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Multiple introductions, polyploidy and mixed reproductive strategies are linked to genetic diversity and structure in the most widespread invasive plant across Southern Ocean archipelagos

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Abstract

Biological invasions in remote areas that experience low human activity provide unique opportunities to elucidate processes responsible for invasion success. Here we study the most widespread invasive plant species across the isolated islands of the Southern Ocean, the annual bluegrass, *Poa annua*. To analyse geographical variation in genome size, genetic diversity and reproductive strategies, we sampled all major sub-Antarctic archipelagos in this region and generated microsatellite data for 470 individual plants representing 31 populations. We also estimated genome sizes for a subset of individuals using flow cytometry. Occasional events of island colonization are expected to result in high genetic structure among islands, overall low genetic diversity and increased self-fertilization, but we show that this is not the case for *P. annua*. Microsatellite data indicated low population genetic structure and lack

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of isolation by distance among the sub-Antarctic archipelagos we sampled, but high population structure within each archipelago. We identified high levels of genetic diversity, low clonality and low selfing rates in sub-Antarctic *P. annua* populations (contrary to rates typical of continental populations). In turn, estimates of selfing declined in populations as genetic diversity increased. Additionally, we found that most *P. annua* individuals are probably tetraploid and that only slight variation exists in genome size across the Southern Ocean. Our findings suggest multiple independent introductions of *P. annua* into the sub-Antarctic, which promoted the establishment of genetically diverse populations. Despite multiple introductions, the adoption of convergent reproductive strategies (outcrossing) happened independently in each major archipelago. The combination of polyploidy and a mixed reproductive strategy probably benefited *P. annua* in the Southern Ocean by increasing genetic diversity and its ability to cope with the novel environmental conditions.

KEYWORDS
biological invasions, breeding systems, clonality, genetic variation, islands, *Poa annua*, polyploidy, population genetics, self-fertilization, sub-Antarctic

1 | INTRODUCTION

One of the dominant features of global change is the spread of invasive species into all ecosystems (Maxwell et al., 2016). Resolving why some species are successful invaders, while others remain localized, is an important challenge (McGeoch & Jetz, 2019). Furthermore, some species have invaded vast regions across large latitudinal gradients, including extremely isolated islands that experience little human impact (Greve et al., 2017; Mairal et al., 2022), with the severity of invasion seemingly increasing with isolation from continents (Brockie et al., 1988).

Many studies have tested the links between certain life-history or functional traits of species and their invasion success (Drenovsky et al., 2012; Liao et al., 2021; Marchini et al., 2018). One trait that has been repeatedly associated with island colonization and the invasion success of alien plants in remote areas is the ability to self-fertilize, commonly referred to as Baker's Rule (Baker, 1959; Razanajatovo et al., 2016). Unlike outcrossing alien plants, self-compatible taxa are not limited by the availability of pollinators or mates in the new range (Ollerton et al., 2012; Schueller, 2004). Thus, population establishment by species known for their high levels of inbreeding can occur following a single dispersal event, even by a single individual (Baker, 1959; Marchini et al., 2016; Pannell et al., 2015). Similarly, clonal propagation (e.g., agamospermy or vegetative reproduction) provides invasive species with the opportunity to rapidly spread when mates are scarce or lacking (Silvertown, 2008; Wang et al., 2017). However, a fundamental evolutionary drawback of these reproductive strategies is a net loss of genetic diversity, and thus adaptive capacity, over time (García-Verdugo et al., 2013; Silvertown, 2008). Clonal reproduction may therefore be particularly detrimental for invasive populations in novel environments stemming from strong founder events (Dlugosch & Parker, 2008). Low genetic diversity is expected to limit the evolutionary potential of invasive populations and lower their chance of harbouring genotypes with high colonization abilities (Dlugosch & Parker, 2008; Smith et al., 2020). Conversely, multiple introductions may benefit colonization success by facilitating admixture that may result in novel genotypes and high genetic diversity (Gillis et al., 2009; Mairal et al., 2022). As with low genetic diversity, constraints may exist at the whole genome level. That is, species with more than two genome copies (i.e., polyploids) are thought to be better colonizers than diploids (te Beest et al., 2012). At the same time, polyploid angiosperms have higher rates of self-fertilization, clonality and life-history traits such as perenniality than their diploid relatives (Van Drunen & Husband, 2019). While life-history traits such as reproductive strategies and population attributes such as genetic diversity, ploidal variation and admixture have been studied in invasive species (Rice et al., 2019), very little is known about their interactions during invasion. In this study we investigate these interactions.

Annual bluegrass, *Poa annua* L. (Poaceae), is a prime example of a successful invasive species that has colonized habitats across a wide latitudinal gradient. The species is now considered one of the most widespread invasive plant species in the world (Molina-Montenegro et al., 2019). It is found from Arctic to Antarctic latitudes and is present in hot deserts and at the highest equatorial peaks (Darmency & Gasquez, 1997; Heide, 2001). In its non-native ranges, the species is a primary colonizer of disturbed habitats, quickly becoming dominant once established (Mao & Huff, 2012; Molina-Montenegro et al., 2019). Its high tolerance to a broad range of environmental conditions has been attributed to its different reproductive strategies and life-history traits such as (i) variability in life forms (annual, biennial and perennial; Lush, 1989), (ii) high rates of self-compatibility (Ellis, 1973; Johnson, 1993), and (iii) polyploid genome and substantial variability in genome size (Frenot et al., 1999; Mowforth & Grime, 1989). These characteristics make *P. annua* a

relevant species for understanding the invasion dynamics of a successful global invader.

P. annua is also the most widespread vascular plant across the extremely remote islands of the Southern Ocean, occurring on all major archipelagos (Shaw et al., 2010). For many of the islands, and indeed for Antarctica, it was the first non-native plant species recorded (Olech, 1996; Skottsberg, 1954). Its initial introduction to the islands has been attributed to the whalers and sealers who visited the islands during the 18th and 19th centuries (Frenot et al., 1999; Greene & Greene, 1963; Schenck, 1906). As a result, it has the longest residence time of any non-native species on many islands, in some instances with records dating back to the 1840s (Shaw, 2013). It is abundant and widespread on almost all islands where it has been introduced (Figure 1), including Macquarie (Copson, 1984), Marion (le Roux et al., 2013), South Georgia (Osborne et al., 2009), Crozet and Kerguelen (Frenot et al., 2001), Campbell (Meurk et al., 1994), Auckland (Johnson & Campbell, 1975), Tristan da Cunha, and Gough and Inaccessible (Roux et al., 1992; Wace, 1960). Meanwhile, on Heard Island and Prince Edward Island, where *P. annua* was more recently introduced, it is not yet abundant (le Roux et al., 2013; Scott, 1989), but is continuously expanding its distribution (le Roux et al., 2013; Scott & Kirkpatrick, 2005). *P. annua* readily colonizes disturbed and nutrient-enriched areas that result from the activity of humans as well as native animals on the Southern Ocean Islands (Haussmann et al., 2013; Mairal et al., 2022; Scott & Kirkpatrick, 1994, 2005). Colonization success of *P. annua* in these habitats might also be due to key traits such as its ability to germinate at low temperatures, high freezing tolerance and potential for reproduction year-round (Chwedorzewska et al., 2015; Dionne et al., 2010; Frenot et al., 2001; Mowforth & Grime, 1989), reflecting acclimatization to polar conditions. Yet, little is known about the role of the species' mating strategies in driving its successful colonization of these remote islands.

In continental habitats, *P. annua* displays high selfing rates, typically between 80% and 85% (Ellis, 1973; Kelley et al., 2009; Koshy, 1969; Mengistu et al., 2000), with apomixis occurring occasionally (Ellis, 1973; Johnson, 1993). The expression of these reproductive strategies is influenced by environmental conditions (Ellis, 1973; Heide, 2001; Koshy, 1969) and may play a fundamental role in the colonization success of *P. annua* on Southern Ocean Islands, which are typified by low mean annual temperatures, low seasonality, and wet and windy conditions. The potential role of genome size variation in the population genetic structure of *P. annua*

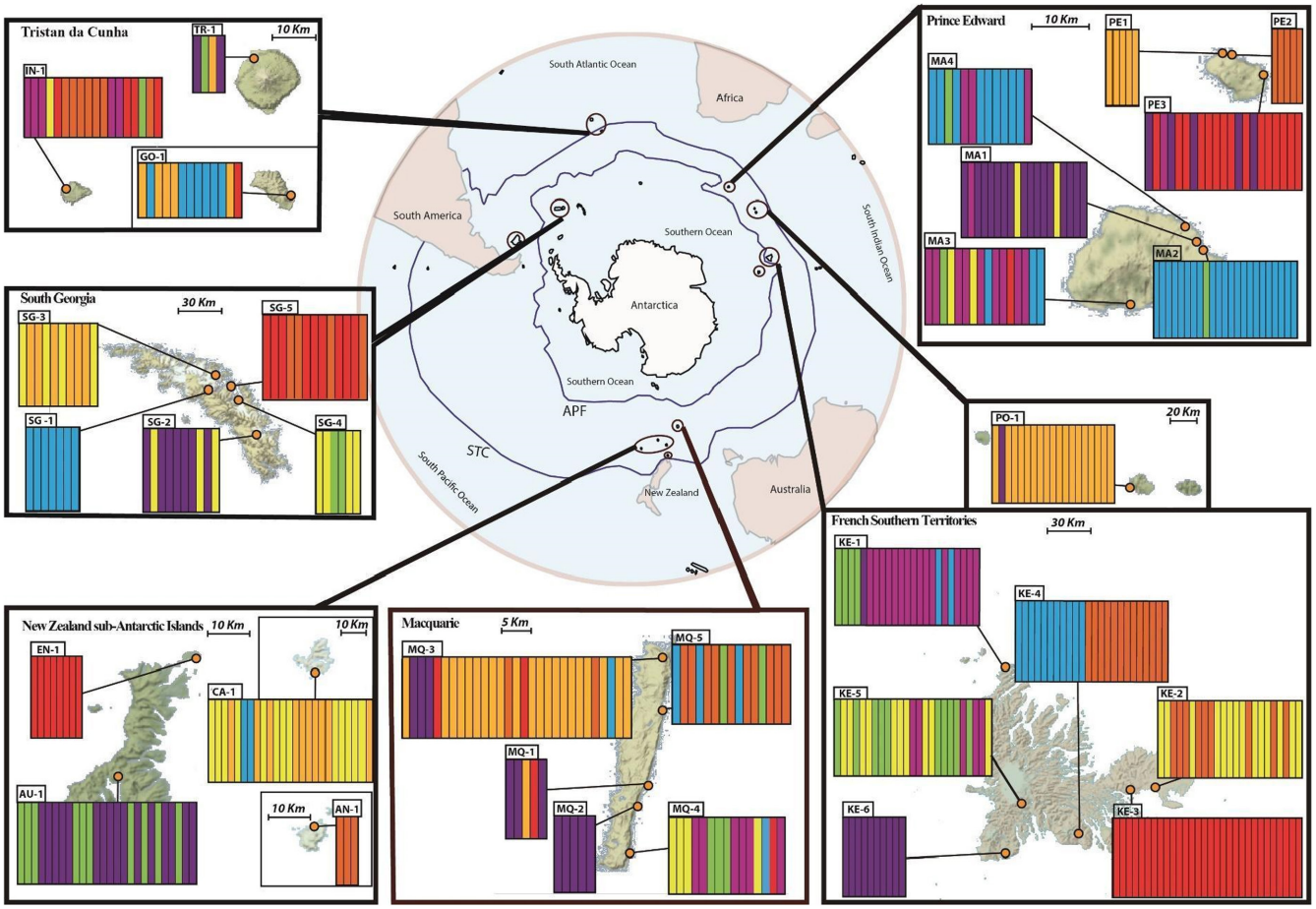

FIGURE 1 Genetic clustering of individuals within each archipelago following AMOVA-based *K*-means of microsatellite data. Each analysis is independent for each archipelago, and they are not related. Each bar represents one individual and colours represent genetically differentiated clusters for each archipelago. Circles around sub-Antarctic islands or nearby archipelagos represent the presence of *Poa annua*. Orange dots correspond to the sampled populations, each with a code given in Table 1 and Table S1 [Colour figure can be viewed at wileyonlinelibrary.com]

is also intriguing and may impact its establishment in the region (Chwedorzewska et al., 2015; Mowforth & Grime, 1989). Preliminary data from Kerguelen and Crozet suggest that sub-Antarctic populations are tetraploid, but previous studies also identified ploidal variation within the species (Frenot et al., 1999; Rodionov et al., 2010) and that genome size can vary substantially within specific cytotypes (Mowforth & Grime, 1989), thus providing opportunities for increased genetic variation that may be geographically structured among archipelagos.

Here, we use population genetic and flow cytometry data to investigate the invasion history and success of *P. annua* across the Southern Ocean Islands. If the species' current distribution in the region has been the result of independent long-distance dispersal events to each archipelago, we expect genetic structure to reflect natural biogeographical barriers within and between islands (i.e., isolation by distance with strong genetic structure among archipelagos; García-Verdugo et al., 2014). In this case, spread within islands could be facilitated via clonal reproduction and selfing, resulting in limited levels of within-island genetic diversity (Frenot et al., 1999; Wouw et al., 2008). Alternatively, if multiple introductions led to the establishment of invasive populations on Southern Ocean Islands, then high levels of within-island genetic diversity could be expected. Because of the recurrent introductions of genetically diverse propagules (Baird et al., 2020; Mairal et al., 2022), population genetic structure among major archipelagos is expected to be low under this scenario. However, some degree of genetic structure is expected within each archipelago, resulting from independent introductions, although this structure may be diluted by secondary dispersal within and between islands (Mairal et al., 2022). Furthermore, if *P. annua* was independently introduced into different archipelagos, it would be especially relevant to explore whether there are convergent genetic and reproductive patterns in each archipelago, which would provide evidence about which reproductive strategies and dynamics are linked to invasion at these latitudes. To test these alternative scenarios, we sampled *P. annua* populations spanning the temperate Tristan da Cunha archipelago and most major sub-Antarctic archipelagos of the Southern Ocean. We generated nuclear microsatellite and genome size data to determine: (i) whether genetic diversity and genome size variation are geographically structured throughout the region; (ii) whether genetic diversity and structure display typical patterns of island biogeography; and (iii) which reproductive strategies (e.g., levels of clonality and selfing) are more common in invasive *P. annua* populations.

2 | MATERIALS AND METHODS

2.1 | Study system and field sampling

Access to Southern Ocean Islands is limited, and only possible with support from National Antarctic Programmes and governments with jurisdictional responsibility for these islands. The possibility of sourcing samples from these archipelagos is not so much related to average visitation rates, but rather to high variability in visit frequency between islands. Some islands are visited regularly by scores of visitors, including tourists, while others are rarely visited owing to their conservation status. For example, Prince Edward Island has been visited more than three times since 2008, while Heard Island was last visited in 2004. Due to these logistical constraints and shipping schedules, sampling of *Poa annua* took place over several years between 2008 and 2018: the Antarctic Circumnavigation Expedition (ACE; including a visit to Prince Edward Island); annual relief expeditions to Marion Island, Tristan da Cunha and Gough islands; field research programmes on South Georgia, Kerguelen, Crozet, Macquarie and Prince Edward Islands; and opportunistic sampling by researchers travelling on tourist ships to Campbell, Auckland, Antipodes and Enderby islands (Table S1). Sampling permits were granted by the national agencies and conservation departments of each island region (for details see the Acknowledgements section). The only major island not sampled was Heard Island, due to its inaccessibility and low visitation. There has been no science expedition to the island since 2004.

Our collection comprised 470 individual plants representing 31 populations, spanning all main Southern Ocean archipelagos (Table 1, Figure 1). Within each population, individuals were sampled at least 10 m apart to avoid resampling the same individual. For large populations, a minimum of 15 individuals were collected throughout the entire distribution of the population. All sampled populations were georeferenced using a handheld GPS (e.g., Garmin eTrex Vista or Trimble Differential GPS unit) and collected material was dried and stored on silica gel until DNA extraction and flow cytometry analysis.

2.2 | Genome size variation

Because *P. annua* is known to have high variation in chromosome numbers, ranging between 14 and 52 (http://ccdb.tau.ac.il; Rice et al., 2015), we first explored genome size variation among our samples. As all our samples collected over a decade consisted of desiccated leaf material, we were restricted to using DAPI flow cytometry rather than propidium iodide for DNA staining to obtain genome size estimates (Suda & Trávníček, 2006). Flow cytometry analysis followed the procedure of Galbraith et al. (1983) using Otto's buffers (Doležel & Göhde, 1995; Otto, 1990). We used *Pisum sativum* var. Ctirad, a well-established standard in flow cytometry, with a genome size of 9.09 pg (Doležel et al., 1998), as a standard for our measurements. Briefly, nuclei were released after chopping 0.5 cm^2 of dry leaf tissue and 0.5 cm^2 of fresh leaf tissue of the internal standard (*Pisum sativum*) with a razor blade in a Petri dish containing 0.5 ml of Otto I buffer (0.1 M citric acid, 0.5% Tween 20). Afterwards, the nuclear suspension was filtered using a 42-μm nylon mesh and stained with a solution containing 1 ml of Otto II buffer (0.4 M $Na_2HPO_4 12H_2O$), 4 mg ml^{-1} of DAPI and 2 mg ml^{-1} of β-mercaptoethanol. After 5 min of incubation, samples were analysed in a Partec PA II flow cytometer (Partec GmbH). The fluorescence of at least 3000 nuclei per sample was analysed using FLOWMAX (version 2.4, Partec GmbH). Because our analyses were based on desiccated leaf material, we accepted histograms with up to a 3.8% coefficient

of variation (CV). In all cases, we only accepted peaks that were clearly identifiable from background noise. This was successful for most of the material collected from 2016 onwards, but less so for older material. In total we accepted histograms for 150 individuals from nine populations, covering all the archipelagos considered in our study (Table 1). The DNA index was calculated for all the samples by dividing the relative fluorescence of the G0/G1 peak of *P. annua* accessions by the relative fluorescence of the G0/G1 peak of *Pisum sativum* cv. Ctirad (2C = 9.09 pg, Schönswetter et al., 2007) used as the internal standard. The G0/G1 peak is always the highest peak in the flow cytometry histogram and represents the standard growing cells not replicating their DNA (i.e., the majority of plant cells).

2.3 | Microsatellite analysis

Genomic DNA was extracted from all samples using a modified cetyltrimethylammonium bromide (CTAB) method (Doyle & Doyle, 1987) with the addition of 0.2 M sodium sulphite to the extraction and wash buffers. DNA quality and quantity were measured using a Nanodrop spectrophotometer (Infinite 200 PRO NanoQuant; Tecan Group), and all DNA samples were diluted to a concentration of 10 ng μl^{-1} and stored at −80°C until further use.

All *P. annua* individuals (n = 470) were genotyped using the set of nine microsatellite loci previously developed by us (Mairal et al., 2022). PCR (polymerase chain reaction) amplification of microsatellites was performed in two multiplex PCRs (see Mairal et al., 2022 for details). Given the sensitivity of multiplex reactions to genotyping errors (e.g., allele dropout), we adopted conditions recommended to minimize such errors, including the use of a standardized DNA concentration (~100 ng μl^{-1}), special buffers for multiplexing, and selection of primers with similar annealing temperatures (Guichoux et al., 2011). All PCRs were carried out in 15-μl reaction volumes containing 1.5 μl diluted template DNA, 7.5 μl KAPA2G Fast Multiplex Mix (Kapa Biosystems), 1.5 μl primer mix (2 μM) and 4.5 μl distilled H_2O. Samples were amplified using the following PCR conditions: 3 min of denaturation at 95°C, 30 cycles of 15 s of denaturation at 95°C, 30 s at multiplex-specific annealing temperature (see Mairal et al., 2022), and 25 s of elongation at 72°C, and a final extension for 10 min at 72°C. Each 96-well PCR plate contained 93 samples plus two randomly selected technical replicates and one negative control (H_2O). All technical replicates (n = 19) were used to count mismatches for scored genotypes and thus to estimate repeatability at each locus. Gel capillary electrophoretic separation of amplified fragments was carried out at the Central Analytical Facility, Stellenbosch University (Stellenbosch, South Africa). All loci were scored using GENEMARKER software version 2.6.4 (SoftGenetics LLC) using the LIZ 500 size standard. We applied a semi-automatic genotype scoring for each allele, followed by manual correction when needed, to reduce scoring errors (DeWoody et al., 2006). Allele scoring was combined across microsatellite loci to generate a multilocus phenotype (i.e., allele variation with unknown dosage) for each individual. In agreement with previous observations of tetraploid species (Frenot et al., 1999; Nannfeldt, 1937), all loci displayed up to four alleles per individual.

Unbiased analyses of microsatellite data in polyploids are hindered by factors such as unknown allele dosage, genotyping errors and unknown mode of inheritance (Meirmans et al., 2018). Although some approaches have been developed to address the first two factors (e.g., Bruvo et al., 2004; Dufresne et al., 2014), not knowing modes of inheritance remains a major challenge when calculating population genetic metrics from allele frequency data (Meirmans et al., 2018). These challenges stem from the fact that the observed allelic patterns in allopolyploids can vary, even among microsatellite loci within species, as the genetic distance between parental taxa strongly determines the level of chromosome pairing in the resulting polyploid (Chester et al., 2012). As a result, a given polyploid species may not fit any of the extremes traditionally defined as allo- and autopolyploid, which may bias population genetic inferences based on allele-frequency calculations (see reviews in Dufresne et al., 2014; Meirmans et al., 2018).

Previous work suggests that *P. annua* originated from a relatively recent hybridization event between two closely related species, *P. infirma* and *P. supina* (Nannfeldt, 1937; Tutin, 1952). As such, *P. annua* would fit Stebbins' (1947) definition of segmental allopolyploidy (i.e., some degree of homology may exist between the chromosomes of parental subgenomes), and cytological and phylogenetic evidence appears to support this view (Hovin, 1958; Soreng et al., 2010). We might therefore expect *P. annua* to follow an intermediate model of disomic inheritance at certain loci, typically expressed as fixed heterozygosity in allelic profiles (e.g., García-Verdugo et al., 2013), and tetrasomic inheritance for loci in chromosomes showing meiotic pairing or occasional recombination between the parental subgenomes (Hovin, 1958). To improve the accuracy of our analyses, we tested this expectation by examining how inbreeding coefficients (F_{IS}) varied across loci. Under a model of complete disomic inheritance, all loci in an allotetraploid are expected to show fixed heterozygosity, leading to negative F_{IS} values, while deviations from this expectation would suggest tetrasomic inheritance (Meirmans & Van Tienderen, 2013). To test this, we calculated inbreeding coefficients at the "locus × population" level by running the approach implemented in GENODIVE version 3.06 (Meirmans, 2020) for testing deviations of allele frequencies from those expected under Hardy–Weinberg equilibrium conditions.

Unlike our previous study that focused on extensive sampling of *P. annua* in the Prince Edward archipelago (Mairal et al., 2022), we found that only three loci in the present data set (i.e., Poa3, Poa8 and Poa288) had significantly negative F_{IS} values (Table S3), whereas the remaining loci tended to have positive values, as would be expected for a predominantly selfing species (Mengistu et al., 2000). To segregate the allelic composition of isoloci (i.e., loci Poa3, Poa8 and Poa288), we used the function "allele. correlations" implemented in the package POLYSAT version 1.6 (Clark & Jasieniuk, 2011) using R 3.2.5 (R Core Team, 2020). However, this approach failed to confidently assign alleles to isoloci, probably because of population genetic structure (see Section 3) or because allele sizes

TABLE 1 Population sample size, genetic diversity indexes (number of effective alleles, N_e; number of alleles, N_a), and estimates of clonality (%) and selfing rate as obtained from the analysis of nuclear microsatellite loci of 31 *Poa annua* sub-Antarctic populations

Archipelagos	Island	Population	*n*	N_e (N_a)	% Clonality (*SD*)	Selfing rate[a] (SE)	2C values (SD)
A	Kerguelen	KE-1	24	2.16 (24)	13.6 (5.9)	0.39 (0.10)	–
A	Kerguelen	KE-2	23	2.25 (24)	4.3 (0.0)	0.43 (0.14)	–
A	Kerguelen	KE-3	30	2.30 (42)	0.0 (0.0)	0.52 (0.10)	3.16 (0.07), *N* = 30
A	Kerguelen	KE-4	24	2.68 (39)	4.2 (0.0)	0.30 (0.36)	–
A	Kerguelen	KE-5	25	2.25 (27)	11.7 (3.5)	0.46 (0.39)	–
A	Kerguelen	KE-6	10	2.10 (25)	0.0 (0.0)	–	–
A	Possession	PO-1	19	2.20 (38)	0.0 (0.0)	0.44 (0.05)	3.14 (0.09), *N* = 15 6.30 (0.16), *N* = 5
B	Marion	MA-1	19	1.76 (26)	19.9 (7.0)	0.39 (0.04)	–
B	Marion	MA-2	23	1.64 (28)	38.3 (9.1)	0.50 (0.05)	3.26 (0.04), *N* = 25
B	Marion	MA-3	15	2.00 (29)	3.3 (5.8)	0.30 (0.41)	3.13 (0.08), *N* = 14
B	Marion	MA-4	13	1.78 (23)	21.2 (5.1)	–	3.09 (0.09), *N* = 9 4.78 (0.12), *N* = 3
B	Prince Edward	PE-1	5	1.40 (14)	23.3 (15.2)	–	–
B	Prince Edward	PE-2	5	1.58 (14)	43.3 (5.8)	–	–
B	Prince Edward	PE-3	21	1.65 (19)	27.5 (6.5)	0.29 (0.06)	–
C	Tristan da Cunha	TR-1	4	1.94 (21)	0.0 (0.0)	–	–
C	Gough	GO-1	13	1.93 (23)	0.0 (0.0)	–	–
C	Inaccessible	IN-1	18	2.88 (36)	3.7 (3.2)	0.20 (0.35)	2.82 (0.27), *N* = 7
D	Enderby	EN-1	8	2.31 (36)	0.0 (0.0)	–	–
D	Auckland	AU-1	26	1.87 (40)	2.5 (0.8)	0.51 (0.05)	–
D	Campbell	CA-1	25	3.01 (55)	0.0 (0.0)	0.52 (0.02)	–
D	Antipodes	AN-1	3	1.42 (15)	0.0 (0.0)	–	–
E	Macquarie	MQ-1	5	2.11 (23)	0.0 (0.0)	–	–
E	Macquarie	MQ-2	5	2.09 (22)	0.0 (0.0)	–	–
E	Macquarie	MQ-3	29	2.44 (42)	0.0 (0.0)	0.49 (0.03)	–
E	Macquarie	MQ-4	16	2.47 (39)	6.3 (0.0)	0.50 (0.02)	3.32 (0.06), *N* = 15
E	Macquarie	MQ-5	15	2.96 (48)	0.0 (0.0)	0.39 (0.33)	3.31 (0.06), *N* = 11 13.79 (0.60) *N* = 3
F	South Georgia	SG-1	7	1.58 (16)	35.3 (8.7)	–	–
F	South Georgia	SG-2	10	2.03 (27)	0.0 (0.0)	–	–
F	South Georgia	SG-3	9	2.73 (32)	0.0 (0.0)	–	–
F	South Georgia	SG-4	6	2.18 (34)	0.0 (0.0)	–	–
F	South Georgia	SG-5	15	3.04 (48)	0.0 (0.0)	0.47 (0.12)	3.38 (0.02), *N* = 9 8.22 (0.22), *N* = 4

Note: Genome size estimates (2C values) obtained from flow cytometry analysis are also indicated for a subsample of individuals. Codes of archipelagos: A = French Southern territories; B = Prince Edward archipelago; C = Tristan archipelago; D = New Zealand sub-Antarctic; E = Macquarie, F = South Georgia.

[a] Based on six tetrasomic microsatellite loci for large populations ($n \geq 15$ individuals).

between parental subgenomes were shared (Clark & Schreier, 2017). Considering these findings, we constructed two data sets to accommodate the heterogeneity among our microsatellite loci in all subsequent analyses, one containing the allelic information generated for all nine loci (hereafter "full data set") and another set containing only the data for the six loci not following a pattern of disomic inheritance (hereafter "partial data set").

2.4 | Estimates of clonality and selfing

To examine the contribution of clonality and self-fertilization to reproduction in *P. annua* populations, we performed a set of population-level statistical analyses. Clonal reproduction was inferred using GENODIVE version 3.06 (Meirmans, 2020). This program estimates the number of clones within populations based on the similarity detected among

multilocus phenotypes, while considering genotyping errors and somatic mutations. Following the recommendations given in the GENODIVE version 3.0 manual (Meirmans, 2022), we based our inferences on the results obtained after running the tests on the "full data set" using different genotyping error and somatic mutation thresholds. Inbreeding may result in highly homozygous loci within populations and can lead to the detection of identical multilocus phenotypes that did not arise from clonal propagation (Halkett et al., 2005). On the other hand, genotyping errors may introduce "mutations" which will decrease inferences of clonality. To account for uncertainty related to these two opposing effects on estimates of clonality, we first ran the function "assign clones" in GENODIVE version 3.0 with a conservative threshold (i.e., equivalent to one mutational step under a stepwise mutation model). If identical allelic composition between two putative clones at a given locus is the result of selfing in an allotetraploid, we would expect allelic variation to be reduced to one variant at each isolocus (Meirmans & Van Tienderen, 2013; Novikova et al., 2017). Following this reasoning, we then calculated the minimum number of clones by filtering the outcome of the previous analysis to retain only those with more than two alleles at the three isoloci displaying fixed heterozygosity (see above). In addition, the maximum number of clones was estimated by rerunning the "assign clones" function but using a threshold for the 2.1% estimated mean genotyping error (i.e., three mutational steps over all genotyped loci; see Results section for more details). Our approach for clonal estimation is thus more conservative than those using three arbitrary thresholds (e.g., Goessen et al., 2022), while controlling for overestimating clonality due to selfing. Population-level mean and SD values of clonality were calculated using the estimates of clonality obtained in each case.

Selfing rates were calculated using the approach described by Hardy (2016) and implemented in SPAGEDI version 1.5 (Hardy & Vekemans, 2002). These estimates are based on multilocus polyploid data and are robust, even when allelic dosage is unknown and in the presence of double reduction (Meirmans et al., 2018), and when assuming polysomic inheritance. For this reason, we obtained our estimates using the "partial data set" but including only one genotype of each unique clone. In addition, because this method is sensitive to small sample sizes (Hardy, 2016), we restricted the analysis to large *P. annua* populations (i.e., ≥15 individuals).

2.5 | Genetic diversity and structure across the Southern Ocean

We tested whether geographical isolation is linked to population genetic variation that primarily resides within, rather than among, islands (García-Verdugo et al., 2014; Mairal et al., 2015). Mengistu et al. (2000) suggested that *P. annua* in temperate regions tends to accumulate most genetic variation within populations. If this is the case in the Southern Ocean, then substantial among-island differentiation may be evident (see Frenot et al., 1999). To determine how genetic variation is structured among different spatial scales, we conducted an analysis of molecular variance (AMOVA; Excoffier et al., 1992) using the "Ploidy Independent Infinite Allele Model" function implemented in GENODIVE version 3.0 (Meirmans, 2020). Population genetic structure among archipelagos was further analysed with the AMOVA-based *K*-means method as described above, using data from all *P. annua* populations ("full data set"). Under a scenario of restricted gene flow among archipelagos, we would expect each population to mainly be assigned to its corresponding archipelago.

We also tested whether island area was a significant predictor of genetic diversity (Johnson et al., 2000). The effective number of alleles (N_e) was estimated at the population level using SPAGEDI version 1.5 (Hardy & Vekemans, 2002), and a Spearman rank correlation between N_e and island size (log km^2) was run with the "cor" function implemented in R 3.2.5 (R Core Team, 2020).

2.6 | Genetic diversity and structure within islands

Previous work suggested that Southern Ocean Islands have been colonized by a limited number of *P. annua* genotypes (Frenot et al., 1999), although this seems to vary among islands and archipelagos (Chwedorzewska, 2008; Mairal et al., 2022). Therefore, we analysed the level of genetic diversity and structure for each archipelago, using the AMOVA-based *K*-means method based on individual genotype data (i.e., no prior population assignment) as implemented in GENODIVE version 3.0 (Meirmans, 2020). We preferred this approach over other genetic assignment methods because it does not make any assumptions about allele frequencies and thus allowed us to use our most comprehensive "full data set." The maximum number of clusters (*k*) on each archipelago was set to the maximum number of populations sampled. Although missing data represented a small fraction of the data set (4.8%), we avoided artificial clustering of individuals by applying the "Fill in Missing Data" function in GENODIVE based on the expected dosage of polyploids. Individual clustering was based on a simulated annealing with 10^6 steps using a Monte Carlo Markov Chain approach, and the optimal value of *k* was selected according to the Bayesian Information Criterion following Meirmans (2012).

Population genetic structure was also explored and visualized using principal coordinate analyses (PCoAs). Bruvo distances (Bruvo et al., 2004) were calculated among all individuals sampled in each archipelago and the first two PCs were extracted and plotted using GENALEX version 6.5 software (Peakall & Smouse, 2012).

Lastly, to test the correlation between population pairwise geographical distances and genetic distances (i.e., isolation-by-distance), we calculated a matrix of pairwise Rho-based geographical and genetic distances among populations within each island, for islands with more than three sampled populations, using SPAGEDI version 1.5. Mantel tests were run in GENALEX version 6.5 including the geographical coordinates obtained from the geometric centre of each population.

3 | RESULTS

3.1 | Genome size variation

Our 2C genome size estimates ranged between 1.19 and 14.47 pg (DAPI from 0.131 to 1.592; Table 1; Figure S1, Table S4). Despite this variation, 90% of the individuals analysed (135 out of 150) had genome size estimates between 2.94 and 3.40 pg. Sixteen individuals had very high genome size estimates (≥4.66 pg). These rare instances were found in populations on Marion (four individuals), Possession (five individuals), South Georgia (four individuals) and Macquarie (three individuals) islands (Figure S1; Table S4). For these individuals with large genome size estimates, we detected rare and private alleles in one individual on Marion Island and six individuals on Macquarie Island.

3.2 | Mating system analysis

Repeatability across individual loci ranged between 94.7% and 100%, with an average score of 97.9% across all loci, or a mean genotyping error rate of 2.1% (see Table S2 for estimates of repeatability at each locus). Using this error threshold, we found evidence for clonality in *Poa annua* populations across the archipelagos included in our study (15 out of 31 sampled populations; Table 1). However, clonality was limited with a mean frequency of 8.3% within populations. When the analysis was run using the "complete data set," clones were not detected between archipelagos. On the other hand, estimates of selfing rates based on six tetrasomic microsatellite loci revealed that levels of self-fertilization ranged between 20% and 52% within large populations (Table 1).

3.3 | Genetic diversity and structure across the Southern Ocean

AMOVA revealed that most genetic diversity (47.5%) resided within populations, followed by within archipelagos (30.5%) (Table 2). Unexpectedly, the least amount of genetic diversity resided among archipelagos (22%, Table 2), in keeping with results at the population level (see below). Indeed, the AMOVA-based *K*-means method was unsuccessful in assigning populations to their corresponding archipelagos (Figure 2).

Within-island genetic diversity (mean number of effective alleles across populations) was only marginally correlated with island size ($n = 13$, $R = .58$, $p = .04$). Such a weak correlation only partially meets the expectations from island biogeography (Johnson et al., 2000; MacArthur & Wilson, 2001) and suggests that some islands may not be at migration–drift equilibrium (e.g., some island introductions may be more recent than others). Furthermore, Mantel tests did not indicate significant links between genetic and geographical distances within islands (Table 3).

TABLE 2 Results of the hierarchical AMOVA obtained from the analysis of nuclear microsatellite loci, based on a ploidy independent Infinite Allele model

Source	df	Var comp	%Var	Rho-value
Among archipelagos	5	0.831	22.0	0.220
Among populations (archipelago)	25	1.152	30.5	0.391
Within populations	436	1.793	47.5	0.525

Note: All levels were significant ($p < .01$) based on 9999 permutations.
Abbreviations: df, degrees of freedom; Var comp, variance components.

3.4 | Genetic diversity and structure within islands

AMOVA-based *K*-means revealed high population genetic structure, both within and between islands (Figure 1). Except for some small populations (i.e., PE1, PE2, SG-1, EN-1, AN-1, MQ-2, KE-6) and one large population (KE-3), all populations were inferred to be composed of individuals assigned to a minimum of two genetic clusters. In contrast, some genetic clusters were shared at larger spatial scales within an archipelago, both among populations within islands (e.g., MA-2, MA-3, MA-4) and between islands of the same archipelago (i.e., PE-3 and MA-1/MA-3 in the Prince Edward archipelago; PO-1 and KE-1/KE-6 in the French Southern Territories). Within-population genetic structure was related to outcrossing rates, since the inferred number of *K*-means clusters was negatively correlated with estimates of selfing rates (Figure 3).

Patterns of genetic structure among populations were also supported by the results of the Bruvo distance-based PCA (Figure 4). In addition, the genetic differentiation between *P. annua* populations on the same island (i.e., KE-3, SG-5) was also highlighted by these analyses. Within each archipelago, PCA showed that individuals with large genome sizes (i.e., higher than expected for tetraploid cytotypes) were not genetically closely related to each other (grey symbols in Figure 4).

4 | DISCUSSION

Islands of the Southern Ocean provide a rare opportunity to study the dynamics of invasive species, given their known, short history of human colonization and low anthropogenic disturbances. We obtained population genetic data for the most widespread invasive plant, *Poa annua*, across the Southern Ocean islands. We identified several consistent patterns across these islands that deviate strongly from observations for the species in continental regions. Furthermore, our results deviated from typical biogeographical patterns of island colonization by plants. We did not find genetic structure among major archipelagos, but we found high genetic structure within archipelagos. Additionally, we found a high frequency of genomes that are similar in size to those previously described for tetraploid *P. annua* (Frenot et al., 1999), high genetic diversity, low rates of self-fertilization and a moderate occurrence of clonality.

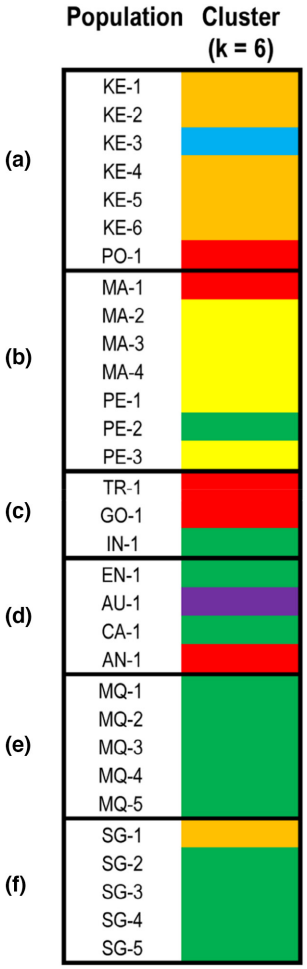

FIGURE 2 Population-based clustering across islands showing the assignment to each island/archipelago. Populations are coded as in Table 1[Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Results of the Mantel tests testing for significant associations between geographical and genetic (Rho) distances on islands with more than four populations sampled (*N*) and across the study area

Island	*N*	R^2	*p*
Kerguelen	6	.08	.24
Macquarie	5	.04	.30
South Georgia	5	.03	.21
Across all islands	31	.008	.10

4.1 | Population genetic structure and diversity of *P. annua* suggest multiple independent introductions into the sub-Antarctic

Population genetic diversity in insular systems is structured by oceanic barriers, usually leading to higher between-island than within-island genetic structure and isolation by distance with strong genetic structure among archipelagos (Franks, 2010; García-Verdugo et al., 2014). This is especially evident in native species with multi-island distributions, given their long residence times and limited long-distance migration (Juan et al., 2000; Mairal et al., 2015). For example, the biota of remote sub-Antarctic islands follows a biogeographical pattern of limited dispersal among different archipelagos (reviewed in Moon et al., 2017). The population genetic structure of invasive alien species might mimic that of island natives, when a limited number of initial introductions act as source of subsequent secondary dispersal events to neighbouring islands. Invasive populations, however, often stem from multiple introductions, involving complex dispersal routes from numerous sources (Cristescu, 2015; Rosenthal et al., 2008; Vicente et al., 2021). In the case of *P. annua*, high levels of within-island genetic diversity and admixture (Figure 1) strongly support this latter scenario.

The overall low genetic differentiation we found among major archipelagos was surprising, being much lower than genetic differentiation among populations within each archipelago (Table 2). At the same time, we did not identify isolation by distance throughout the Southern Ocean or on large islands (Table 3). Overall, *P. annua* populations showed remarkably weak population genetic structure and high genetic diversity throughout the region. This may be explained by the visitation history of these islands. Since the discovery of the Southern Ocean Islands and their early human history (late 1700s to late 1800s), ships visited them from multiple ports around the world, often from regions where *P. annua* is present, including the east coast of the United States, southern New Zealand, Hobart in Australia and Cape Town in South Africa (Downes, 1997; Hooker, 1847). At the same time, it should be noted that, in general, each major archipelago has its own jurisdiction and is governed by a different country, so most visits come from similar ports and sources, with visits among archipelagos being extremely rare, since the cessation of sealing in the 1800s.

In the early days of exploration, there were no biosecurity protocols in place, resulting in the introduction and establishment of numerous non-native species (Convey & Lebouvier, 2009). Despite more stringent biosecurity protocols nowadays (de Villiers et al., 2006) there are still many pathways for the introduction of alien species to Southern Ocean Islands (Chown et al., 2012; Lee & Chown, 2009; le Roux et al., 2013), for example resulting in new grass invasions in recent years (Pertierra et al., 2016; Shaw, 2013). In fact, *P. annua* has been one of the top three species that visitors have unintentionally transported into the region as seed contaminants on gear and clothing (Huiskes et al., 2014).

The high population genetic structure of *P. annua* we identified within and between islands belonging to the same archipelago (i.e., nearby islands) may be explained by multiple introductions to each archipelago. For example, this seems evident across the New Zealand sub-Antarctic archipelago, where *P. annua* populations consist of unique genetic clusters on each island, despite their geographical proximity (Figure 1). Similarly, within larger islands such as South Georgia and Kerguelen, populations are highly differentiated (Figures 1 and 4) and have higher genetic diversity than those on smaller islands. This may be due to large islands having greater infrastructure, several ports of entry, multiple historic

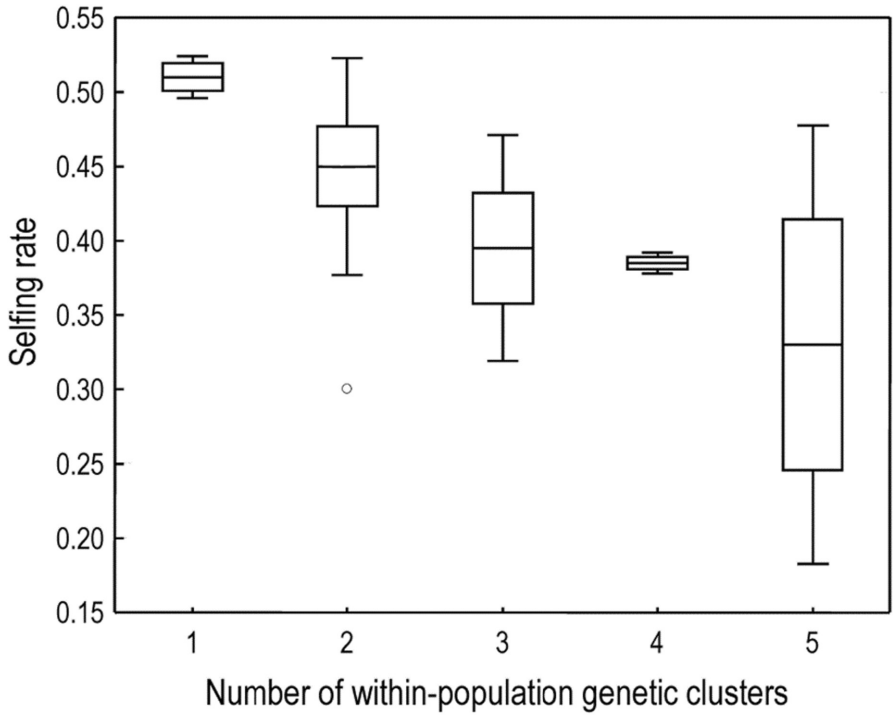

FIGURE 3 Relationship between estimates of selfing rate and genetic heterogeneity (number of *K*-means clusters) within populations of *Poa annua* as inferred in our study system using nuclear microsatellite data ($N = 18$ populations)

settlement sites, higher human visitation and more visiting vessels (both currently for research, and historically for sealing) than small islands (Chown et al., 2005; Frenot et al., 1999; Greene & Greene, 1963). This presents a greater opportunity for propagules to be introduced at different times and from different sources. The short residence time of some populations, the low rates of within-island natural dispersal in *P. annua* (le Roux et al., 2013) or the rugged orography dominated by steep slopes and glaciers on larger islands may have prevented subsequent gene flow between these populations. Nonetheless, some admixture is observed within and between nearby neighbouring islands and may be the result of multiple introductions followed by human-mediated secondary introductions within and between islands (e.g., Genton et al., 2005; Gillis et al., 2009; Mairal et al., 2022), which may benefit the colonization success of *P. annua* (Genton et al., 2005; Hodgins et al., 2018; Sherpa & Després, 2021). A previous genetic study suggested that a population of *P. annua* in the Antarctic Peninsula was founded by multiple introductions from different sources (Chwedorzewska, 2008). Similarly, human transport and multiple introductions probably underlie the genetic structure of invasive soil fauna in the sub-Antarctic (Baird et al., 2020).

Without chromosome counts, we cannot confirm whether most of the *P. annua* individuals collected are indeed tetraploid. The DAPI method we used is known to suffer from biases from preferentially binding to AT-rich regions. Thus, genome size estimates depend on genome composition (Doležel et al., 1998). Yet, we found 90% of *P. annua* individuals (135 out of 150) to have genome size estimates ranging between 2.94 and 3.40 pg, similar to genome size estimates previously reported for tetraploid cytotypes of the species (Frenot et al., 1999). Importantly, Frenot et al. (1999) also used the DAPI method to estimate genome sizes. Our genome size estimates are lower than those obtained for *P. annua* from the Kerguelen Islands by Siljak-Yakovlev et al. (2020). These authors analysed 16 tetraploid individuals and found genome sizes to vary between 4.12 and 4.29 pg. These values probably differ from our values and those reported by Frenot et al. (1999) because they were determined using propidium iodide. We also identified several high-order polyploids (often in geographically distant archipelagos; Table 1; Figure S1). These incidences, albeit rare in the context of our study, may represent multiple, independent introductions of different cytotypes not yet reported in *P. annua* (Mairal et al., 2022). Alternatively, these polyploids may have arisen following hybridization between *P. annua* and one or more of the about 15 native and five non-native *Poa* species present on the Southern Ocean Islands. Some of these high-order polyploids had private and rare alleles, possibly due to interspecific hybridization with resident *Poa* species (e.g., Lorenz-Lemke et al., 2006), which may represent an unnoticed, but significant, threat to Southern Ocean Island biodiversity (Rhymer & Simberloff, 1996). However, more detailed analyses of cytogenetic and genetic diversity, including of other *Poa* species, on these islands are required to investigate the performance of higher order polyploids in these habitats or the impact of *P. annua* on the genetic composition of native species.

4.2 | Mating system changes in *P. annua*

The levels of genetic diversity present in populations are highly dependent on the mating systems of plants (Booy et al., 2000). As selfing predominates in *P. annua*, the species is expected to have low population genetic diversity (Jullien et al., 2019), a phenomenon that may be exacerbated by the colonization of remote oceanic archipelagos

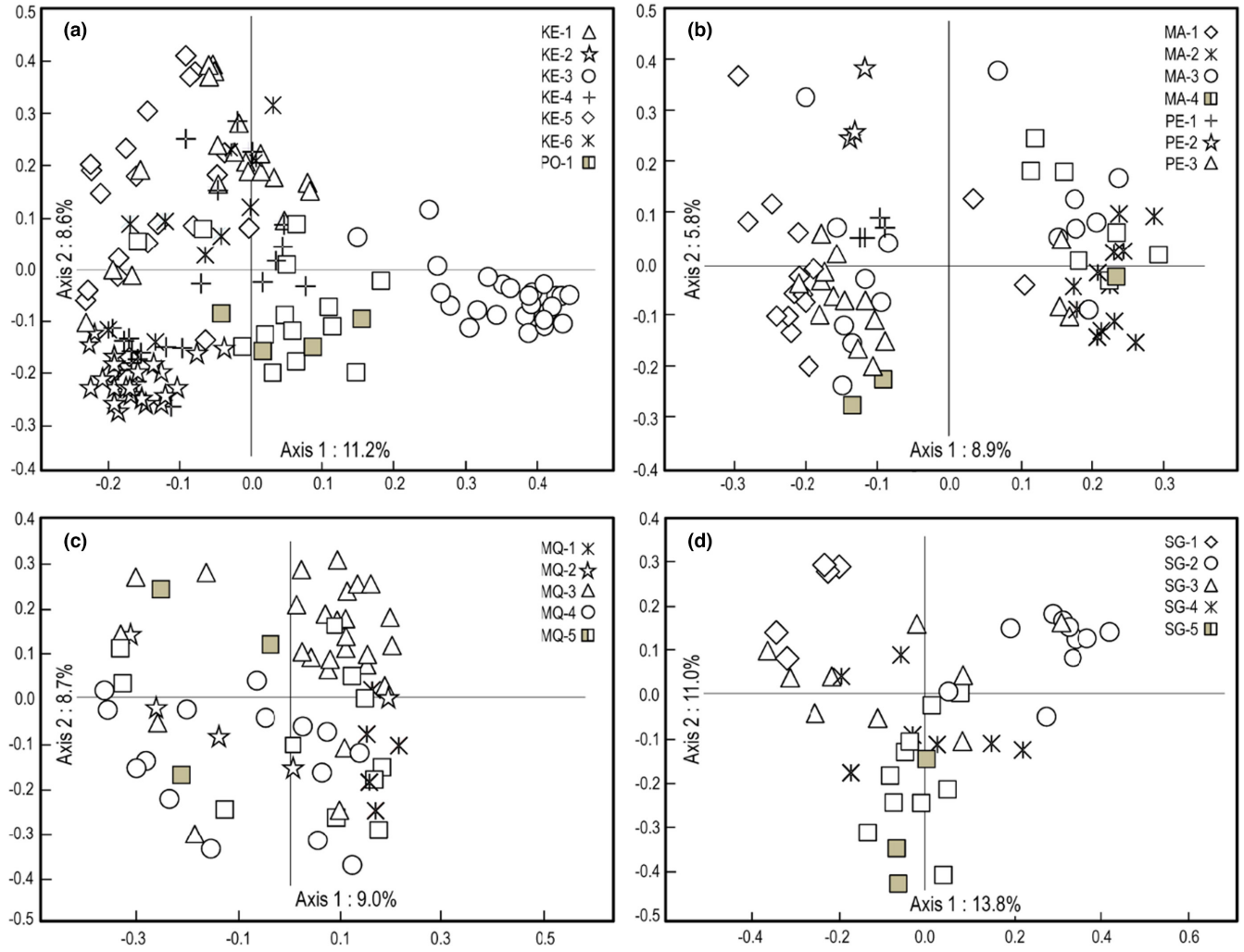

FIGURE 4 PCA of genetic structure based on Bruvo distances conducted on archipelagos with more than four sampled populations: (a) Kerguelen, (b) Prince Edward archipelago, (c) Macquarie and (d) South Georgia. Individuals with high genome size estimates (≥4.66 pg) are coloured in grey [Colour figure can be viewed at wileyonlinelibrary.com]

(Baker, 1959). Conversely, *P. annua* seems to have accumulated high genetic diversity levels on the Southern Ocean Islands (Table 1). At the same time, we found the genome size of *P. annua* across the region to conform predominantly to those of tetraploid cytotypes (Frenot et al., 1999), which may further elevate genetic diversity (de Paz & Caujapé-Castells, 2013). These results contrast strongly with those expected for a predominantly inbreeding species, since the latter should result in low genetic diversity and homogenization within populations (Wright et al., 2013). A plausible explanation for the high genetic diversity we found might be that *P. annua* underwent changes in its reproductive strategy in the Southern Ocean Islands (Ellegren & Galtier, 2016). In fact, while continental populations of the species typically have selfing rates of up to 85% (Chen et al., 2003; Ellis, 1973; Mengistu et al., 2000), our estimated rates were substantially lower, with an average of 42% across populations (Table 1). While selfing rates reported for continental populations are based on different experimental approaches to ours, we found a range of estimates that consistently supported lower selfing rates on Southern Ocean islands and, importantly, in the presence of high levels of genetic variation (Table 1). In agreement with this observation, we also found higher within-population genetic structure (i.e., number of *K*-means clusters) to be related to lower levels of selfing (Figure 3). This result, in turn, could be related to the establishment of genetically diverse and divergent groups of *P. annua* on these islands. Switching from selfing to outcrossing, linked to environmental stress and population density, has also been reported in island species (e.g., Barrett, 2013). To investigate this possibility in *P. annua*, future reproductive biology work should include comparisons of selfing rates between Southern Ocean Island populations and continental source populations of the species. The sub-Antarctic climate may have further acted as a filter to promote the survival of polyploid individuals with greater genetic diversity, as well as a common reproductive strategy, independently in all major archipelagos.

Our data identified several instances where clonality could be inferred with high confidence (Table 1). Both our sampling design (collection of samples separated a minimum of 10 m apart) and the repeated observation of clones within different archipelagos support the notion that these *P. annua* populations can also reproduce

clonally. The ecological conditions of sub-Antarctic islands (i.e., isolated habitats, strong abiotic selection associated with extreme climate conditions, distributional range-edge for the species) have probably promoted the adoption of clonal reproduction by *P. annua* in the region (Hörandl, 2006; Tilquin & Kokko, 2016). Interestingly, while *P. annua* is predominantly an annual plant, in the Southern Ocean Islands it has shifted to larger, perennial plants, especially at sites where animal disturbance is high (Selkirk et al., 1990; Williams et al., 2018). These life-history shifts in life forms may favour vegetative propagation (i.e., dispersal of plant fragments by animals, and potential for reproduction year-round) over apomixis, and deserves further research. This is also consistent with the idea that polyploids often colonize disturbed areas (Rice et al., 2019; Silvertown, 2008). The low frequency of clonality in *P. annua* in our study populations suggests that this mechanism probably contributes to the initial spread of the species, but not its continuing spread. For example, incidences of clonality appear to be higher on recently colonized islands such as those in the Prince Edward archipelago (Table 1; Huntley, 1971). Because our estimates of clonality are conservative, our results open a new avenue for research on the interaction of polyploidy, selfing and clonality in the critical stage of population establishment in invasive plants.

5 | CONCLUSIONS

The most widespread invasive plant in the Southern Ocean, *Poa annua*, is characterized by populations that harbour high levels of genetic diversity and that are genetically distinct within individual islands. The overall low genetic differentiation we found among major archipelagos was surprising, being much lower than among populations within each archipelago. These patterns deviate from typical biogeographical patterns of island colonization by plants and are consistent with an invasion history characterized by multiple introduction events from diverse sources and secondary dispersal events within archipelagos, leading to genetically diverse and admixed populations on Southern Ocean Islands. Following independent colonizations of each archipelago, the predominantly perennial invasive populations probably adapted similar reproductive strategies, characterized by low levels of selfing and clonality. These strategies probably enable *P. annua* to maintain high genetic diversity and avoid the accumulation of deleterious mutations and, therefore, to cope with stressful environmental conditions (Jullien et al., 2019). Worryingly, future human-mediated disturbance in the region may facilitate further genetic admixture between invasive populations (e.g., Mairal et al., 2022) that are likely to result in novel genotypes given the high levels of genetic diversity we identified. There is growing evidence that genetic admixture fosters invasiveness (Keller & Taylor, 2010; Li et al., 2018; Smith et al., 2020), and this may further enhance the invasion success of *P. annua* in the Southern Ocean. Alternatively, if new founding populations of *P. annua* suffer from bottlenecks, asexual reproduction, coupled with the species' wide environmental tolerance, may allow plants to invade new areas (Le Roux et al., 2008). Our study illustrates the importance of flexible reproductive strategies to maximize opportunities for the establishment and spread of non-native species, especially in harsh and remote areas.

AUTHOR CONTRIBUTIONS

M.M., C.G.V., J.S., S.L.C. and J.J.L.R. designed the study. J.S., M.M., S.L.C. and J.H.C. performed sampling of biological material. M.M., J.J.L.R. and Z.M. generated the data. C.G.V. and M.M. analysed data. M.M. led the writing, with major contributions from C.G.V. and J.J.L.R. and contributions and final approval from all co-authors.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data available at 10.5061/dryad.zs7h44jdk.

DATA AVAILABILITY STATEMENT

Microsatellite matrix of *Poa annua*. Dryad Dataset: https://doi.org/10.5061/dryad.zs7h44jdk.

BENEFIT-SHARING STATEMENT

Benefits generated from the sharing of our data and results on public databases.

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