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Human activity strongly influences genetic dynamics of the most widespread invasive plant in the sub-Antarctic

Mario Mairal[1,2] | Steven L. Chown[3] | Justine Shaw[4] | Desalegn Chala[5] | John H. Chau[6] | Cang Hui[7,8] | Jesse M. Kalwij[6,9] | Zuzana Münzbergová[10,11] | Bettine Jansen van Vuuren[6] | Johannes J. Le Roux[1,12]

[1]Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa

[2]Departamento de Biodiversidad, Ecología y Evolución, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, Ciudad Universitaria, Madrid, Spain

[3]Securing Antarctica's Environmental Future, School of Biological Sciences, Monash University, Victoria, Australia

[4]School of Biological Sciences, The University of Queensland, St Lucia, Queensland, Australia

[5]Natural History Museum, University of Oslo, Oslo, Norway

[6]Centre for Ecological Genomics and Wildlife Conservation, Department of Zoology, University of Johannesburg, Auckland Park, South Africa

[7]Centre for Invasion Biology, Department of Mathematical Sciences, Stellenbosch University, Stellenbosch, South Africa

[8]Biodiversity Informatics Unit, African Institute for Mathematical Sciences, Cape Town, South Africa

[9]Institute of Geography and Geoecology, Karlsruhe Institute of Technology, Karlsruhe, Germany

[10]Department of Botany, Charles University, Prague, Czech Republic

[11]Department of Population Ecology, Czech Academy of Science, Průhonice, Czech Republic

[12]Department of Biological Sciences, Macquarie University, Sydney, New South Wales, Australia

***Correspondence**
Johannes J. Le Roux and Mario Mairal, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa.
Emails: jaco.leroux@mq.edu.au; mariomairal@gmail.com

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Abstract

The link between the successful establishment of alien species and propagule pressure is well-documented. Less known is how humans influence the post-introduction dynamics of invasive alien populations. The latter requires studying parallel invasions by the same species in habitats that are differently impacted by humans. We analysed microsatellite and genome size variation, and then compared the genetic diversity and structure of invasive *Poa annua* L. on two sub-Antarctic islands: human-occupied Marion Island and unoccupied Prince Edward Island. We also carried out niche modelling to map the potential distribution of the species on both islands. We found high levels of genetic diversity and evidence for extensive admixture between genetically distinct lineages of *P. annua* on Marion Island. By contrast, the Prince Edward Island populations showed low genetic diversity, no apparent admixture, and had smaller genomes. On both islands, high genetic diversity was apparent at human landing sites, and on Marion Island, also around human settlements, suggesting that these areas received multiple introductions and/or acted as initial introduction sites and secondary sources (bridgeheads) for invasive populations. More than 70 years of continuous human activity associated with a meteorological station on Marion Island led to a distribution of this species around human settlements and along footpaths, which facilitates ongoing gene flow among geographically separated populations. By contrast, this was not the case for Prince Edward Island, where *P. annua* populations showed

high genetic structure. The high levels of genetic variation and admixture in *P. annua* facilitated by human activity, coupled with high habitat suitability on both islands, suggest that *P. annua* is likely to increase its distribution and abundance in the future.

KEYWORDS
biological invasions, dispersal, human commensalism hypothesis, island conservation, polyploidy, propagule pressure

1 | INTRODUCTION

The establishment and spread of alien species to the point at which they become impactful or even dominant members of local assemblages encompass the major critical stages of biological invasion (Blackburn et al., 2011). While extensive data on invasion dynamics exist for many species (Hui & Richardson, 2017), the underlying drivers can be complex because of the simultaneous impacts of human activity and climate change (Hulme, 2017). Separating these two confounding factors from those of intrinsic plant population dynamics remains a key challenge in invasion science and requires comparisons of invasions of the same species between areas of high and limited human pressure, with the latter being rare anywhere on Earth.

Much can be gained from a genetic perspective on the likely drivers of invasion dynamics and what various genetic signatures may reveal about the invasion process (Bock et al., 2015; Cristescu, 2015; Estoup, & Guillemaud, 2010). Important issues, amongst others, include tracing the origins and routes of invasion, detecting multiple introductions, tracking demographic processes of invasive populations, understanding pathways of secondary spread, identifying genetic admixture and detecting genomic regions under selection (Berthouly-Salazar et al., 2013; Diedericks et al., 2018; Hudson et al., 2019; Jansen van Vuuren & Chown, 2007; Thompson et al., 2012; Yadav et al., 2019). Genetic approaches can be especially helpful in adjudicating the roles of particular processes during the establishment and spread of the invaders (Chown et al., 2015).

In this study, we considered two hypotheses regarding the impact of human activity on invasion dynamics. The first hypothesis assumes that increased propagule pressure through multiple introductions results in higher levels of genetic diversity in invasive populations, which, in turn, may lead to a higher likelihood of establishment and spread through a variety of mechanisms (Bock et al., 2015; Dlugosch & Parker, 2008; Luque et al., 2016; Roman & Darling, 2007; Simberloff, 2009). Although an increasing number of experimental studies provide evidence in support of this idea (Hovick & Whitney, 2019; King & Howeth, 2019; Sinclair et al., 2019), they have also drawn attention to the context dependency of the outcome. For example, differences in invasion success may also be a consequence of variation in climate, biotic resistance, or other aspects of the receiving environment (Balestri et al., 2018; Cheng et al., 2019; Liu et al., 2020; Seebens et al., 2019; Vahsen et al., 2018). Other studies have suggested that genetic diversity may be less important for success in establishment and spread (Le Cam et al., 2020; Chown et al., 2015; Richards et al., 2012; Le Roux et al., 2007; Schrieber & Lachmuth, 2017; Wang et al., 2020). Much scope therefore exists for further examination of the relationship between propagule pressure, genetic diversity and invasion success in the context of the progression from introduction to spread of an alien species.

In the second hypothesis, human activity is thought to be a significant contributor to dispersal, both by establishing new spatial pathways for invasion in a local environment and by enhancing genetic diversity within these new populations to an extent greater than expected with natural colonisation processes (Bertelsmeier & Keller, 2018; Bertelsmeier et al., 2018; Wilson et al., 2008). Here, population genetic approaches provide a means to distinguish between natural and human-mediated dispersal because of the different expectations for genetic diversity and structure. Low spatial genetic structure is expected from frequent human-assisted long-distance dispersal, whereas localised dispersal by natural processes is expected to result in higher spatial genetic structure (Wilson et al., 2008). Yet, this is difficult to test because few areas exist where humans do not dominate the environment (Watson et al., 2016).

The Antarctic region, including its surrounding islands, provides unique opportunities for investigating both hypotheses. The region includes some of the least visited places on Earth (Leihy et al., 2020), yet has a suite of invasive species recorded at sites where human presence is prolonged and significant (Frenot et al., 2005; Greve et al., 2020). The sub-Antarctic islands are of particular interest because on several archipelagos, multiple islands lie in close proximity and share similar climate conditions and biodiversity, generally differing only in their extent of human visitation (Leihy, Duffy, & Chown, 2018; Leihy, Duffy, Nortje, et al., 2018; De Villiers et al., 2006). In many cases, the islands have been colonised by the same alien species (Chapuis et al., 1994; le Roux et al., 2013; Shaw et al., 2010), making for natural experiments where recipient environments are similar, yet histories of human visitation and activity are very different. Such sub-Antarctic archipelagos offer an opportunity to study parallel invasions of the same species in areas with similar abiotic and biotic conditions, but a contrasting history of anthropogenic impact. While new insights about invasion dynamics in this part of the world are emerging for invertebrates (Myburgh, Chown, Daniels, & Jansen Van Vuuren, 2007; Baird et al., 2020), little

is known for plants. Of particular interest are grasses (Pyšek et al., 2012), which can be highly invasive and have a significant impact on local sub-Antarctic and Antarctic ecosystems (Gremmen et al., 1998; Molina-Montenegro et al., 2019).

Among the grasses, *Poa annua* L. (vernacular name: annual bluegrass or annual meadow grass) is an exemplar invasive species, being the most widespread invasive plant in the broader Antarctic region (McGeoch et al., 2015; Shaw et al., 2010). As a ruderal species, *P. annua* is an excellent coloniser of exposed and highly disturbed areas and can quickly become dominant once established (Chwedorzewska et al., 2015; Molina-Montenegro et al., 2019; Scott & Kirkpatrick, 2005). The species is established on many sub-Antarctic and maritime Antarctic islands and on the Antarctic Peninsula (Frenot et al., 1997; Hughes et al., 2010; Molina-Montenegro et al., 2019; Olech & Chwedorzewska, 2011; Pertierra et al., 2017; Roy, 1990). In addition, it is the only alien plant species with successful generative reproduction on the Antarctic continent (Chwedorzewska et al., 2015). One of the island groups in the region where the species occurs is the Prince Edward Islands archipelago (PEA).

The PEA, comprising Marion Island and Prince Edward Island, represents an ideal model system to study the impact of human activity on the invasion dynamics of human commensals like *P. annua*. The archipelago contains relatively simple and species-poor communities that include some shared alien species (Greve et al., 2017). Both islands have very similar biotic and abiotic conditions (Chown & Froneman, 2008) and are home to similar animal and plant communities (e.g., both islands share the same 21 native vascular plant species; Chau et al., 2020). To date, only three alien plant species have been recorded on Prince Edward Island (*Cerastium fontanum* Baumg., *P annua*, *Sagina procumbens* L.), while more than 21 alien plant species are known from Marion Island (Greve et al., 2017, 2020). Despite differences in their physical size (Marion Island, 290 km^2 vs. Prince Edward, 45 km^2), the two islands experience very similar ecological processes (Chown & Froneman, 2008), with both supporting large aggregations of seals and seabirds, including species such as gulls and sheathbills that are known to disperse grasses in some settings (Parnikoza et al., 2018). Thus, natural dispersal opportunities for plant propagules are considered to be similar on both islands. *Poa annua* is one of the earliest-established and most abundant invasive plant species on both islands (le Roux et al., 2013). The species was first collected on Marion Island in 1948 (Greene & Greene, 1963), and on Prince Edward Island in 1965 (Huntley, 1971). While no earlier observations of the species have been recorded (Chown & Froneman, 2008; Huntley, 1971), it may have reached the PEA in the 1800s when explorers and sealers frequently visited the islands (Chown & Froneman, 2008), as was the case on other sub-Antarctic islands at similar latitudes (Frenot et al., 2001; Williams et al., 2018).

Despite their close geographic proximity, Marion and Prince Edward Islands have experienced very different levels of human impact over time. Prince Edward Island has remained largely unvisited, making it one of the world's most pristine islands (Chown et al., 2001). Since the annexation of the PEA by South Africa in 1948, Prince Edward Island has been infrequently visited by only a small number of researchers undertaking short stays in summer and autumn (Bester et al., 2003; Cooper et al., 2009). Between 1965 and 1985, 103 days of research visits had accumulated across 26 visits (Cooper & Avery, 1986). The current management plan limits visits to one every four years, for up to 10 people, and for a maximum duration of eight days (PEIMP, 2010). The last visit to Prince Edward Island was in March 2011. The impact of invasive species on this island has been considered largely negligible (Gremmen & Smith, 1999). On Marion Island, however, there has been a year-round operational presence of overwintering teams since 1948 and many more visitors and researchers stay on the island during annual resupply visits (Chown & Froneman, 2008; Cooper et al., 2009; Greve et al., 2020).

Here, we aimed to test the two major hypotheses outlined above using evidence from newly developed microsatellite loci, flow cytometry analyses, and niche modelling techniques. For the propagule pressure hypothesis, we expected higher genetic diversity and genome size variation on Marion Island due to higher human visitation and thus introduction opportunities than on Prince Edward Island. If multiple independent introductions have taken place on Marion Island, then a higher number of unique genetic lineages are expected compared to Prince Edward Island. For the human-mediated dispersal hypothesis, we expect clear differences in the spatial genetic structure of *P. annua* between the two islands, even if habitat suitability and natural dispersal opportunities are similar across both islands. Specifically, we expect to see higher levels of genetic admixture and lower population differentiation (i.e., higher gene flow) on Marion Island compared to Prince Edward Island.

2 | MATERIALS AND METHODS

2.1 | Field sampling

Field sampling was designed to cover the human entry points to the islands, as well as scattered localities around the islands spanning a range of minimum residence times (following le Roux et al., 2013). Since le Roux et al. (2013) did not observe *P. annua* during their systematic grid survey on both islands, we used their ad hoc presence data only. Sampling on Prince Edward Island was conducted during the biological survey of December 2008 (Cooper et al., 2009). Sampling on Marion Island was performed during several annual relief expeditions between 2009 and 2018. This resulted in samples for 225 individuals from 34 locations (Table 1): 26 localities from Marion Island (174 individuals) and eight localities from Prince Edward Island (51 individuals). From larger populations, a minimum of ten individuals was collected from across the entire distribution of each population. All individuals were sampled for populations comprising fewer than five individuals. Care was taken to collect only individuals that were spatially separated (i.e., that are not clonal). Trypot Beach, an area frequently visited by humans

TABLE 1 Details of *Poa annua* populations sampled in this study

Population locality	Population code	Number of samples	Latitude	Longitude	Minimum residence time
Prince Edward Island					
Kent Crater	1	1	−46.6309	37.8883	2008
Creek above camp	2	5	−46.6128	37.9252	2001
Hope Stream – Escarpment	3	5	−46.6087	37.9277	2001
Foot of escarpment – Gentoo penguin colony	4	5	−46.6128	37.9394	2008
Foot of Vaalkop	5	4	−46.6044	37.9158	2008
Hope Stream	6	5	−46.6081	37.9248	2001
Near Hope Stream	7	5	−46.6090	37.9281	2001
Cave Bay	8	21	−46.6421	37.9971	1965
Marion Island					
Kaalkoppie	9	4	−46.9138	37.5990	2007
Kaalkoppie - Kampkoppie	10	2	−46.9086	37.6009	1975
Kampkoppie	11	4	−46.9038	37.6013	1965
Base to Rockhopper Bay	12	19	−46.8703	37.8565	1975
West Goney Plain's Lake	13	12	−46.8425	37.7830	1975
King Penguin Bay	14	7	−46.8410	37.8003	1965
Piew Crags (inland)	15	1	−46.8877	37.8077	2018
First of Three Sister Hills	16	4	−46.8642	37.8216	2018
Ship's Cove	17	13	−46.8561	37.8437	1965
Skua Ridge	18	2	−46.8616	37.8487	1975
Rockhopper Bay	19	21	−46.8700	37.8571	1975
Gentoo Lake - Trypot Beach	20	1	−46.8814	37.8636	1965
Trypot Beach 1 (2018)	21	9	−46.8846	37.8687	1965
Trypot Beach 2 (2016)	22	23	−46.8846	37.8687	1965
Trypot Beach 3 (2009)	23	22	−46.8846	37.8687	1965
Trypot Beach – Macaroni Bay	24	1	−46.8908	37.8702	1975
East Cape	25	2	−46.9006	37.8977	2007
Middelrooikop	26	1	−46.9382	37.8100	2018
Kildalkey Bay	27	4	−46.9653	37.8471	1965
Black Haglet Valley	28	1	−46.9469	37.8029	2007
Watertunnel Stream	29	1	−46.9505	37.7799	2007
Santa Rosa Valley - East	30	3	−46.9627	37.7246	2007
Grey-Headed Alb. Ridge - Hut	31	1	−46.9618	37.7085	1975
Santa Rosa Valley - West	32	1	−46.9629	37.7099	1975
Grey-Headed Albatross Ridge	33	13	−46.9620	37.7074	1975
Goodhope Bay	34	2	−46.9625	37.6893	1975

Notes: The sources for the minimum residence time (i.e., year of establishment) are based on previous reports: Huntley, 1971; Gremmen, 1975; Bergstrom & Smith, 1990; Gremmen & Smith, 1999; Ryan et al., 2003; le Roux et al., 2013

on Marion Island, was sampled across three different years (2009, 2016 and 2018; populations 23, 22 and 21, respectively; Figure 1). All sampled populations were georeferenced using a handheld GPS (typically a Garmin eTrex, though models varied). We specifically collected individuals from populations that span a wide range of minimum residence times (i.e., populations discovered from 1948 to 2018; see Supporting Information "Selection of minimum residence times of *Poa annua*" for additional details) based on previous reports (Bergstrom & Smith, 1990; Greene & Greene, 1963; Gremmen, 1975; Gremmen & Smith, 1999; Huntley, 1971; le Roux et al., 2013; Ryan et al., 2003), including the presumed locations of the oldest documented populations on both islands. We estimated the minimum residence time for our populations from an updated data set of le Roux et al. (2013), following the same 30 arc seconds grid cell

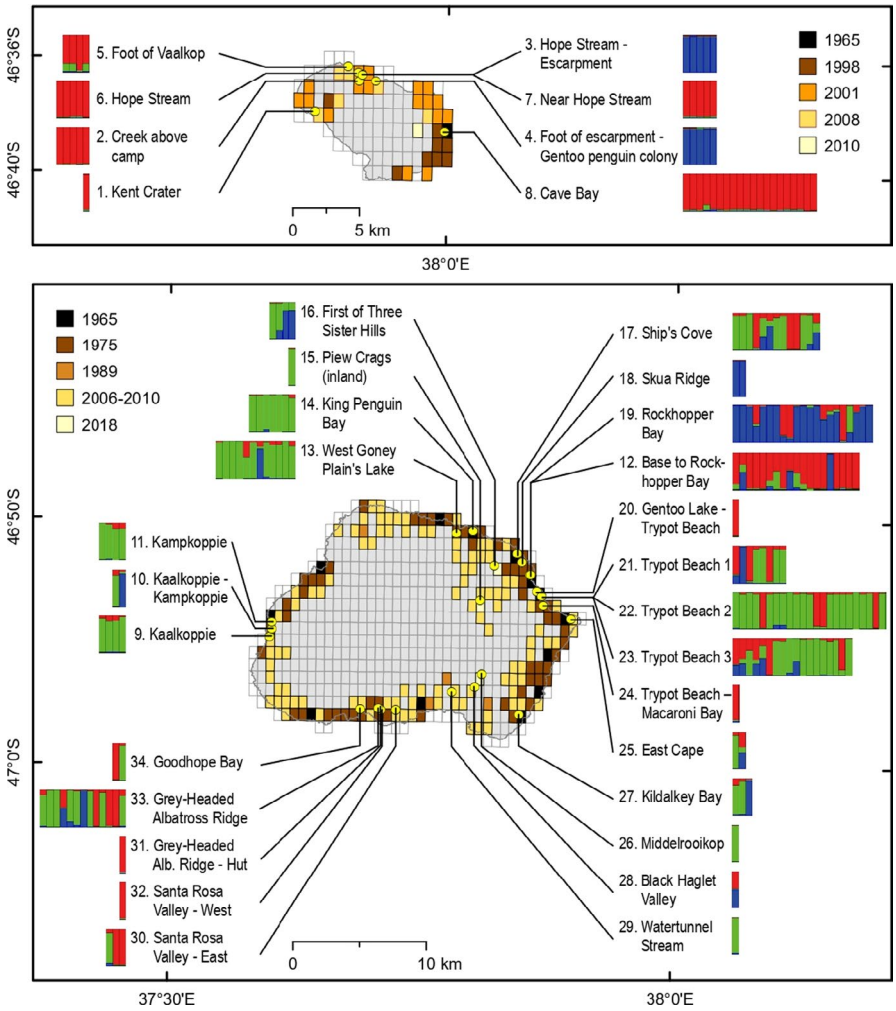

FIGURE 1 Bayesian structure analysis for all sampled *Poa annua* populations from the Prince Edward Islands archipelago (upper panel = Prince Edward Island, lower panel = Marion Island). Population numbers follow Table 1. Barplots show assignment values of individuals where different colours represent the proportion of an individual's membership to each of the inferred genetic clusters. Grid cells show the minimum residence time at a 30 arc second resolution following le Roux et al. (2013), complemented with our own observations. Map projection: Transverse Mercator

resolution. Based on these data and previous reports, we sampled populations with the following minimum residence times: 1948–1966 (n = 9), 1975 (n = 10), 2001 (n = 4), 2007–2008 (n = 8), 2018 (n = 3). In 2018, samples were taken from single individuals or small populations (<5 individuals) along footpaths or around nesting areas of birds. All collected material was dried and stored on silica gel until DNA extraction.

2.2 | Ploidal variation

Although *P. annua* is generally considered to be an allotetraploid, several different ploidal levels have been reported for the species (Mao & Huff, 2012). We therefore first estimated genome size variation within sampled populations prior to genetic analyses using flow cytometry. Flow cytometric analysis followed the procedure of Galbraith et al. (1983) using Otto's buffers (Doležel & Göhde, 1995; Otto, 1990). In all cases, we only accepted peaks that were clearly identifiable from background noise. DNA indices were calculated for all samples by dividing the relative fluorescence of the G0/G1 peak of *P. annua* accessions with the relative fluorescence of the G0/G1 peak of our internal standard, *Pisum sativum* cv. Ctirad (2C = 9.09 pg, Schönswetter et al., 2007).

2.3 | Microsatellite genotyping

Microsatellite-containing sequences were identified by Ecogenics GmbH (Balgach, Switzerland). Size-selected fragments from *P. annua* genomic DNA were enriched for nuclear microsatellites using magnetic streptavidin beads and biotin-labelled tri- and tetramer repeat oligonucleotides. The enriched library was sequenced on a Roche 454 platform using the Roche GS FLX Titanium technology (Roche Diagnostics Corporation). This resulted in 861 reads containing microsatellite motifs with at least six tri- or tetra-nucleotide repeat units. Primers were designed for 24 of these loci to test for both ease of amplification and polymorphism. We also included one previously described locus (Poa228; Kindiger et al., 2013). Of these, 13 loci were discarded due to amplification failure in most samples or poor electrophoretic profiles. Primer sequences for the remaining 12 microsatellites are provided in Table S1.

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 Ltd), and all DNA samples were diluted to 10 ng/μl and stored at −80°C until further use. Amplification of microsatellites was

performed in two multiplex PCR reactions (Table S1). All PCR reactions were carried out in 15 µl reaction volumes containing 1.5 µl 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 of annealing (at 60°C for multiplex 1 and at 61.5°C for multiplex 2), 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). Gel capillary electrophoretic separation of amplified fragments was carried out at the Central Analytical Facility, Stellenbosch University (Stellenbosch, South Africa). All microsatellite loci were scored using GeneMarker software (version 2.6.4; SoftGenetics LLC, State College, Pennsylvania, USA) with the LIZ 500 size standard. We applied semi-automatic genotype scoring for each allele, with visual inspections of each sample, following Dewoody et al. (2006), to reduce scoring errors. After this, three more loci were eliminated (Poa5, Poa6 and Poa12) because of low levels of variation or band stuttering.

We evaluated data quality by testing for the rate of meiotic error, the presence of null alleles and homoplasy between isoloci. For this, we analysed genotypes under the assumption of random segregation and assigned alleles to isoloci in POLYSAT (Clark & Schreier, 2017). The algorithm processDatasetAllo indicated significant positive correlations between alleles at locus Poa1. However, we ruled out the possibility of scoring errors at this locus because the positively correlated alleles did not have similar amplicon sizes (tetranucleotide motif). After scoring of genotypes, some loci (Poa1, −3, −8, −9 and −11; Table S1) were split into two isoloci, resulting in a final data set of 14 loci.

2.4 | Genetic diversity and population structure

Microsatellite loci generally did not show high levels of ploidal variation, and we detected only four individuals with more than four alleles per locus (i.e., tetraploid or higher ploidy). However, fragment-based inferences are not always reliable for detecting differences in ploidal levels since allele dosage can be difficult to estimate from microsatellite markers (Clark & Jasieniuk, 2011). Our population-level flow cytometry analysis indicated the presence of genome size variation, which could be related to ploidal variation (see Results section). However, previous studies on *P. annua* found genome size variation to be unrelated to ploidal variation, and that individual tetraploid populations can show up to 80% variation in genome size (Mowforth & Grime, 1989). Most of our analysed individuals (87.3%) had genome size values conforming to tetraploid cytotypes (see Results). Therefore, we decided to omit data from individuals with uncertain ploidal levels and treated the overall data set as allotetraploid. We used POLYSAT (Clark & Jasieniuk, 2011) to calculate a matrix of genotype dissimilarities using a band-sharing metric and a neighbour-joining tree (Clark, 2019). This approach did not identify individuals that were highly dissimilar from the rest, confirming the prevalence of tetraploid individuals in our data.

We also used POLYSAT to estimate genetic diversity metrics and population genetic differentiation. This program allows analyses of microsatellite data of any ploidal level, and assumes that allele copy number is ambiguous in partial heterozygotes (Clark & Jasieniuk, 2011). We used POLYSAT to calculate the number of alleles (N_A) and genotype diversity statistics based on genotype frequencies using Shannon and Simpson estimates (Shannon & Weaver, 1963; Simpson, 1949) and to determine the genetic differentiation between different populations as fixation indices (F_{ST}). We decided not to analyse presence/absence of alleles, due to the loss of information using this approach.

To explore the genetic structure of *P. annua* populations, we used Bayesian assignment tests implemented in STRUCTURE v2.3 (Pritchard et al., 2000) and pairwise distance matrices based on Bruvo distances to perform principal coordinate analyses (PCoA) for: (i) all populations from the PEA, (ii) populations from Prince Edward Island only, and (iii) populations from Marion Island only. For these analyses, we used an admixture model with correlated allele frequencies among groups. We ran 500,000 Markov chain Monte Carlo iterations after a burnin of 100,000 iterations for *K* values (i.e., number of genetic clusters) between 1–15, with 15 iterations for each value of *K*. The most probable value of *K* was determined using the Delta-K method of Evanno et al., (2005) as implemented in STRUCTURE Harvester (Earl, 2012).

We also calculated an admixture index (H_A) using a standardised version of the Shannon–Wiener diversity index (see Keller & Taylor, 2010, for details) for each individual, as:

$$H_A = \frac{-\sum_{i=1}^{n}\left(f_i ln(f_i)\right)}{ln(n)}$$

where f_i is the fractional assignment of an individual to STRUCTURE-identified genetic cluster *i* and *n* is the total number genetic clusters. We did this for the assignment results of the Prince Edward Island, Marion Island, and the PEA analyses.

We assessed the fit of quadratic and linear models for relationships between residence time and genetic diversity metrics (i.e., allelic richness and admixture indices). In all instances, delta-AIC values indicated that quadratic models did not significantly improve model fitting over linear models (χ^2 =3.841, p >.05). After checking for linearity and homoscedasticity in our data using residual and quantile-quantile plots (Figure S3), we ran generalised linear models with gamma distributions in R (R Core Team, 2020) to test for the effects of minimum residence time on allelic richness and levels of admixture. We also ran models using 1975 as the baseline date to calculate minimum residence time for populations presumed to be older than the date of the first systematic survey of *P. annua*'s distribution on the PEA (Gremmen, 1975).

To quantify the partitioning of genetic variance, hierarchical analyses of molecular variance (AMOVA) were performed using Poppr v2.8.3 (Kamvar et al., 2014) for Prince Edward Island, Marion

Island and the PEA. We considered (i) the populations on each island separately, (ii) the genetic clusters identified by STRUCTURE for Prince Edward Island, Marion Island, and the PEA and (iii) populations grouped by considering the main topographic barriers (e.g., ridges, calderas, etc.) on each island. For the latter we identified three groups for Prince Edward Island: (i) Kent Crater (population 1), (ii) north (populations 2–7), and (iii) Cave Bay (population 8); and four groups for Marion Island: (i) north (populations 12–14, 17–25), (ii) south (populations 27–34), (iii) west (populations 9–11), and (iv) central (populations 15, 16, 26). We used Poppr v2.8.3 to calculate private alleles and to implement a Mantel procedure with 999 permutations. We tested the correlation between population pairwise geographic distances and genetic distances (i.e., isolation-by-distance). We also tested the correlation between footpath distances among populations (measured as pedestrian path distances in Google Earth Pro 7.3.2.577) and genetic distances for Marion and Prince Edward Island separately.

2.5 | Ecological niche modelling

To estimate a reasonable niche for *P. annua*, we modelled its current habitat suitability based on occurrence data obtained from a large geographic range between 10° and 60°S latitude, including southern parts of Africa, Australia and other circum-Antarctic islands, spanning a wide range of habitats. These occurrence records were obtained during fieldwork expeditions to these islands (40 records) and from the Global Biodiversity Information Facility (GBIF; 1,829 records). We relied on two model algorithms for modelling: a general additive model (GAM; Wood, 2011), and a gradient boosting model (GBM; Elith et al., 2008). For absence data, we generated 10,000 random points (weighed against the number of presences) for GAM, while we generated random points equivalent to the number of presence points for the GBM (Chala et al., 2019). For both algorithms, we randomly divided the presence and pseudoabsence data sets in a 3:1 ratio, and used 75% of the data for training the models and the remaining 25% for model validation.

We downloaded 19 bioclimatic variables at a spatial resolution of 30 arc seconds from WorldClim Version 2 for current climate (Fick & Hijmans, 2017), which is approximately 926 × 635 m at the latitude of our study area. The WorldClim data do not overlap perfectly with the coastal zone of the PEA, which includes three of our sampling points and thus these points were not used for modelling. To avoid the confounding effects of variable collinearity, a drawback previously pointed out for WorldClim data in sub-Antarctic island systems (Leihy, Duffy, Nortje, et al., 2018), we filtered out highly correlated variables following Chala et al. (2019) and avoided the use of unreliable variables for Southern Ocean Islands (Leihy Duffy, Nortje, et al., 2018). This led to eight retained variables used for all model runs: mean diurnal range of temperature, isothermality, temperature seasonality, minimum temperature of coldest month, mean temperature of wettest and driest quarters, as well as precipitation of warmest and coldest quarters.

The selected environmental variables and the training data set were used in both algorithms. The GAM modelling was done with the k parameter in the spline smoother function in the mgcv R package set to "3" (Wood, 2011). To obtain the most parsimonious model we dropped variables with no significant contributions one at a time using ANOVA chi-square tests until two consecutive models revealed a significant difference in the proportion of explained variation. For GBM, several models were generated by setting the back fraction and tree complexity level to the default values (0.75 and 2, respectively; Elith et al., 2008), but slightly varying values of learning rates ranging from 0.0001 to 0.05 from the gbm.step function in the gbm package (Ridgeway et al., 2013). This way, the learning rate value that yielded the lowest cross-validation deviance was chosen as the optimal model. This final model was further simplified by removing variables with less significant contributions by setting n.drops to auto in the gbm.simplify function. We then projected the selected models from both algorithms onto emission scenarios. The accuracy of the modelling approach was assessed using the area under the receiver operator characteristic curve (AUC).

Using three thresholding approaches (maximum sum, prevalence and maximum kappa), we produced six binary maps for the current potential distributions of *P. annua* (two algorithms × three thresholds). Maximum sum refers to the probability value of the predicted habitat suitability at which the sum of sensitivity (fraction of correctly predicted presences) and specificity (fraction of correctly predicted absences) are the highest. Prevalence refers to the occurrence rate of a species in the total data set. Maximum kappa threshold refers to the probability value that provides the maximum kappa coefficient (Sor et al., 2017). We stacked these six binary maps and clipped the output to our study area. We then defined habitat suitability classes based on the level of agreement among pixels from these binary maps in predicting habitat suitability localities, such that where more than 60% of the binary maps predict habitat suitability, a locality is considered one with high certainty of suitable habitat (Chala et al., 2016).

3 | RESULTS

3.1 | Genome size variation

Flow cytometry analysis was successful for most of the material collected in 2018, but less so for older material. In total, we obtained reliable 2C genome size estimates for 126 individuals from 27 localities (three from Prince Edward Island and 24 from Marion Island), with DAPI indices ranging from 0.131 to 0.920 (1.191–8.363 pg; Figure S4a, Table S2). Despite this variation in genome size, 87.3% of individuals had indices between 0.305 and 0.364 (2.772–3.308 pg), values conforming to previously published tetraploid genome sizes for *P. annua* in the French sub-Antarctic archipelagos (mean values of 2.952 pg ±0.142 for 2C-DNA; Frenot et al., 1999). Populations from Prince Edward Island had lower genome size values (DAPI: 0.131–0.261; 1.190–2.372 pg), than those from Marion Island (DAPI

≥0.305), except for one individual from Rockhopper Bay (population 19; DAPI =0.149; Figure S4a). Individuals with the highest genome size estimates (DAPI >0.51) were mainly restricted to the Marion Island populations at Trypot Beach and Ship's Cove (Table S2). The analysis of DNA content of nuclei isolated from leaf tissue showed that most of the nuclei were in G0/G1 phase of the cell cycle and formed three dominant peaks in histograms of DNA content (Figure S4b). The mean genome size was significantly lower in Prince Edward Island populations compared to populations from Marion Island (*t* test, t = 9.59, *p* = .00004).

3.2 | Genetic diversity and population structure

For the 225 *P. annua* individuals analysed, we detected 27 alleles in the Prince Edward Island populations and 58 alleles in the Marion Island populations. The average number of alleles per locus was 1.57 (SD = 0.94) for Prince Edward Island populations and 4.42 (SD = 3.44) for Marion Island populations. Allelic richness was significantly lower for Prince Edward Island than for Marion Island (*t* test; *t* = 1.49, *p* = .0005). Overall genetic diversity values (Shannon Index) were 0.35 for Prince Edward Island and 0.62 for Marion Island. We found that minimum residence time significantly affected allelic richness in populations on Marion Island (*t* = 3.49, *p* = .0014) with older populations generally having higher levels of allelic richness. This effect remained significant after we recalculated minimum residence time using 1975 as the baseline date for populations older than the first systematic survey of *P. annua* in PEA (*t* = 3.24, *p* = .0027). Conversely, minimum residence time did not affect levels of admixture in populations on Marion Island, irrespective of baseline date (for 1965 t = 1.489, *p* = .076 and for 1975 *t* = 1.776, *p* = .0883). The Trypot Beach population showed an increase in both diversity and admixture between 2009 and 2018 (see populations 21–23 in Table 2). Overall, older populations also harboured the highest number of private alleles. For example, Cave Bay, the oldest known population on Prince Edward Island, had 11 private alleles and was the only population on the island containing private alleles (Table 2).

Bayesian assignment tests identified the most likely number of genetic clusters as *K* = 3, when including all *P. annua* populations in the model (Figure 2). Analyses of individual islands indicated that Prince Edward Island populations consist of two genetic clusters, and the Marion Island populations of three genetic clusters (Figure 2). Populations from Prince Edward Island showed almost no admixture among the two identified genetic clusters, while Marion Island populations showed high levels of admixture among all three clusters (Figures 1,2). When considering the overall analyses, ~92% of all *P. annua* genotypes from Prince Edward Island had genome assignment values >0.9 to one of the two identified genetic clusters (average H_A = 0.094; Figure 1). On the other hand, on Marion Island only 62% of genotypes had similarly high (i.e., >0.9) assignment values to any one of the three genetic clusters (Figure 1), while admixture indices were significantly higher (average H_A =0.172; *t* test, *t* = −1.855, *p* = 0.021). These differences in within-island admixture were supported by the island-specific analyses, with populations from Prince Edward Island harbouring no admixed individuals, while 53.21% of Marion Island individuals were admixed between the three genetic clusters on it (Figure 2b). Distinct genetic clusters were further supported by our PCoA visualisation of genetic structure (Figure S5). The PCoAs also showed that two Prince Edward Island populations (populations 3 and 4; hereafter the "Scarp group") were clearly differentiated from all other populations, while the rest of the Prince Edward Island populations clustered with older Marion Island populations (Figure S5a). The PCoA including only Prince Edward Island populations further supported this structure (Fig. S5b).

Hierarchical AMOVAs indicated that a large proportion of genetic variation resided among STRUCTURE-identified genetic clusters (61.21% for Prince Edward Island; 25.39% for Marion Island; 40.17% for PEA; Table 3). The higher levels of genetic variation found to reside within genetic clusters on Marion Island (e.g., 58.67% for *K* = 3) are expected for panmictic populations and contrast with the Prince Edward Island populations (e.g., 23.51% for *K* = 2). Low or negative values of variance for the distribution of population genetic diversity according to island geography are indicative of no genetic structure (Cochran, 1977; −29.72% for Prince Edward Island; 6.3% for Marion Island; 7.51% for PEA).

Mantel tests found no significant relationship between pairwise genetic distance and geographic distance for Prince Edward Island, but a significant positive relationship for Marion Island (*r* = 0.2055, *p* = .0003; Figure S6). Similarly, Mantel tests between pairwise genetic and footpath distances found no isolation by distance on Prince Edward Island, but a significant positive relationship on Marion Island (*r* = 0.2419, *p* = .002; Figure S6). When considering all data, we found that some populations from Prince Edward Island had higher genetic similarity to populations on Marion Island than to some populations on Prince Edward Island. For example, the oldest population on Prince Edward Island (population 8, Cave Bay) had highest genetic similarity to various populations on Marion Island (i.e., populations 17, 23, 33). Similarly, the Scarp group on Prince Edward Island (i.e., populations 3 and 4) had highest genetic similarity to Marion Island populations close to the scientific station (i.e., populations 18, 19). Interestingly, older populations generally had lower genetic differentiation despite their geographic isolation, for example, populations 20 and 33 on Marion Island and population 8 on Prince Edward Island. Older populations on Marion Island close to the scientific station (populations 12, 14, 17) showed low genetic differentiation with all other populations. Inland populations on Marion Island (populations 15 and 26) generally had low differentiation with older populations on the island or the populations close to the scientific station (Table S3). The highest genetic differentiation was generally found between the Scarp Group (populations 3 and 4) and all other PEA populations, including neighbouring populations on Prince Edward Island (e.g., populations 2 and 5).

TABLE 2 Genetic diversity indices of *Poa annua* populations included in this study (ordered by island and minimum residence time)

Year	Population number	Population	Number of alleles	Allele diversity	Simpson Index	Shannon Index	Number of private alleles
Marion Island							
1965	17	Ship's Cove	23	1.642	0.830	0.281	0
	23	Trypot Beach 3	35	2.5	0.807	0.405	1
	22	Trypot Beach 2	28	2	0.854	0.278	0
	21	Trypot Beach 1	24	1.714	0.825	0.270	0
	27	Kildalkey Bay	20	1.428	0.810	0.206	1
	11	Kampkoppie	17	1.214	0.917	0.089	0
	14	King Penguin Bay	23	1.642	0.844	0.236	0
	20	Gentoo Lake - Trypot Beach*	16	1.142	NA	0	0
		Average	**23.25**	**1.663**	**0.841**	**0.252**	
1975	18	Skua Ridge*	15	1.071	1.000	0	0
	19	Rockhopper Bay	29	2.071	0.787	0.411	5
	12	Base to Rockhopper Bay	26	1.857	0.825	0.310	1
	24	Trypot Beach – Macaroni Bay	16	1.142	NA	0	2
	33	Grey-Headed Albatross Ridge	29	2.071	0.784	0.374	2
	31	Grey-Headed Alb. Ridge - Hut	15	1.071	NA	0	0
	32	Santa Rosa Valley - West	13	0.928	NA	0	0
	10	Kaalkoppie – Kampkoppie*	18	1.285	0.786	0.148	0
	13	West Goney Plain's Lake	27	1.928	0.772	0.371	2
	34	Goodhope Bay	17	1.214	0.917	0.049	0
		Average	**20.5**	**1.463**	**0.838**	**0.166**	
2006–2010	25	East Cape	17	1.214	0.929	0.049	0
	28	Black Haglet* Valley	15	1.071	NA	0	0
	29	Watertunnel Stream	13	0.928	NA	0	1
	30	Santa Rosa Valley -East	18	1.285	0.897	0.090	0
	9	Kaalkoppie	17	1.214	0.917	0.089	0
		Average	**16**	**1.142**	**0.914**	**0.076**	
2018	16	First of Three Sister Hills*	23	1.642	0.726	0.333	1
	26	Middelrooikop*	17	1.214	NA	0	0
	15	Piew Crags (inland)*	16	1.142	NA	0	0
		Average	**18.6**	**1.332**	**0.726**	**0.111**	
Prince Edward Island							
1965	8	Cave Bay	19	1.357	0.921	0.138	11
2001	2	Creek above camp	14	1	0.9	0.096	0
	3	Hope Stream - Escarpment	13	0.928	0.967	0.035	0
	6	Hope Stream	15	1.071	0.923	0.083	0
	7	Near Hope Stream	14	1	1.000	0	0
		Average	**11.5**	**0.999**	**0.947**	**0.071**	0
2006–2010	5	Foot of Vaalkop	13	0.928	0.958	0.040	0
	4	Foot of escarpment – Gentoo penguin colony	14	1	0.917	0.083	0
	1	Kent Crater	13	0.928	NA	0	0
		Average	**13.3**	**0.625**	**0.625**	**0.041**	

Populations for which all individuals were sampled are indicated by asterisks (*).

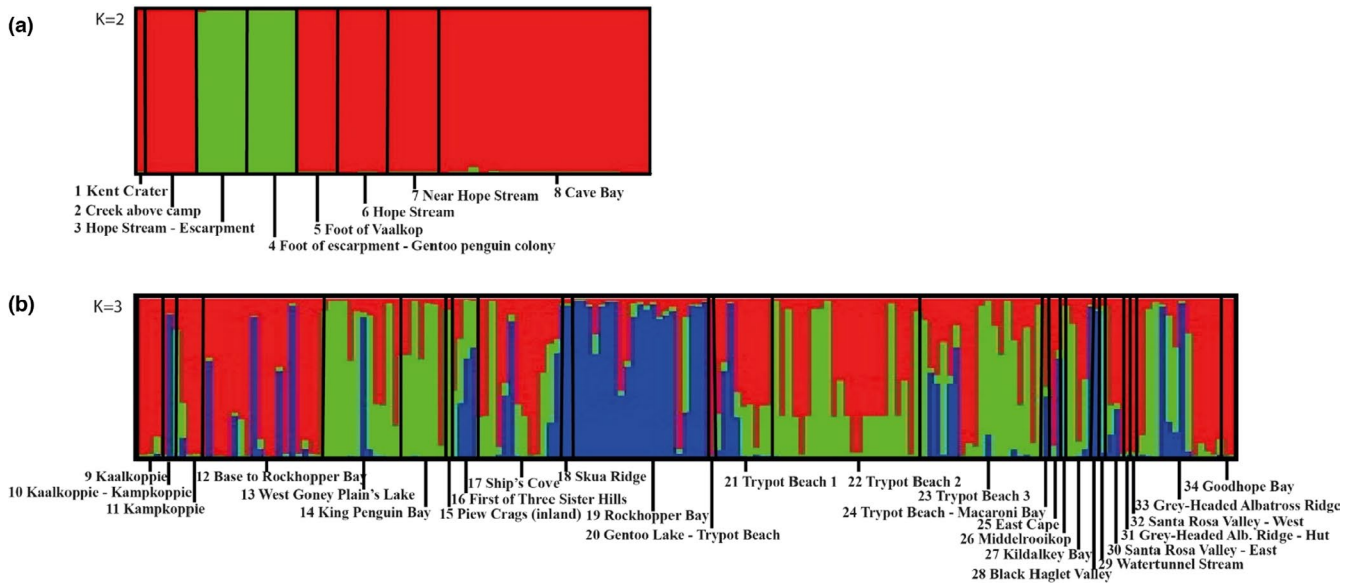

FIGURE 2 Results of the STRUCTURE analyses for (a) Eight *Poa annua* populations on Prince Edward Island and (b) 24 populations on Marion Island. Barplots show assignment values of individuals where different colours represent the proportion of an individual's membership to each of the inferred genetic clusters

3.3 | Ecological niche modelling

Our models had high performance (AUC >0.97). Although most of the occurrence records of *P. annua* were confined to coastal areas, our model showed that almost the entire PEA (>90% of landmass) is suitable to *P. annua* under current climate conditions (Figure 3). In this way, a substantial mismatch might exist between the realised niche (current actual distribution) and the potential niche available to the species. Importantly, the model showed that all of Prince Edward Island is climatically suitable for *P. annua*, whereas the interior, higher elevation areas of Marion Island are less suitable for the species (Figure 3). These results should be interpreted with caution for several reasons. First, all predictor variables we used have been interpolated from a single weather station on Marion Island. Second, in high elevation areas on Marion Island, *P. annua* appears restricted to the entrance of bird burrows (Bergstrom & Smith, 1990), suggesting that microsite conditions (e.g., soil nutrients) may restrict the distribution of *P. annua* at high elevations, despite suitable climatic conditions.

4 | DISCUSSION

4.1 | Introduction history of *Poa annua* to the Prince Edward Islands archipelago

In this study we set out to test two hypotheses. First, that a positive relationship between propagule pressure and genetic diversity exists, leading to an expectation that *P. annua* would show higher genetic diversity on the more frequently visited Marion Island than on its less visited neighbour, Prince Edward Island. This expectation was supported.

The high genetic diversity of the Marion Island populations may be related to multiple introductions, or, alternatively, a single introduction from a diverse source (Androsiuk et al., 2019; Genton et al., 2005; Le Roux et al., 2011). In support of multiple independent introductions, we detected three distinct genetic clusters on Marion Island, each showing some affinity with at least one of the oldest populations found on the island (Figure 1, Figure S5; Table 3). We also found that older populations on Marion Island have high levels of genetic diversity and admixture, suggesting that they could have benefitted from the accumulation of genetic diversity from independent introductions, a common phenomenon for many invasive species (Dlugosch & Parker, 2008; Vicente et al. 2021). By contrast, the low genetic diversity and near-absence of gene flow between the two genetic clusters on Prince Edward Island (i.e., an absence of admixture, including in the oldest known populations such as Cave Bay; Figures 1,2), suggests that these populations have resulted from lower propagule pressure and fewer founding individuals. The number of genetic clusters and high level of genetic diversity found in Marion Island populations thus reflect multiple introductions.

Further support for this pattern is found in the relationship between centres of human activity, and genetic diversity and structure on both islands. On Marion Island, the oldest populations of *P. annua* were located in close proximity to human settlements, such as the scientific station, huts and historic sealing sites (Figure 1; populations 17 and 33), while on Prince Edward Island the oldest population was located at Cave Bay (Figure 1; population 8), which is typically the camp site for the few visitors during infrequent visits to the island. We also observed high genetic diversity in older populations linked to human settlements. Moreover, the two genetic clusters on Prince Edward Island were closely related to Marion Island populations near the scientific station (Figures 1,2; Table S3;

TABLE 3 Hierarchical analysis of molecular variance (AMOVA) for *Poa annua* based on microsatellite data at different spatial scales

AMOVA groups	Number of genetic clusters (K)	Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation	Φ Statistics
Prince Edward Island							
STRUCTURE	2	Among groups	1	16.15	0.89	61.21	0.76
		Among populations	6	9.40	0.22	15.27	0.39
		Within populations	43	14.74	0.34	23.51	0.61
Island geography	3	Among groups	2	5.77	−0.25	−29.72	0.59
		Among populations	5	19.78	0.74	88.98	0.68
		Within populations	43	14.74	0.34	40.74	−0.29
Marion Island							
STRUCTURE	3	Among groups	2	20.66	0.17	25.39	0.41
		Among populations	44	33.00	0.10	15.93	0.21
		Within populations	124	48.82	0.39	58.67	0.25
Island geography	4	Among groups	3	5.89	0.04	6.30	0.27
		Among populations	22	29.37	0.13	21.08	0.22
		Within populations	145	67.23	0.46	72.61	0.06
PEA							
STRUCTURE	3	Among groups	2	34.37	0.26	40.17	0.56
		Among populations	43	29.14	0.10	16.01	0.26
		Within populations	146	41.55	0.28	43.80	0.40
Prince Edward Island, Marion Island	2	Among groups	1	5.97	0.04	7.51	0.35
		Among populations	32	45.52	0.17	27.92	0.30
		Within populations	188	73.14	0.39	64.56	0.075

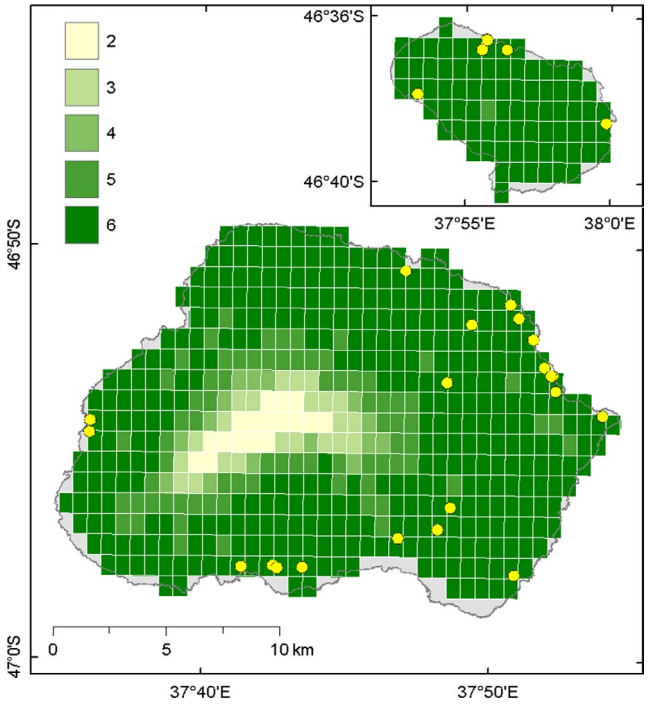

FIGURE 3 Habitat suitability map for *Poa annua* under current climate conditions obtained by overlaying six binary habitat suitability maps. The grid cell colour depicts the suitability range from highest (dark green) to lowest suitability (cream) and are based on a 30 arc second grid (white mesh). Numerical values indicate the number of binary maps predicting a suitable habitat for the respective grid cell. Occurrences included in the habitat suitability model are shown as yellow points. Map projection: Transverse Mercator

Figure S5), suggesting that these populations acted as sources for Prince Edward Island invasions.

Genetic markers with rare or private alleles, such as microsatellites, are especially sensitive to founder events (Dlugosch & Parker, 2008; Spencer et al., 2000). On Prince Edward Island we found 11 private alleles in the oldest known population (Cave Bay, the usual human entry point to the island), while we found no additional private alleles in populations elsewhere on the island. The two highly structured genetic clusters on Prince Edward Island (Figures 1,2) further suggest that at least two independent introductions have occurred from Marion Island.

In sum, the genetic diversity and genome size variation on the PEA indicate a history of multiple introductions, followed by secondary colonisation events within the archipelago (Figures 1,2). For example, the Marion Island population at Rockhopper Bay (Figure 1; population 19) showed very close genetic affinity to the Scarp group on Prince Edward Island (Figures 1,2; Table S3; populations 3 and 4). By contrast, Rockhopper Bay (population 19) showed higher genetic differentiation with adjacent populations on Marion Island (Figure 1, Table S3).

Propagule pressure and the establishment success of alien species on remote sub-Antarctic islands are correlated with human visitation rates to these islands (Chown et al., 1998; le Roux et al., 2013). On Marion Island, a significant number of alien species continues to reach the island as contaminants of building material, cargo, and clothes (Bergstrom & Smith, 1990; Lee & Chown, 2009), with most new arrivals being first detected around the scientific station (le Roux et al., 2013). This island has been visited by a supply ship at least once a year since 1948, while visits to Prince Edward Island have been rare and subject to strict quarantine measures since 1986 (Cooper & Avery, 1986; Cooper et al., 2009). *Poa annua* is an extremely common ruderal weed of urban habitats, including in Cape Town, South Africa, the usual departure port for voyages to Marion Island (Lee & Chown, 2009). We know that the first collection of *P. annua* on the PEA coincided with the building of the first scientific station on Marion Island by the South African research team in 1948 (Greene & Greene, 1963; Greve et al., 2017; le Roux et al., 2013), suggesting that it may have been introduced from Cape Town. It is also possible that *P. annua* reached Marion Island before 1948 (Chown & Froneman, 2008), being introduced inadvertently by whalers and sealers, as was the case for most other sub-Antarctic islands (Frenot et al., 1999; Schenck, 1906).

4.2 | Range dynamics of *Poa annua* on the PEA

Despite the high habitat suitability for *P. annua* on both islands (Figure 3), the species' genetic structure contrasted strongly at the population level between islands: on Marion Island most populations were highly admixed, while on Prince Edward Island this was not the case (Figures 1,2). This provides support for our second hypothesis; that low spatial genetic structure is expected due to frequent human-assisted dispersal, whereas infrequent human-assisted dispersal and consequent slow dispersal of invasive species by natural processes is expected to result in much higher population genetic structure (Wilson et al., 2008).

The genetic structure on Marion Island suggests that populations have been benefitting from frequent anthropogenic disturbance and human-assisted dispersal. By contrast, the genetic structure of Prince Edward Island populations suggests the opposite. On Prince Edward Island, even long-established populations such as the Cave Bay population (minimum residence time >50 years; Bergstrom & Smith, 1990; Ryan et al., 2003), showed no evidence for genetic admixture. This interpretation is supported by previous estimates of dispersal rates for *P. annua* on both islands. On Marion Island the species is spreading ~2.5 times faster than on Prince Edward Island (1.48 and 0.22 km^2/year, respectively), in keeping with the much higher level of human presence on Marion Island (le Roux et al., 2013).

Other vectors such as wind, water, and animals, could also have played a significant role in the spread of *P. annua* between and within the islands (Scott & Kirkpatrick, 2005; Shaw, 2013). Long-distance dispersal of plants by animals, especially birds, has been shown on sub-Antarctic islands (Kalwij et al., 2019; Malfasi et al., 2020; Parnikoza et al., 2012, 2018). *Poa annua* seeds have been found at high elevation at the entrances of petrel burrows and also attached

to the hair of marine mammals (Shaw, 2013), suggesting that animals have further facilitated its range expansion (Bergstrom & Smith, 1990). This may well be the case for the Scarp group (Figure 1; blue genetic cluster on Prince Edward), which is located some 6.4 km from the only area of occasional human presence. Indeed, birds were suggested to have introduced *C. fontanum* to the Scarp area (Bergstrom & Smith, 1990). If birds, wind or water, rather than humans, had been the primary agents of dispersal of *P. annua* in the PEA, then these agents would need to act differently on Marion and Prince Edward Islands in order for the genetic structure observed here to have been generated. This is the case for pelagic birds, to some degree. Invasive terrestrial predators (feral cats *Felis catus* L. (now-eradicated) and house mice *Mus musculus* L.) have reduced avian species richness and abundance on Marion Island, whereas these predators have never been present on Prince Edward Island (Van Aarde, 1979; Berruti, 1981; Jones et al., 2019; Preston et al., 2019). More importantly, however, higher bird abundance on Prince Edward Island should have resulted in lower genetic structure of *P. annua* populations, yet the opposite was observed (Figure 1). In contrast to the findings of Ryan et al., (2003), who undertook no formal analysis for *P. annua* (the work by Gremmen and Smith (1999) which they refer to for information on Marion Island contains no quantitative spread rate data for *P. annua*), the range expansion data of le Roux et al., (2013) suggest that *P. annua* is not spreading more rapidly on Prince Edward Island (0.22 km^2/year) than on Marion Island (1.48 km^2/year). Our genetic data are in keeping with this finding, suggesting that seabird density differences between the islands have little role in differential dispersal rates or variation in genetic structure of *P. annua* between the two islands.

Residence time may also affect population genetic structure, whereby long-established populations may acquire higher genetic structure than more recently-established populations, an expectation not supported by our findings. Heterogenous climate conditions in the invasive range may also cause strong population genetic structure to develop in invasive populations (e.g., Cao et al., 2019). This is unlikely to be the case for *P. annua* in the PEA as Marion Island and Prince Edward Island have highly similar climate conditions (Chown & Froneman, 2008; Leihy, Duffy, Nortje, et al., 2018). Moreover, *P. annua* is mostly restricted to disturbed areas around huts and along footpaths on Marion Island (but see Haussmann et al., 2013). Therefore, the primary means of dispersal of *P. annua* is anthropogenic (see also discussion in le Roux et al., 2013).

The difference in admixture between islands holds important implications for the ecology of *P. annua*. The general consensus is that genetic admixture between distinct genetic lineages often benefits invasive populations (Smith et al., 2020). Admixture frequently creates novel genotypes, resulting in enhanced performance in the new range and release from environmental constraints (Lavergne & Molofsky, 2007; Smith et al., 2020). Worryingly, this could be aggravated due to the high current suitability of most of the archipelago for colonisation by *P. annua* (Figure 3). The ongoing range expansion of *P. annua* provides an ideal model system to investigate the link between genetic admixture and population dynamics in more detail. Future work, such as common garden experiments, should determine whether a relationship exists between population fitness and genotype composition for *P. annua* on the respective islands.

4.3 | Conclusions

Our work has used a highly unusual opportunity where two closely located sub-Antarctic islands differ substantially in their extent of human activity, to test whether increased propagule pressure leads to higher genetic diversity, and whether historic human activities can be detected from current population genetic structure. We found support for both ideas. Our findings also indicate that preventing further introductions to Prince Edward Island is essential to avoid an increase in genetic diversity, which may result in an increase of *P. annua* abundance. The most important management action is to ensure that no additional seed is introduced or dispersed to both islands through human activity. This would not only reduce genetic admixture, but also mitigate future spread, especially as the islands' climates continue to change and previously unsuitable sites become more susceptible to invasion (Chown et al., 2013; le Roux & McGeoch, 2008).

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AUTHOR CONTRIBUTIONS

M.M., S.L.C., J.S. and J.J.L.R. designed the study. M.M., J.S., J.H.C. and S.L.C. performed sampling of biological material. M.M., J.J.L.R. and Z.M. generated the data. M.M., J.M.K. and D.C. analysed data. M.M., J.J.L.R. and S.L.C. led the writing, with contributions and final approval from all coauthors.

DATA AVAILABILITY STATEMENT

Microsatellite matrix of *Poa annua* has been made available in Dryad (https://doi.org/10.5061/dryad.76hdr7st7).

ORCID

Mario Mairal https://orcid.org/0000-0002-6588-5634
Steven L. Chown https://orcid.org/0000-0001-6069-5105
Desalegn Chala https://orcid.org/0000-0002-8045-6950
John H. Chau https://orcid.org/0000-0002-8913-6451
Cang Hui https://orcid.org/0000-0002-3660-8160

Jesse M. Kalwij https://orcid.org/0000-0002-8685-9603
Bettine Jansen van Vuuren https://orcid.org/0000-0002-5334-5358
Johannes J. Le Roux https://orcid.org/0000-0001-7911-9810

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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