproduce under sub-optimal conditions (Bernström, 1950) and has been shown to be important in the invasion success of *Hieracium pilosella* (Trewick *et al.*, 2004) and *O. pes-caprae* (Castro *et al.*, 2007). This flexibility might also counteract the reduced fertility that is often found in polyploids. Moreover, when a polyploid is introduced into a new environment in the absence of the diploid progenitor, one of its main challenges, i.e. minority cytotype exclusion, is removed, increasing successful establishment and possibly colonization of the new environment.

Several consequences of genome duplication, such as lower growth rates or larger seed mass, may also clearly reduce invasiveness. However, these traits are not necessarily disadvantageous to plants in general. For example, whereas lower seed mass has been shown to positively affect adult density and, hence, dominance (Rejmánek and Richardson, 1996; Ordonez *et al.*, 2010), higher seed mass positively affects seedling and sapling establishment and persistence (Moles and Westoby, 2006), and may therefore increase success in the long term. This raises the question of how to quantify the success of an invasive plant. Should this be related to abundance or to the extent of its geographic range? The life history attributes usually associated with polyploids suggest that polyploidy often favours successful establishment and subsequent persistence, rather than the achievement of the high local densities that are often associated with successful invasive species and that lead to negative impacts on biodiversity and ecosystem services (Parker *et al.*, 1999; Vilà *et al.*, 2011). This is further supported by studies that show that the distribution of polyploids is often more widespread and less fragmented than that of diploids (Watanabe, 1986; Lumaret, 1988; Van Dijk and Bakx-Schotman, 1997; Münzbergová, 2007). Indeed, for invasive trees and shrubs listed by Richardson and Rejmánek (2011) in their global review of invasive woody plants for which data on ploidal levels are available ($n = 54$; Appendix), the number of known ploidal levels within particular taxa is significantly positively correlated with the number of regions invaded ($P = 0.03$, $R^2 = 0.01$). However, there was no significant relationship between the highest known ploidal level and the number of regions invaded ($P = 0.054$, $R^2 = 0.07$). Therefore, it is likely that polyploid plants have a higher chance of becoming naturalized, but not necessarily invasive. However, the same is suggested for species with smaller rather than larger genome sizes (Kubešová *et al.*, 2010), although this is often linked to ruderal behaviour. There are also many examples of polyploid invaders that can become extremely dominant. For example, among woody plants: *Ailanthus altissima*, *Chromolaena odorata*, *Cytisus scoparius*, *Fallopia japonica*, *Lantana camara*, *Leucaena leucocephala*, *Psidium cattleianum*, *Rosa rubiginosa*, *Salix fragilis*, *Schinus terebinthifolius* and *Ulex europaeus* are all major transformer species (*sensu* Richardson *et al.*, 2000). Among the many herbaceous polyploids that can qualify as transformer species, *S. anglica* can completely replace native communities in European salt marshes (Thompson, 1991).

It has been proposed that broad ecological tolerance may predispose polyploid lineages to successful colonization in novel environments, i.e. pre-adaptation (Buggs and Pannell, 2007). Even though this hypothesis remains controversial (Soltis *et al.*, 2010), it is supported by evidence from some invasive species. For example, the invasion success of tetraploid *Centaurea stoebe* in North America has been partly attributed to pre-adaptation of native European tetraploids to wider climate ranges compared with diploids and, following the initial introduction, tetraploids may have further adapted to drier continental conditions (Treier *et al.*, 2009; Henery *et al.*, 2010). Similarly, introductions of pre-adapted highland tetraploids from southern Africa that are more cold tolerant than lowland diploid populations have been suggested as an explanation for the invasion success of *Senecio inaequidens* in Europe (Lafuma *et al.*, 2003; Bossdorf *et al.*, 2008; Lachmuth *et al.*, 2010). Other examples include the invasion of tetraploid *Rubus alceifolius* on islands in the Indian Ocean (Amsellem *et al.*, 2001), the invasion of tetraploid *Lythrum salicaria* in North America (Kubátová *et al.*, 2008) and the invasion of tetraploid *Solidago gigantea* in Europe (Schlaepfer *et al.*, 2008; Hull-Sanders *et al.*, 2009).

These examples are all characterized by the dominance or sole occurrence of one invasive polyploid cytotype. In addition to the explanation that the polyploid lineage is pre-adapted and therefore more successful in the new habitat than diploid lineages, there are several other explanations for this phenomenon. Strong founder effects may favour the cytotype with the most effective reproduction and, hence, highest fitness, and cause shifts in cytotype frequency or even exclusion of other cytotypes (Kliber and Eckert, 2005; Bakker *et al.*, 2009). Alternatively, different introduction pathways could also influence the presence of one or more ploidal levels in the new range. For example, a single introduction of a species might by chance cause a polyploid to establish, whereas in the case of multiple introductions the mixing of cytotypes could be expected. Accidental or deliberate introductions also play an important role. Deliberate introductions of crops and ornamental plants have been recognized as a major pathway of plant invasions (Dehnen-Schmutz *et al.*, 2007). Since inducing polyploidy is an important tool in agriculture and horticulture to breed and improve new cultivars (Väinölä, 2000; Ramanna and Jacobsen, 2003), deliberate introductions of crops and ornamental plants are more likely to be polyploid due to previous breeding programmes. Ploidy manipulation (triploid

production) has also been proposed to produce sterile, non-invasive cultivars in invasive ornamental plants, such as *Lantana camara* (Czarnecki and Deng, 2009).

It is generally accepted that the stochasticity typically associated with biological invasions will greatly influence the pace of contemporary evolution, i.e. introductions typically characterized by genetic bottlenecks, strong genetic drift, novel selection pressures, etc. will act rapidly to facilitate genetic change and local adaptation in new environments. Clear evidence for rapid evolutionary change in invasive plants has been repeatedly found when intraspecific hybridization (admixture) between previously allopatric lineages occurs in the invasive range(s) (e.g. Hurka *et al.*, 2003; Lavergne and Molofsky, 2007; Keller and Taylor, 2010). Admixed individuals often show broader ecological tolerance, increased levels of phenotypic plasticity and increased vigour compared with parental lineages. It is therefore not surprising that allopolyploids show similar but more pronounced changes, combining the complete genomes of two divergent species. Indeed, successful invasions often arise as a result of allopolyploidization (Ellstrand and Schierenbeck, 2000), indicating that invasiveness may evolve following interspecific hybridization coupled with genome duplication, so-called 'evolution of invasiveness'. The link between invasiveness and autopolyploidization is less clear. However, given that numerous genomic processes are profoundly influenced by genome doubling, it is conceivable that autopolyploidy can contribute to invasion success (e.g. Schlaepfer *et al.*, 2008).

It is, however, important to distinguish the immediate evolutionary effects of polyploidy from effects that arose following polyploidization (Soltis *et al.*, 2010). For example, when comparing 'historical' diploid–polyploid systems, the phenotypic and ecological consequences of genome duplication *per se* will be overestimated. Recently, Ramsey (2011) reported on historical and contemporary evolutionary effects of polyploidization using field transplants of tetraploid and hexaploid *Achillea borealis* with a parallel experiment on neohexaploids – first-generation autopolyploid mutants. The use of neohexaploid cytotypes provides a direct measure of the phenotypic effects of genome duplication *per se*, whereas the comparison of neopolyploids with established polyploids reveals post-polyploidization evolution such as allele substitutions and gene silencing. Ramsey (2011) found that established hexaploids have a 5-fold fitness advantage over tetraploids in dune habitats and that 70 % of this fitness advantage was retained in neohexaploids. These results suggest that genome duplication can immediately facilitate ecological differentiation in plants. Insights from studies on neopolyploids are otherwise limited (e.g. Bretagnolle and Lumerat, 1995; Husband *et al.*, 2008; Maherali *et al.*, 2009) and, while having great potential for the study of polyploid evolution, some evolutionary aspects of current-day established 'historical' polyploid populations may be overlooked by this approach (Ramsey, 2011).

Fawcett *et al.* (2009) proposed that genome doubling helped numerous plant lineages to survive the large-scale Cretaceous–Tertiary mass extinction. This observation of greater polyploid survival generates two questions that are essential for our understanding of the role of polyploidy in species success. Did only the existing polyploids survive or did species actively 'create' polyploids in order to survive? We hope to have made clear in this review that due to lower growth rates, higher seed mass, increased drought and temperature tolerance, flexible breeding behaviour, etc., polyploids may indeed have a higher survival rate under harsh environmental conditions, with all the implications of such for current-day survival in new environments and fragmented habitats, caused by anthropogenic disturbances and/or global change. The second question 'did species actively 'create' polyploids in order to survive?' is perhaps even more interesting since this implies that polyploidy is a 'survival' mechanism for species and, hence, an important factor in their success and potentially their invasiveness. Further evidence for this comes from the observation that the production of unreduced gametes increases with increasing environmental stress, e.g. strong temperature fluctuations, frost, drought, lack of nutrients, wounding and/or herbivory (Bretagnolle and Thompson, 1995; Ramsey and Schemske, 1998; Parisod *et al.*, 2010). This suggests that natural environmental variation, as well as large-scale climate change, could substantially alter the dynamics of polyploid evolution and subsequent species success. Unfortunately, however, data on unreduced gamete formation in natural systems are few (Ramsey and Schemske, 1998).

Various approaches have been used to address the question of whether polyploidy mediates ecological differentiation, adaptation and, ultimately, range expansion. Observational studies that describe the distribution of and habitat differentiation between different ploidal levels within a single species or between closely related species (e.g. Baldwin, 1941; Lumaret *et al.*, 1987; Ståhlberg, 2009; Treier *et al.*, 2009; Sonnleitner *et al.*, 2010) are important in providing the cytological and ecological context for further experimental research. Large-scale correlative studies comparing the flora of certain regions (Stebbins, 1984; Brochmann *et al.*, 2004) or studies comparing large sets of diploid and polyploid species provide information on patterns, for example, with regard to differences in ecological range (Stebbins and Dawe, 1987; Petit and Thompson, 1999) or in range breadth and climatological position (Martin and Husband, 2009). Ultimately, experimental studies of diploid–polyploid systems, such as field transplant (e.g. Flégrová and Krahulec, 1999; Baack and Stanton, 2005; Buggs and Pannell, 2007; Raabová *et al.*, 2008; Ramsey, 2011), common garden (e.g. Bowden, 1940; Garbutt and Bazzaz, 1983; Bretagnolle and Thompson, 1996, 2001; Petit and Thompson, 1997; Münzbergová, 2007; Schlaepfer *et al.*, 2010) and greenhouse studies (Sudová *et al.*, 2010; Thébault *et al.*, 2010, 2011) are needed to test hypotheses about ecological adaptation in polyploids and its consequences for species invasiveness. However, relatively few experimental studies have been undertaken considering the amount of efforts that have been put into polyploidy research in recent years. Many more studies, especially combining observations and experimentation, are needed in the years to come to test rigorously the hypothesis that polyploidy provides plants with novel features that allow them to invade new environments or expand their geographic range.

In summary, we suggest that polyploidization may indeed increase the success of plant invaders through a combination of pre-adaptation, where polyploids have a higher survival rate and fitness in the earliest establishment phase, as, for example, in *Centaurea stoebe*, and the possibility for

subsequent adaptation due to a larger gene pool that may result in the 'evolution of invasiveness', as, for example, in *Fallopia* taxa. Alternatively, polyploidization may play an important role by restoring sexual reproduction after hybridization, as, for example, in *Spartina anglica* or, conversely, allowing for asexual reproduction in the absence of suitable mates, as, for example, in *Oxalis pes-caprae*. We have shown that polyploidy might be an important factor in species invasion success and suggest that ploidy must be considered in any general model that seeks to explain why some species are more successful than others as invaders.

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APPENDIX

Ploidal levels reported for 128 of the world's most widespread invasive plant species (those known to be invasive in at least three regions of the world according to Weber, 2003)

Species	Family	Ploidal level(s)[†]
Acacia dealbata	Fabaceae	2, 3, 4
Acacia longifolia	Fabaceae	2
Acacia saligna	Fabaceae	2 (3)
Acer negundo	Sapindaceae	2
Acer pseudoplatanus	Sapindaceae	4
Agave americana	Asparagaceae	2, 4*
Ageratina adenophora	Asteraceae	6*
Ageratina riparia	Asteraceae	6
Ailanthus altissima	Simaroubaceae	8
Alliaria petiolata	Brassicaceae	6 (2, 4, 5)
Ammophila arenaria	Poaceae	4 (2, 8)
Amorpha fruticosa	Fabaceae	4
Ardisia crenata	Primulaceae	2, 4
Arundo donax	Poaceae	2, 6, 9
Berberis thunbergii	Berberidaceae	4
Carpobrotus edulis	Aizoaceae	2
Casuarina equisetifolia	Casuarinaceae	2

Continued

TABLE *Continued*

Species	Family	Ploidal level(s)[†]
Cenchrus ciliaris	Poaceae	4, 6
Cinchona pubescens	Rubiaceae	–
Cinnamomum camphora	Lauraceae	2
Cirsium arvense	Asteraceae	2 (4)*
Cirsium vulgare	Asteraceae	4 (2)*
Clidemia hirta	Melastomataceae	2*
Colocasia esculenta	Araceae	4, 6 (5)
Conium maculatum	Apiaceae	2
Cortaderia jubata	Poaceae	12
Cortaderia selloana	Poaceae	8
Crataegus monogyna	Rosaceae	2 (3)*
Cynara cardunculus	Asteraceae	2*
Cytisus scoparius	Fabaceae	8 (4)
Delairea odorata	Asteraceae	2
Egeria densa	Hydrocharitaceae	2*
Ehrharta erecta	Poaceae	2, 4
Eichhornia crassipes	Pontederiaceae	4, 8
Elaeagnus umbellata	Elaeagnaceae	4
Elodea canadensis	Hydrocharitaceae	2, 4
Eucalyptus globulus	Myrtaceae	2
Eugenia uniflora	Myrtaceae	2, 3
Euphorbia esula	Euphorbiaceae	(2) 6
Fallopia japonica	Polygonaceae	8 (3, 4, 5, 6)
Festuca arundinacea	Poaceae	6 (4, 8, 10)
Furcraea foetida	Asparagaceae	6
Gleditsia triacanthos	Fabaceae	4
Gunnera tinctoria	Gunneraceae	2*
Hedera helix	Araliaceae	6, 12
Hedychium flavescens	Zingiberaceae	2, 3*
Hedychium gardnerianum	Zingiberaceae	2, 3*
Heracleum mantegazzianum	Apiaceae	2
Holcus lanatus	Poaceae	2
Hydrilla verticillata	Hydrocharitaceae	2, 3, 4
Chromolaena odorata	Asteraceae	6, 12
Impatiens glandulifera	Balsaminaceae	2
Imperata cylindrica	Balsaminaceae	2, 4, 6
Ipomoea indica	Convolvulaceae	2*
Lantana camara	Verbenaceae	2, 3, 4, 5, 6
Lepidium draba	Brassicaceae	8 (4)
Leptospermum laevigatum	Myrtaceae	2
Leucaena leucocephala	Fabaceae	8 (4)
Ligustrum sinense	Oleaceae	2*
Lonicera japonica	Caprifoliaceae	2
Lupinus arboreus	Fabaceae	8
Lupinus polyphyllus	Fabaceae	8
Lycium ferocissimum	Solanaceae	2
Lythrum salicaria	Lythraceae	2, 4, 6 (3)
Macfadyena unguis-cati	Bignoniaceae	8
Melia azedarach	Meliaceae	4
Melinis minutiflora	Poaceae	4
Mikania micrantha	Asteraceae	4, 8
Mimosa pigra	Fabaceae	2
Myriophyllum aquaticum	Haloragaceae	–
Myriophyllum spicatum	Haloragaceae	2, 4, 5, 6
Nassella trichotoma	Poaceae	4
Nicotiana glauca	Solanaceae	2 (3, 4)
Opuntia dillenii	Cactaceae	2, 4, 6
Opuntia ficus-indica	Cactaceae	2, 5, 8
Opuntia stricta	Cactaceae	2, 4
Oxalis pes-caprae	Oxalidaceae	2, 4, 5

Continued

Species	Family	Ploidal level(s)†
Panicum maximum	Poaceae	2, 4, 5, 6
Paspalum dilatatum	Poaceae	4, 5, 6
Passiflora edulis	Passifloraceae	2
Passiflora tripartita var. *mollissima*	Passifloraceae	2
Pennisetum clandestinum	Poaceae	4
Pennisetum purpureum	Poaceae	3, 4, 8
Pennisetum setaceum	Poaceae	2, 3, 6
Phalaris arundinacea	Poaceae	2, 4, 5, 6, 8
Phragmites australis	Poaceae	3, 4, 6, 7, 8, 9, 12, 14, 16, 20
Pinus nigra	Pinaceae	2
Pinus patula	Pinaceae	2
Pinus pinaster	Pinaceae	2
Pinus radiata	Pinaceae	2
Pistia stratiotes	Araceae	4
Pittosporum undulatum	Pittosporaceae	2
Psidium cattleianum	Myrtaceae	4, 8
Psidium guajava	Myrtaceae	2 (3)
Pueraria montana	Fabaceae	2
Pyracantha angustifolia	Rosaceae	2*
Rhamnus catharticus	Rhamnaceae	4
Ricinus communis	Euphorbiaceae	2
Robinia pseudoacacia	Fabaceae	2
Rosa multiflora	Rosaceae	2, 3, 4
Rosa rubiginosa	Rosaceae	5
Rubus fruticosus	Rosaceae	3, 4
Rubus ulmifolius	Rosaceae	2 (4)
Salix fragilis	Salicaceae	4 (2, 3, 6)*
Salvinia molesta	Salviniaceae	5

Continued

Species	Family	Ploidal level(s)†
Securigera varia	Fabaceae	4
Senecio inaequidens	Asteraceae	2, 4
Senna didymobotrya	Fabaceae	4
Senna pendula	Fabaceae	4
Schinus terebinthifolius	Anacardiaceae	4*
Silybum marianum	Asteraceae	2*
Solanum mauritianum	Solanaceae	2
Solidago altissima	Asteraceae	2, 4, 6
Spartina anglica	Poaceae	12*
Sphagneticola trilobata	Asteraceae	8
Sporobolus indicus	Poaceae	4, 5, 6
Stenotaphrum secundatum	Poaceae	2, 3, 4
Syzygium cumini	Myrtaceae	2
Syzygium jambos	Myrtaceae	4
Tagetes minuta	Asteraceae	4
Tamarix ramosissima	Tamaricaceae	2
Tecoma stans	Bignoniaceae	4
Tradescantia fluminensis	Commelinaceae	3, 4, 5, 6, 9, 11, 12, 14
Ulex europaeus	Fabaceae	4, 8, 12
Urochloa mutica	Poaceae	4
Verbascum thapsus	Scrophulariaceae	4
Vinca major	Apocynaceae	4*
Vulpia bromoides	Poaceae	2

Ploidy data were compiled from various sources and families according to Angiosperm Phylogeny Group (2009).

†Taxa with a high (secondary) basic chromosome number are denoted by an asterisk. Rare ploidal levels (usually with only one literature record) are given in parentheses.