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The importance and prevalence of allopolyploidy in Aotearoa New Zealand

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ABSTRACT
Allopolyploids arise when two or more species hybridise to form an entirely new species with a duplicated genome. Although initially met with an array of potentially catastrophic challenges triggered by the combination of two diverged parental subgenomes within a single cell, countless allopolyploids worldwide demonstrate exceptional biological resilience by not only living under these unique circumstances, but thriving. The archipelago of Aotearoa New Zealand is home to an unexpectedly large number of allopolyploid species, both indigenous and introduced. Here, we review the prevalence and importance of these species from a local perspective. The benefits of allopolyploid species permeate multiple facets of life in New Zealand, from pastoral health and arable crop yield, to long-established viticulture and brewery practices, to the intrinsic nature of the land through the presence of diverse native allopolyploid flora. Consequently, the motivation behind the pursuit of New Zealand's allopolyploid research extends beyond improvement of the global knowledgebase and also aims to drive tangible economic and cultural impacts on the country and the lives of its people.

Introduction

Polyploidy, the heritable phenomenon that generates species with increased chromosomal content, is a major force in evolution (Ren et al. 2018). It is widely accepted that polyploidy encompasses a continuum spanning its two primary classifications, autopolyploidy and allopolyploidy (Tayalé and Parisod 2013; Spoelhof et al. 2017). Autopolyploids, the prefix 'auto-' meaning 'same', are generated from whole genome duplication within species. Conversely, allopolyploids ('allo-', meaning 'different') originate from the hybridisation of two or more different species (Comai 2005). This continuum of polyploidy accounts for intermediates whose chromosomes exhibit both homologous (as in autopolyploids) and homeologous (as in allopolyploids) pairing during cell division. Intermediacy in polyploids was described in the seminal works by Stebbins (1947, 1950), who later

asserted the inefficiency of selection in duplicated genomes, deeming polyploids to be evolutionary dead-ends (Stebbins 1971). Stebbins' view, the 'dead-end hypothesis', has seen increasing opposition through subsequent discoveries of recurrent polyploidy (Soltis and Soltis 1999), substantial dynamism within polyploid genomes (Scannell et al. 2006; Flagel and Wendel 2009; Parisod et al. 2009; Chester et al. 2012; Wang et al. 2015; Wang et al. 2018) and the presence of an ancestral polyploidy event at the base of the major land plant radiation (Jiao et al. 2011).

The genetic consequences of allopolyploidy

Allopolyploidy appears almost as an antithesis of conventional Darwinian evolution, where new species evolve from a single common ancestor, typically conceptualised as a bifurcating tree (Darwin 1859). In allopolyploidy, multiple ancestral species instead hybridise to form a single new species. Allopolyploid formation has been shown to be accompanied by extensive structural and biochemical changes to the genome, which have been described as 'genome shock' (McClintock 1984). Indeed, this phrase aptly captures the essence of this potentially catastrophic array of structural and biochemical changes that can occur, near-instantaneously, from ploidy elevation and hybridisation within the nascent allopolyploid genome. The suite of potential biological responses, both rapid and longer term, employed by the allopolyploid in response to genome shock have many potential manifestations, including genomic restructuring (Lim et al. 2008; Wu et al. 2015; Qin et al. 2016; Wang et al. 2018) and gene loss (Scannell et al. 2006; Gordon et al. 2009; Vallejo-Marín et al. 2015). Although the impact of allopolyploidy is most often viewed through the lens of nuclear genomic studies, organellar genomes (Sloan et al. 2018), small RNAs (Ha et al. 2009; Jiao et al. 2018) and the gene expression profiles of allopolyploid species (Yoo et al. 2014; Jung et al. 2015) are also affected. Extensive changes in allopolyploid gene expression ('transcriptome shock') are driven by the mixing of two dissimilar and poorly co-adapted sets of transcription factors and chromatin signatures (Cox et al. 2014).

The relative influences of hybridisation and ploidy elevation in driving post-allopolyploidisation genetic changes are highly debated, with these causal factors exhibiting lineage-specific differences. In allopolyploid *Fragaria* (strawberry) species, DNA methylation changes appear to be predominantly driven by genome doubling, whereas both genome doubling and hybridisation appear to impact gene expression changes (Wang et al. 2016). In contrast, comparative analysis of *Arabidopsis* auto- and allopolyploids has suggested that gene regulation is more influenced by hybridisation (Wang et al. 2006). A further study of synthetic allopolyploids obtained from *Chrysanthemum nankingense* (chrysanthemum) x *Tanacetum vulgare* (tansy) hybrids proposed that it is the interaction between the two processes that is important (Qi et al. 2018).

Nascent polyploids must adapt to an instantaneous increase in genomic material, with potential downstream consequences for cell regulatory functions. Such consequences are typically generated through non-proportional cellular expansion (Melaragno et al. 1993; Robinson et al. 2018), producing a stoichiometric imbalance between chromatin components and envelope proteins (Corredor et al. 2005). This scaling relationship may be further observed at the organismal level, particularly in polyploid plants (the gigas effect) (Sattler et al. 2016; Robinson et al. 2018), or there may be a compensatory reduction

in cell number that lessens the impact of increased cell size on organ size changes (Tsukaya 2008; Del Pozo and Ramirez-Parra 2014; Czesnick and Lenhard 2015). Diploidisation, the process by which a polyploid genome returns to a state of diploidy, commonly follows ploidy elevation, suggesting that the challenges associated with whole genome duplication are often too complex to allow the establishment of the nascent polyploid species (Wolfe 2001; Leitch and Bennett 2004). Alternatively, diploidisation may be triggered by the unavailability of any required ecological drivers, such as novel niche availability (Baduel et al. 2018). As a result, some presumed classical diploid lineages are in fact paleo-polyploids, having experienced single or multiple rounds of polyploidisation and diploidisation in their evolutionary history (Wolfe and Shields 1997; Wolfe 2001; Ozkan and Feldman 2009; Qiao et al. 2019).

As well as genomic changes, allopolyploidy can also yield novel phenotypes, largely through the diversity introduced by hybridisation (Hedrick 2013). Allopolyploids may be morphologically intermediate between both parents due to homeolog (parental gene copy) co-dominance at a given locus (Szymura and Farana 1978). Alternatively, hybrids may show a phenotypic similarity to one parent as a result of subgenome dominance or genomic imprinting (Heslop-Harrison 1990; Edger et al. 2017; Bird et al. 2018), or they may exhibit a phenotype beyond the range of either parental species, generated through transgressive expression (Rieseberg et al. 1999; López-Caamal and Tovar-Sánchez 2014). It is possible that some phenotypic changes observed in allopolyploids result from genome doubling, rather than hybridisation, with the multiple gene copies produced through duplication able to perform different functions. Support for this hypothesis is also provided by the phenotypic differences observed between autopolyploids, whose origin does not involve hybridisation, and their diploid ancestors (Segraves and Thompson 1999).

Advantages of allopolyploidy

The persistence of allopolyploidy across Eukarya (Yoo et al. 2013; Cox et al. 2014; Sehrish et al. 2014; Session et al. 2016; Matos et al. 2019) suggests that successful adaptation to all of these challenges may grant the allopolyploid advantages previously unavailable to its parent lineages. Their doubled and hybrid genomes can facilitate intergenomic heterosis (hybrid vigour); a phenotypic consequence where hybrid species demonstrate increased biological fitness when compared with either parental line (Baranwal et al. 2012; Fujimoto et al. 2018). At a molecular level, allopolyploid hybrid vigour may manifest as a buffering effect against deleterious recessive mutations (Gu et al. 2003), novel gene function innovation through neo- or subfunctionalisation of genes (Adams and Wendel 2005), and the evolution of complementary parental homeologs at a given genetic locus (Paterson 2005). Heterosis and transgressive phenotypes can enable some allopolyploids to outcompete their parents within the same ecological niche, or to colonise niches that are more extreme than those of either parental species. Thus, allopolyploidy is often associated with invasiveness (Ainouche et al. 2008; Kim et al. 2008; Pandit et al. 2011).

Allopolyploidy in New Zealand

New Zealand allopolyploids include introduced species; both those that underwent allopolyploidy prior to their arrival and those that were allopolyploids upon introduction, as well

Table 1. Prominent New Zealand allopolyploid taxa, with origin and commercial significance.

Origin	Taxon	Common name	Status	Study	Industry
Introduced	*Epichloë* spp.	Ryegrass endophyte	Allopolyploid	Campbell et al. (2017)	Agriculture
	Trifolium repens	White clover	Allopolyploid	Griffiths et al. (2019)	Agriculture
	Salmo salar	Atlantic salmon	Allotriploid	Harvey et al. (2017)	Aquaculture
	Saccharomyces pastorianus	Lager yeast	Allopolyploid	Casaregola et al. (2001)	Brewing
	Humulus lupulus	Hops	Intraspecific triploid	Beatson and Brewer (1994)	Brewing
	Saccharomyces cerevisiae	Brewer's yeast	Allopolyploid	Wolfe (2001); Pfliegler et al. (2012)	Brewing/ viticulture
	Dekkera bruxellensis	Wine spoilage yeast	Putative allopolyploid	Borneman et al. (2014)	Brewing/ viticulture
	Actinidia spp.	Kiwifruit	Possible allopolyploid origin	Atkinson et al. (1997)	Horticulture
	Avena sativa	Oats	Allopolyploid	Liu et al. (2017)	Horticulture
	Brassica napus	Oilseed rape	Allopolyploid	Chalhoub et al. (2014)	Horticulture
	Coffea arabica	Coffee	Allopolyploid	Lashermes et al. (2014)	Horticulture
	Gossypium spp.	Cotton	Allotetraploid	Wendel et al. (1995); Hu et al. (2015)	Horticulture
	Malus spp.	Apple	Possible allopolyploid origin	Chevreau and Laurens (1987); Tatum et al. (2005)	Horticulture
	Nicotiana tabacum	Tobacco	Allopolyploid	Bindler et al. (2011)	Horticulture
	Pyrus spp.	Pear	Possible allopolyploid origin	Evans et al. (2008)	Horticulture
	Triticum aestivum	Wheat	Allopolyploid	Ozkan et al. (2003)	Horticulture
	Zea mays	Maize	Putative allopolyploid	Gaut et al. (2000)	Horticulture
	Pilosella officinarum	Hawkweed	Allopentaploid	Morgan-Richards et al. (2004); Trewick et al. (2004)	Invasive weed
Native	*Acanthoxyla* spp.	Stick insect	Putative mosaic allotriploid	Buckley et al. (2008); Myers et al. (2013)	Native fauna
	Asplenium spp.	Spleenwort	Allopolyploid	Shepherd, Perrie, et al. (2008)	Native flora
	Lepidium spp.	Scurvy grass	Allopolyploid	Mummenhoff et al. (2004)	Native flora
	Leptinella spp.	Button daisy	Allopolyploid	Himmelreich et al. (2014)	Native flora
	Lobelia angulata	Pānakenake	Allopolyploid	Murray et al. (2004)	Native flora
	Pachycladon spp.	New Zealand rockcress	Allopolyploid	Joly et al. (2009); Mandáková et al. (2010)	Native flora
	Plantago spp.	Plantain	Allopolyploid	Ishikawa et al. (2009); Murray et al. (2010)	Native flora
	Polystichum neozelandicum	Shield fern	Allooctoploid	Perrie et al. (2003)	Native flora
	Sphagnum australe	Peat moss	Allotriploid	Karlin et al. (2009)	Native flora
	Sphagnum falcatulum	Peat moss	Allotriploid	Karlin et al. (2009)	Native flora

as an array of native and endemic allopolyploid taxa (Table 1). Allopolyploid species play an important role in the country's industries and economy, as well as in the *mauri*, or 'vital essence', of the land. Studies of New Zealand native allopolyploids offer complementary information and a unique perspective to global allopolyploid research, while improving our understanding of the evolution of a unique biota. Here, we discuss the importance and prevalence of allopolyploidy in Aotearoa New Zealand, in the context of the outcomes, timings and locations of their formation.

When Māori arrived in New Zealand from tropical Polynesia around AD 1250, they brought with them a number of tree and root crops (Leach and Stowe 2005). Only six of these species, whose cultivation was mostly marginal in New Zealand's temperate climate, are known to have survived into European times: *aute* (paper mulberry, *Broussonetia papyrifera*), *hue* (bottle gourd, *Lagenaria siceraria*), *kūmara* (*Ipomoea batatas*), *taro* (*Colocasia esulenta*), *tī pore* (*Corydyline fruticosa*) and *uwhi* (yam, *Dioscorea alata*). Polyploidy is inferred in the origins of three of these species – *kūmara* (Roullier et al. 2013), *tī pore* (Hinkle 2004) and *uwhi* (Nemorin et al. 2012) – but research to date indicates that these origins lie in autopolyploidy rather than allopolyploidy.

In contrast, post-colonial agriculture, which forms the backbone of the New Zealand economy today (Brooking 2006; Peden 2008), relies heavily on allopolyploids (Figure 1). Most introduced allopolyploids formed prior to their introduction to New Zealand, but there are also examples of allopolyploidy events occurring post-introduction.

Allopolyploidisation pre-introduction

Agricultural exports exceed NZD$25 billion per annum, most of which are products derived from pasture-grazing livestock (Ministry of Business, Innovation & Employment 2018). The 2017 census quantified national sheep, dairy cattle and beef cattle numbers at 27.5, 6.5 and 3.6 million, respectively (Stats NZ 2018). The human population of New Zealand is approaching 5 million. For the agricultural sector to maintain these consistently
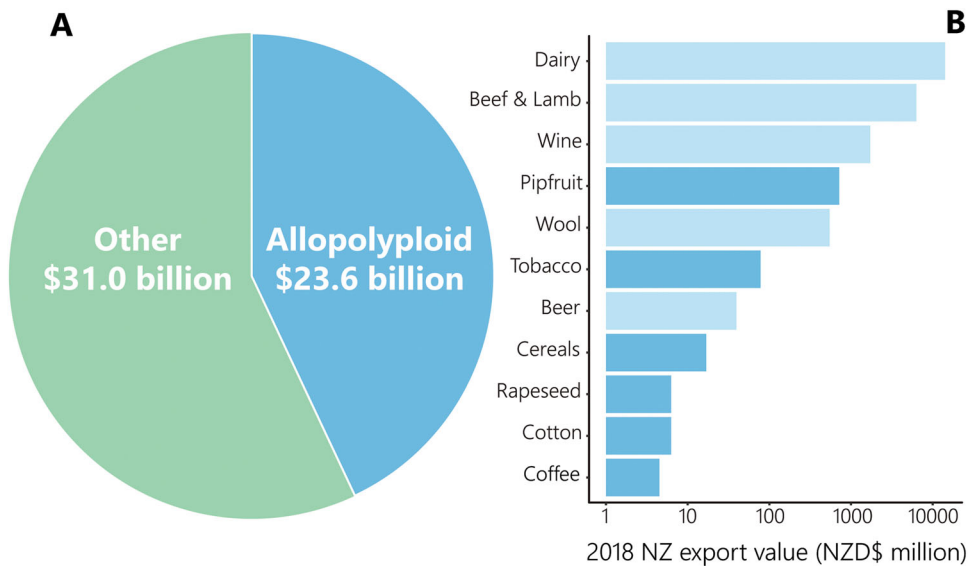

Figure 1. Economics of New Zealand allopolyploids. **(A)** Pie chart of New Zealand's total exports in 2018, separated into goods that derive directly or indirectly from systems that are reliant on allopolyploid species (blue) and other goods (green). Data were obtained using the New Zealand Trade Dashboard (Stats NZ 2019; accessed 24 June 2019) for the categories 'exports', 'goods' and '2018'. **(B)** Breakdown of allopolyploid export goods based on their individual contributions to the New Zealand economy in 2018 (NZ dollars, millions). Goods that are directly allopolyploid are represented by dark blue bars. Goods that derive indirectly from allopolyploid species are represented by pale blue bars. The *x*-axis is a log (base 10) scale.

high economic contributions, it is heavily reliant on pastoral quality and condition. Endophyte species of the genus *Epichloë* live as obligate symbionts of the cool-season grasses found in New Zealand pastures, particularly perennial ryegrass (*Lolium perenne*). An unexpectedly large number of *Epichloë* species have arisen via allopolyploidisation, with the genus subsequently becoming an emerging model system for studying fungal allopolyploidy (Schardl et al. 1994; Schardl et al. 2013; Cox et al. 2014; Campbell et al. 2017). Although central to New Zealand's agronomy, *Epichloë* species seldom form symbioses with native grasses (Rolston et al. 2002), although endemic *Epichloë* species are often allopolyploid (Leuchtmann et al. 2019). Agricultural strains were first introduced via seed brought by British immigrants during the 1800s (Stewart 2006). The coevolution between *Epichloë* endophytes and their hosts is thought to drive the specialisation and mutualistic cooperation of these symbioses (Leuchtmann et al. 1997; Saikkonen et al. 2004; Saikkonen et al. 2016). Able to persist asymptomatically within their host tissue, *Epichloë* fungi produce beneficial secondary metabolites that act as natural insecticides and enhance the survival of their grass host, in addition to improving the vegetative growth and drought tolerance of the pasture (Song and Nan 2015; Saikkonen et al. 2016).

Epichloë species are estimated to contribute NZD$200 million to the New Zealand economy per annum (Johnson et al. 2013). Given that one endophyte strain, *E. festucae* var. *lolii* AR37, introduced commercially at the 2006 Fieldays, is estimated to have taken NZD$12 million in development costs (Ministry of Business, Innovation & Employment 2018), this return has proved an immensely rewarding investment for New Zealand and its future. Different *Epichloë* strains make different compounds that protect their grass host from insect herbivory, with allopolyploid species often producing the most diverse array of compounds. While AR37 is not an allopolyploid, other allopolyploid strains such as *E. hybrida* Lp1 have been commercialised in other agricultural settings, and due to their diverse mechanisms of anti-insect protection, many contenders for third-generation commercial products are also allopolyploids. Beyond these economic incentives, *Epichloë* research also contributes fundamental information, such as the impacts of allopolyploidy on modulating fungal gene expression, to the growing global knowledgebase on allopolyploid species (Cox et al. 2014).

Epichloë endophytes are not the only allopolyploid species central to the functioning of the agricultural sector. White clover (*Trifolium repens*) is a key pastoral plant, owing to its quality forage material and nitrogen-fixing abilities (Charlton 2008). White clover emerged following an allopolyploidisation event between two European clover species confined to markedly different coastal and alpine habitats. Genetic analyses suggest that their unlikely co-habitation was driven by the reconfigured European landscape during the last glacial period (Griffiths et al. 2019). New Zealand's history of white clover research extends back some 80 years, incentivised by its advantages for pastoral agriculture. Nitrogen fixation by white clover has enabled pasture establishment in regions with significant mineral deficits, including the volcanic plateau and Northland gumlands (Brock et al. 1989). Moreover, a higher pastoral clover content has been positively correlated with dairy cow milk yields (Harris et al. 1998). White clover is a remarkable example of allopolyploidy-facilitated niche expansion that produced a ubiquitous temperate forage crop able to outcompete its two highly-specialised parental species, with surprising benefits for the modern pastoral economy. Continued research in New Zealand on the

interactions between the two parental subgenomes will enable the selection of superior white clover strains for use in pastoral breeding programmes (Griffiths et al. 2019).

Since the 1850s, pastoralism has dominated agricultural production in New Zealand, but crop production still constitutes an important source of economic gain in the agricultural sector (Peden 2008). New Zealand's major arable crops include a number of allopolyploid species formed prior to their introduction (Table 1). Cotton crops (*Gossypium* species) are a striking example of hybrid vigour through the evolution of complementary parental homeologs. Modern-day cotton cultivars are naturally-formed allotetraploids whose extinct diploid parental species, most closely related to extant *G. arboreum* and *G. raimondii* (Wendel et al. 1995), hybridised 1–2 million years ago (Hu et al. 2015). Notably, *G. raimondii* possesses a phenotype devoid of any spinnable fibre qualities (Hu et al. 2015). The natural union of complementary homeologs from these two divergent genomes in a common allopolyploid nucleus, in combination with intense human-mediated artificial selection, has seen the development of cotton species whose maximum yield, and fibre strength, length and fineness consistently surpass those of their parental species (Paterson 2005). New Zealand's cotton exports, a sector not widely recognised, exceeded NZD\$6 million in 2018 (Figure 1B), mainly in the form of woven cotton fabrics, as opposed to combed or carded raw cotton fibres (Stats NZ 2019).

As yet another example of allopolyploidy in agriculture, many areas of New Zealand, including Nelson, Hawke's Bay and Central Otago, provide an ideal climate for the cultivation of apples (*Malus* species); a purportedly allopolyploid crop (Chevreau and Laurens 1987; Tatum et al. 2005) that has been grown on New Zealand soil since European settlement and exported since the 1880s. Several new apple varieties have been developed in New Zealand, including Royal Gala, Jazz and Lemonade. The sequencing of the domestic apple genome in 2010 gave unprecedented insight into the evolutionary history of the *Malus* genus, postulating a polyploidy event that occurred over 50 million years ago in the ancestral lineage from which another pipfruit, pears (*Pyrus* species), have also originated. This duplication may have enabled the expansion of key gene families, such as those implicated in carbohydrate metabolism, a gene family over-represented in apples (Velasco et al. 2010), and those responsible for the commonly observed red fruit-skin pigmentation (Chagné et al. 2013). However, contrary to earlier studies, more recent genomic analysis is favouring the view that apples may have originated through autopolyploidy (Velasco et al. 2010). The evolutionary history of pears is also unclear, with some studies supporting an allopolyploid origin (Evans et al. 2008), while others support the autopolyploidy hypothesis (Li et al. 2019). The latter study drew their conclusions from the observed unbiased subgenome evolution in the pear genome; a common trend among paleo-autopolyploids, but one that has also been observed in some paleo-allopolyploid lineages (Sun et al. 2017; Li et al. 2019).

Introduced allopolyploid taxa of importance to the New Zealand economy are also prevalent well beyond the agricultural and horticultural sectors. *Saccharomyces*, the fungal genus of the model organism *S. cerevisiae* (brewer's and baker's yeast), is instrumental in brewery practices worldwide. *Saccharomyces cerevisiae* is the descendent of an ancient allopolyploidisation event, although genetic analyses have revealed extensive diploidisation, resulting in only minor retention of duplicated gene copies, most commonly those associated with beneficial novel properties (Wolfe 2001; Pfliegler et al. 2012; Marcet-Houben and Gabaldón 2015; Wolfe 2015). Notably, *S. cerevisiae*, an ale

(top fermenting) yeast, is also a parent of the allopolyploid lager (bottom fermenting) yeast, *S. pastorianus* (Casaregola et al. 2001; Lodolo et al. 2008). However, it is the genomic contribution of its other parental species, *S. eubayanus*, that granted *S. pastorianus* the specific sugar and sulphite metabolism changes necessary for its lager-brewing domestication (Libkind et al. 2011).

The establishment of New Zealand vineyards also began in the early 1800s. Domesticated allopolyploid *S. cerevisiae* of course plays a central role in wine making too, dominating the initial (Mangado et al. 2018) and late (Bagheri et al. 2017) stages of fermentation due to its high sugar processing rates and ethanol tolerance. Recent evidence suggests that *S. cerevisiae* not only dominates this ecosystem, but also directly influences the other constituent species (Bagheri et al. 2017). Seemingly in parallel with the allopolyploidy observed in brewing yeasts, strains of *Dekkera bruxellensis*, a prominent industrial wine fermentation contaminant, also appear to be allopolyploids (Borneman et al. 2014). The separation of the *Saccharomyces* and *Dekkera* lineages occurred at least 200 million years ago, preceding the ancient allopolyploidisation event in the *S. cerevisiae* lineage (Schifferdecker et al. 2014). Perhaps this genotypic convergence has been driven by the biological pressure from an evolutionary arms race between these two fermentative yeasts. A purported link exists between the ploidy level of *Saccharomyces* species and culture productivity (Albertin and Marullo 2012), and is a plausible explanation for the strong presence of allopolyploids among brewing yeasts, particularly when considered in conjunction with hybrid vigour. Subsequently, it is in the interest of New Zealand brewers to explore the existence of novel local allopolyploid strains that may provide a unique new edge to New Zealand's longstanding brewing and viticultural practices.

Allopolyploidisation post-introduction

Allopolyploid taxa whose hybridisation occurred following their introduction to New Zealand are less common than the examples above where allopolyploidisation preceded their arrival in New Zealand. One case of hybridisation subsequent to arrival, which has benefited the brewing industry, is triploid hops (*Humulus lupulus*). The New Zealand brewing industry pioneered the development of triploid hops, first releasing a commercial variety in 1972 in response to the growing global demand for a seedless phenotype. Today, 24 New Zealand-developed triploid cultivars are available (New Zealand Hops Ltd. 2018), distinguishable beyond their seedlessness by their superior growth and lushness relative to diploid cultivars (Trojak-Goluch and Skomra 2018). Although strictly autopolyploids, triploid hops are formed by controlled crosses between genetically extremely distinct cultivars; most often between a tetraploid female and diploid male, and thus nonetheless contain diverse parental genomes (Beatson and Brewer 1994; Beatson et al. 2003).

New Zealand's large population of introduced flora provides ample opportunity for naturally-occurring allopolyploidy events among taxa following their arrival. Given the purported role of polyploidy (Pandit et al. 2011; te Beest et al. 2012; Baduel et al. 2018) and hybridisation (Ellstrand and Schierenbeck 2000; Hovick and Whitney 2014; Gaskin 2016) in plant invasions, it will be important to remain vigilant to such occurrences. Certainly, allopolyploidy appears to have been central to the invasiveness of the aggressive hawkweed (*Pilosella officinarum*), which was accidentally introduced over 100 years ago

and has since become the bane of New Zealand's high country (Morgan-Richards et al. 2004; Morgan-Richards et al. 2009). Data suggests that the hybridisation of *P. officinarum* with a related species (likely *Hieracium praealtum*) has occurred at least three times within New Zealand, generating plants that appear phenotypically similar to *P. officinarum*, but that may act as conduits for increased gene flow between the species and possess the potential to colonise from single seeds, an ability likely to facilitate the rapid spread of an invasive species (Morgan-Richards et al. 2004; Trewick et al. 2004). In contrast to the direct genetic manipulation of triploid hops, allopolyploid hawkweed appears to have arisen as a consequence of human-induced habitat disturbance (Morgan-Richards et al. 2009).

Native flora and fauna

Introduced allopolyploid species have become an integral part of the country: for its industries, its economy and its food-chain. Many of these species are relatively well studied, due to their analogous roles on a global scale and their economic importance (Figure 1). However, New Zealand native allopolyploid species are significantly less well understood than their non-native counterparts. This knowledge gap belies the importance of native allopolyploids to the distinctiveness of the New Zealand biota. Concordant with the global trend (Jiao et al. 2011; Barker et al. 2016), a wealth of native allopolyploid diversity is found in New Zealand's flora, with documented examples across mosses, ferns and angiosperms (flowering plants). Allopolyploidy is possibly largely absent from New Zealand native fauna, even for species with otherwise unusual reproductive strategies (Morgan-Richards et al. 2019). The sole case known to us is an ancient hybridisation inferred in the formation of the mosaic allotriploid, parthenogenetic *Acanthoxyla* stick insects (Buckley et al. 2008; Myers et al. 2013) (Table 1). Triploidy has been documented in the New Zealand freshwater snail *Potamopyrgus antipodarium* (Soper et al. 2013), although its origin appears to lie in autopolyploidy (Neiman et al. 2011).

Mosses

Mosses are considered to be one of the earliest forms of land plant that evolved in adaptation to the higher CO_2 levels present from the early Paleozoic Era (Shaw et al. 2011). New Zealand is home to more than 500 moss species, approximately 20% of which are considered endemic (Glenny et al. 2011). Although mosses are haploid-dominant organisms (Graham and Wilcox 2000), researchers have identified two species of the New Zealand native *Sphagnum* mosses (peat moss) that lack haploid gametophytes (Karlin et al. 2009; Karlin and Smouse 2017). *Sphagnum australe* and *S. falcatulum* are found throughout the South Island only as allodiploid or allotriploid cytotypes, and it further appears that the allotriploids are the predominant plant form, perhaps due to a competitive advantage over their allodiploid counterparts that allows them to inhabit a broader ecological niche. Hybridisation and polyploidy are relatively common within the *Sphagnum* genus (Ricca et al. 2008; Karlin et al. 2014), as is interploidal hybridisation (i.e. hybridisation between different ploidy levels) relative to angiosperms (Flatberg et al. 2006; Karlin et al. 2009; Meleshko et al. 2018). For *S. australe* and *S. falcatulum* allotriploids, one of the parental species is their respective allodiploid species (or ancestor

thereof). Both taxa also display intersectional allopolyploidy, with *S. australe* appearing to have parental species from the sections *Sphagnum* and *Rigida*, and *S. falcatulum* from the sections *Subsecunda* and *Cuspidata* (Karlin et al. 2009).

Ferns

Ferns are another prominent feature of the damp understory of forested areas throughout New Zealand; the number of distinct species is unusually high for a temperate country (approximately 200, with 44% endemicity) (Schönberger et al. 2018). Among vascular plants globally, ferns demonstrate the highest frequency of polyploid species, with polyploidy implicated in up to 31% of speciation events (Wood et al. 2009). Consequently, ferns have long been used as a model system for studying polyploidy and its genetic repercussions (DeMaggio et al. 1971). The genus *Asplenium* (spleenworts) contains more than 700 species worldwide. Its Austral group, a polyploid complex centred in New Zealand (Brownsey 1977; Shepherd, Holland, et al. 2008), is unique when compared with European and North American groups of the same genus due to its absence of diploid organisms (Dawson et al. 2000; Perrie and Brownsey 2005). Seven tetraploid and eight octoploid *Asplenium* species are found in New Zealand, with allopolyploidy implicated in the origin of seven of the octoploid species (Shepherd, Perrie, et al. 2008), mirroring the high frequency of allopolyploidy found in *Asplenium* worldwide (Lovis 1978; Reichstein 1981; Wagner et al. 1993; Schneider et al. 2017). Interestingly, one of the tetraploids is thought to be the parent of five of the octoploids, suggesting that this single species has played a central role in the evolution of this fern complex (Shepherd, Perrie, et al. 2008). Despite extensive sympatry and having the same parental species, the allopolyploids *A. cimmeriorum* and *A. gracillimum* have each evolved independently at least twice, with the four lineages reproductively isolated (Perrie et al. 2010), thus emphasising the importance of allopolyploidy in the generation of biological diversity. It is possible that the octoploids *A. shuttleworthianum* and *A. northlandicum* have extinct parental species; nuclear sequences of the *LFY* gene obtained from the allopolyploids could not be identified among the tetraploid taxa analysed by Shepherd, Perrie, et al. (2008). However, it is also possible that these sequences were inherited from unsampled Pacific species.

The genus *Polysticum* (shield ferns) contains an allopolyploid complex located in New Zealand, and provided the first evidence-based demonstration of allopolyploidy in the New Zealand fern flora (Perrie et al. 2003). Initially considered to be a single species with very high levels of morphological variability (Allan 1961; Brownsey and Smith-Dodsworth 1989), *P. richardii* is now recognised as an allopolyploid complex containing four unique evolutionary lineages: two allooctoploid subspecies and two purportedly-parental tetraploid species. Allooctoploid *P. neozelandicum* is widely distributed throughout New Zealand, including on several outer islands. However, the individual distributions of its two subspecies do not overlap. Notably, allooctoploid *P. neozelandicum* subsp. *zerophyllum* has a wider geographical distribution than either of its tetraploid parental species, despite possessing relatively lower intra-lineage genetic variability (Perrie et al. 2003). It is possible that the New Zealand *Polystichum* complex represents a further example of allopolyploidy-mediated niche expansion and hybrid vigour. However, a wider study of the geographic ranges of all New Zealand ferns and lycophytes has found no obvious correlation between range sizes and polyploidy (Mountier et al. 2018).

Angiosperms

Angiosperms are the largest group of vascular plants, numbering over 300,000 species worldwide. Phylogenomic evidence has implicated an ancient whole genome duplication event in the ancestry of all extant angiosperm lineages (Jiao et al. 2011). Allopolyploidy, specifically, has been instrumental in the evolution of many of these (Osabe et al. 2012; Lyu 2016), and importantly, the link between New Zealand and allopolyploid angiosperms extends well beyond those species that make major contributions to the economy via crop production. Among New Zealand native angiosperms, there is an excess of species with even haploid numbers (i.e. the number of chromosomes within a single set), and an excess of those with haploid numbers greater than 10–14. These two karyotypic features are strong indicators of polyploid ancestry and substantiate the key role of polyploidy in the evolution of the New Zealand flora (Murray and de Lange 2011).

Perhaps the best-studied example of native allopolyploidy is *Pachycladon* (New Zealand rockcress), a genus in the Brassicaceae that is related to the model organism *Arabidopsis thaliana*. The number of species in the *Pachycladon* genus increased from one to eleven in the last million years following an allopolyploidisation event during the Pleistocene (Joly et al. 2009; Mandáková et al. 2010). Today, ten *Pachycladon* species are endemic to the South Island, and exhibit considerable morphological and habitat diversity in mainly alpine environments. Phylogenetic modelling and molecular studies have provided strong evidence for an adaptive radiation in the New Zealand group, despite the absence of clear phenotypic adaptations (Joly et al. 2014), with allopolyploidy and subsequent genomic restructuring within the founding species being the purported driving force (Joly et al. 2009; Mandáková et al. 2010). An adaptive radiation in *Pachycladon* is an impressive example of hybridisation between significantly diverged parental species. The level of divergence between the parents prior to their hybridisation is thought to be greater than that of allopolyploids in *Gossypium*, a genus that has long boasted one of the highest known parental genetic divergences among allopolyploids (Joly et al. 2009).

Polyploidy is also frequent among the more than 200 species of the globally-widespread genus *Plantago* (Murray et al. 2010). Commonly known as plantains, *Plantago* primarily comprises small herbaceous plants and shrubs. The eleven species of *Plantago* in New Zealand are not monophyletic and form three distinct lineages that appear to derive from at least three relatively-recent long-distance dispersal events, likely from Australia (Tay et al. 2010). Cytological and molecular studies suggest that most, if not all, New Zealand polyploid *Plantago* are allopolyploids (Ishikawa et al. 2009; Murray et al. 2010). This feature appears to have been central to their evolutionary history and taxonomic complexity, generating six ploidy levels, from diploid to 16-ploid, and forming many sympatric species within the New Zealand group (Rahn 1957; Rattenbury 1957; Groves and Hair 1971; Murray et al. 2010; Meudt 2011).

Looking forward

Allopolyploid species, both native and introduced, are central to many key aspects of life in New Zealand, and thus the benefits they confer to the country and its people are vast, far-reaching and surprisingly underappreciated. Duplicated, hybrid genomes give allopolyploids access to a suite of potential benefits otherwise unavailable to their ancestral

species, assuming they survive the initial genome shock. The prevalence of allopolyploid species throughout New Zealand attests not only to their resilience in overcoming these challenges, but also to their ability to thrive and oftentimes surpass the biological fitness of their parental species. In some cases, such as the allopolyploid hawkweed, this ability is clearly demonstrated through invasiveness. In others, humans have been able to control the distribution of allopolyploid species, and even manipulate their ploidy level. New Zealand demonstrates a high level of polyploidy among its vascular plants: early studies characterised polyploidy in approximately 63% of angiosperms (Hair 1966). This value is concordant with the globally-observed positive correlation between polyploidy and latitude (Stebbins 1984; Brochmann et al. 2004; te Beest et al. 2012), but contrasts with the chromosomal stasis (i.e. the absence of chromosomal change) seen in other Pacific island groups (Murray and de Lange 2011; Stuessy et al. 2014). It has been postulated that the high number of introduced plant species (approximately 50%) among the native biota has generated both the opportunities, and the pressure, for increased hybridisation within New Zealand (Morgan-Richards et al. 2009). New Zealand allopolyploid research would benefit from a dedicated survey of the prevalence of allopolyploid taxa, both native and introduced, in place of the current rough estimates made from the independent prevalence of hybridisation and polyploidy, and the incomplete lists of known allopolyploid cases.

Statistics New Zealand data (2019) suggest that allopolyploids, either directly or indirectly, collectively contribute around NZD\$23 billion to the economy per annum (Figure 1A), with this value excluding the largest economic sector, tourism. The need to continue to invest in the development of superior crop strains that deliver higher yields with reduced energy, water and land area requirements is strengthened by the rapidly growing global population: by 2050, the world's population is projected to reach 9.8 billion people; 11.2 billion by the year 2100 (United Nations Department of Public Information 2017). The optimisation of arable crops is imperative to feed this rapidly growing global population, and the interests of New Zealand in pursuing this research rest not only on its own food sufficiency, but also on export opportunities to the rest of the world. Beyond these critical subsistence applications, allopolyploid species play an integral role in the long-established traditions of brewing and viticulture, which also make significant contributions to the New Zealand economy (Figure 1B). These practices could gain a distinctive and competitive edge in both sensory profile and culture productivity through the discovery and implementation of novel native allopolyploid yeast strains.

Questions remain about the role of allopolyploidy in the evolution of New Zealand's indigenous flora. The vast majority of New Zealand native plant species arrived via long distance dispersal (Winkworth et al. 2002; Wallis and Jorge 2018). Were the successful colonisers polyploid when they arrived, or did polyploidy occur subsequently in New Zealand? There is evidence that both situations occurred (Murray and de Lange 2011), but the relative contribution of allo- versus autopolyploidy has not yet been assessed. There are also questions about the timing of allopolyploidy events. Many Northern Hemisphere allopolyploids have Pleistocene origins (Abbott and Brochmann 2003), with the harsh environmental conditions of glacial periods thought to increase both hybridisation (Soltis et al. 2004) and the production of unreduced gametes (Mable 2004), and leading to an increased efficiency of allopolyploid species in colonising newly deglaciated areas

(Comai 2005). The age of many of New Zealand's allopolyploids are unknown but Pleistocene origins have been postulated for New Zealand *Asplenium* (Shepherd, Holland, et al. 2008), *Pachycladon* (Joly et al. 2009), *Lepidium* (Mummenhoff et al. 2004) and *Leptinella* (Himmelreich et al. 2014). The creation of time-calibrated phylogenies for additional taxa has the potential to provide insight into the geological drivers of allopolyploid formation within New Zealand's island context.

Finally, how will these allopolyploids, both of agricultural and environmental importance, adjust to a changing climate? Will increased plasticity from multiple genomes mean that allopolyploid species are more resistant to climate change? Or will allopolyploids tend to be more transient on the landscape as many early writers originally proposed? Ten years ago, Morgan-Richards et al. (2009) concluded their review of genetic analyses of hybridisation in New Zealand with an acknowledgement that hybridisation is a continuing focus of evolutionary biology. Today, it feels more important than ever to prioritise local allopolyploidy research to continue to improve the crops on which the economy depends, as well as to understand the processes that have generated the unique national biota of Aotearoa New Zealand.

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Disclosure statement

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