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# Evidence of strong small-scale population structure in the Antarctic freshwater copepod *Boeckella poppei* in lakes on Signy Island, South Orkney Islands

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## Abstract

Environmental conditions were particularly severe during the Last Glacial Maximum, altering the distribution of the Southern Hemisphere biota, particularly at higher latitudes. The copepod *Boeckella poppei* is the only macroscopic continental invertebrate species known to be distributed today across the three main biogeographic regions in Antarctica as well as in southern South America. Signy Island (South Orkney Islands) is a unique location for the study of Antarctic freshwater ecosystems due to its location and geographic isolation; it contains 17 lakes in several low altitude catchments. We conducted phylogeographic and demographic analyses using the *cox*1 gene on 84 individuals of *B. poppei* from seven lakes across Signy Island. We recorded low levels of genetic diversity and a strong genetic differentiation signal between the eastern and western valleys within the island. Phylogeographic structure and demographic inference analyses suggested at least one asymmetrical dispersal event from west to east. Demographic inference detected a strong signal of population growth during the deglaciation process, which may have followed either (1) a strong genetic bottleneck due to a reduction in population size during the last glacial period, or (2) a founder effect associated with postglacial recolonization of Signy Island from elsewhere. The genetic architecture of this island's populations of *B. poppei* shows that historical events, rather than continuous dispersal events, likely played a major role in the species' current distribution. Finally, our study considers possible mechanisms for dispersal and colonization success of the most dominant species in the Antarctic freshwater community.

During the Quaternary, Antarctica underwent a characteristic cycle of slow build-up to full glacial conditions, followed by rapid ice melting and deglaciation to interglacial conditions (Williams et al. 1990). These continuous cycles of expansion and contraction of Antarctic ice sheets resulted in the displacement of terrestrial, freshwater, and shallow marine ecosystems, causing widespread extinction at high latitudes (Bergstrom et al. 2006; Convey et al. 2008, 2009). Environmental conditions were particularly severe during the Last Glacial Maximum (LGM), between 23,000 and 18,000 years before present (YBP), with thicker and more extensive ice sheets covering low-altitude terrain in continental and maritime Antarctica, including the Scotia Arc archipelagos as well as sub-Antarctic South Georgia, Patagonia and parts of New Zealand (Hodgson et al. 2014; Brown et al. 2017).

Several hypotheses have been proposed to explain how these Quaternary glaciations shaped the demography and consequently the genetic architecture of higher latitude terrestrial

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(Bennet et al. 1991; Taberlet et al. 1998; Hewitt 2000) and marine (Maggs et al. 2008; Marko et al. 2010; Díaz et al. 2011; Allcock and Strugnell 2012; Gonzalez-Wevar et al. 2013) biota. They rely upon the expansion–contraction (E–C) model (Provan and Bennett 2008), which describes the response of populations and species to past glacial–interglacial climate oscillations (Taberlet et al. 1998; Marko et al. 2010). According to the basic E–C model, most cool-temperate species survived in lower latitude glacial refugia, only repopulating higher latitudes through range expansion following the LGM (Hewitt 2004). An alternative scenario for the E–C model, "cryptic or in situ refugia", proposes that some populations may have persisted throughout the period of glaciation in suitable high-latitude refugia within the affected area, from which they recolonized the impacted area during deglaciation (Stewart and Lister 2001; Provan and Bennett 2008; Fraser et al. 2014).

This model also gives rise to predictions routinely tested using genetic data. In particular, it predicts that, once habitats became available again during the Holocene, recently colonized higher-latitude populations should retain the genetic signature of a short demographic history, denoting recent population expansion following the loss of genetic variation due to a prior reduction in population size (i.e., genetic bottleneck) and low levels of current genetic diversity (Hewitt 2000, 2004).

Today's continental (i.e. terrestrial and freshwater) fauna are restricted to ice-free area, corresponding to ca. 0.3% of Antarctic continent (Convey 2017) and are currently found predominantly near the coast and to a lesser extent in inland, higher-altitude mountain ranges (nunataks, Newman et al. 2009). The fauna is dominated by small ($\sim$ 200 μm to 5 mm) and inconspicuous invertebrates, usually associated with simple vegetation (lichens, mosses, algae). At least 12 species of Crustacea, including copepods, cladocerans, ostracods, and an anostracan, have been reported from freshwater lakes of the Antarctic continent, Antarctic Peninsula, and the maritime Antarctic South Shetland Islands and South Orkney Islands (Pugh et al. 2002; Gibson and Bayly 2007; Dartnall 2017; Diaz et al. 2019). There has been a long debate about the origin of the Crustacea that inhabit Antarctic lakes. An essential requirement for long-term survival of freshwater fauna on the continent is the continued existence of lakes (Newman et al. 2009). It has been generally considered that during glacial periods the ice-sheet extent wiped out freshwater fauna, implicitly inferring recolonization of Antarctica from extra-continental sources during interglacial periods (Ellis-Evans and Walton 1990; Pugh et al. 2002; Newman et al. 2009). However, the recent discovery that some lakes in continental Antarctica have been in continual existence for upwards of 120,000 years (Hodgson et al. 2005) challenges this paradigm and raises the question of whether any of the fauna currently present survived successive glaciations in situ.

Freshwater invertebrate propagules commonly have impressive resistance capacity and can provide a long-term reservoir capable of persisting through periods of harsh conditions including freezing and drying (Mellors 1975; Marcus et al. 1994; Jiang et al. 2012). These stages can remain viable and become active after months to possibly hundreds of years of dormancy, when appropriate environmental conditions resume (e.g., the earlier observations of Proctor 1964; Jiang et al. 2012). This characteristic is particularly important in extreme and highly seasonal environments such as sub-Antarctic and Antarctic regions. These propagules can potentially be transported by water (hydrochory, Hawes et al. 2007*a*), wind (anemochory, Pugh 2003; Muñoz et al. 2004; Cowie and Holland 2006; Hawes et al. 2007*b*), and animals (zoochory, Pugh 1994; Figuerola and Green 2002), including humans (anthrochory, Pugh 1994). Among these potential vectors, birds have repeatedly been suggested as the most likely biotic-mediated transport, sometimes over very long distances, especially along migration routes (Darwin 1859; Mayr 1963; Valdevenito et al. 1990; Figuerola and Green 2002; Gillespie et al. 2012). All of these vectors of passive dispersal have been suggested to be potentially important for continental biota in an Antarctic context (Hawes 2009).

Several studies have focused on biotic- and abiotic-mediated transport of freshwater organisms or their propagules (Bilton et al. 2001; Figuerola and Green 2002; Bohonak and Jenkins 2003 and the references therein; Havel and Shurin 2004; Muñoz et al. 2004; Cowie and Holland 2006; Rivas et al. 2018). However, relatively few such studies have focused on Antarctic continental ecosystems, including springtails (Hawes et al. 2007*a*; Collins et al. 2019), vascular plants (Fuentes-Lillo et al. 2016; Parnikoza et al. 2018), mosses (Marshall 1996; Marshall and Convey 1997; Pugh 2003), and the freshwater fairy shrimp *Branchinecta gaini* (Hawes 2009). Even though there is a substantial body of evidence supporting passive dispersal in freshwater invertebrates generally, phylogeographic analyses have revealed clear genetic differentiation between geographically close populations in copepods (Marrone et al. 2013), rotifers (Gomez et al. 2000), cladocerans (Cox and Hebert 2001; Hebert et al. 2003; Xu et al. 2009; Ventura et al. 2014), amphipods (Witt and Hebert 2000), and springtails (Liu et al. 2003), suggesting lower levels of gene flow in these groups than previously supposed. The "Monopolization Hypothesis" (De Meester et al. 2002) has provided a potential mechanism which may cause this dispersal-gene flow paradox in lentic habitats. This hypothesis states that the genetic differentiation pattern among neighboring populations is the result of founder and priority effects, with rapid local adaption and monopolization of resources by the early arriving individuals reducing the establishment success of new colonizers. Therefore, a complete understanding of the underlying mechanisms of dispersal and colonization success, with particular attention to the role of passive vectors and ecological-evolutionary priority effects during the colonization of freshwater habitats, is yet to be achieved (Pantel et al. 2015; De Meester et al. 2016; Viana et al. 2016*a*, 2016*b*).

Signy Island (60°43′S, 45°38′W; Fig. 1) is a relatively small island with a total area of about 20 km$^2$, length (from north to south) of 8 km, maximum width of 5 km and greatest elevation

of 280 m (Holdgate 1967). It is located in the South Orkney Islands south of the Antarctic Polar Front within the maritime Antarctic (Holdgate 1977; Convey 2017) and was highly impacted during Quaternary glaciations (Hodgson et al. 2014). Marine geomorphological mapping obtained from the South Orkney Islands plateau provides evidence of an expanded ice cap, which may have completely covered Signy Island during the LGM (Sudgen and Clapperton 1977; Herron and Anderson 1990; Smith 1990). A minimum age for onshore deglaciation inferred from the onset of lake sediment accumulation is between 7292 and 7517 YBP (Hodgson et al. 2014). The South Orkney Island archipelago is remote from the other Scotia Ridge archipelagos (South Georgia, South Sandwich Islands, and South Shetland Islands). Approximately 32% of the island is currently glaciated, mainly at higher altitudes (above 200 m). The island has 17 lakes in the valleys and plains of its coastal lowlands, which are usually seasonally snow- and ice-free and lie within a small area which is geologically and climatically homogeneous (Heywood et al. 1980). The presence of aquatic mosses and different types of substrates provides a great diversity of habitats and variation in the community of phytoplankton and zooplankton (Jones 1996). These multiple lakes were the focus of an almost 30-year long and year-round monitoring program between the 1960s and 1990s, meaning that they have arguably the most detailed environmental and biological characterization of any lake systems in maritime Antarctica. With this background, Signy Island represents an exceptional location in the Southern Ocean for examining demographic and genetic hypotheses and represents a unique area for the study of Antarctic freshwater ecosystems.

The freshwater fauna of Signy Island is depauperate, primarily composed of microscopic groups, along with a small number of species of anostracan, cladoceran, and copepod crustaceans (Heywood 1970; Convey et al. 2008). The calanoid copepod *Boeckella poppei* is the only macroscopic terrestrial or freshwater invertebrate species known to be distributed across the three main biogeographic regions in Antarctica as well as southern South America. It is also the most abundant and dominant of the pelagic metazoan species on the island (Heywood 1970; Butler et al. 2005). Paleolimnological studies of lake sediment cores have confirmed the presence of *B. poppei* in the basal sediments of Sombre and Heywood lakes, very soon after the lakes first formed around 5,500 YBP as ice retreated after the LGM (Jones et al. 2000). *B. poppei* exhibits the broadest distribution of any species in the genus (Maturana et al. 2018, 2019), also being reported in lakes of the Antarctic continent (King Charles Mountains, Bayly and Burton 1993; Bayly et al. 2003; Gibson and Bayly 2007; East Antarctic Peninsula, Nedbalová et al. 2009), Alexander Island (Heywood 1977) and northward along the Antarctic Peninsula, the South Shetland Islands, and South Georgia as well as in the southern tip of South America (Menu-Marque et al. 2000; Bayly et al. 2003; Maturana et al. 2018). Jiang (2012) reported the presence of egg banks of *B. poppei* in the sediments of two lakes in the northern Antarctic Peninsula, suggesting that they remained viable after $\sim$ 100 years. In the traditional view of high-dispersal ability in freshwater invertebrates it might be predicted that once habitats become available after deglaciation, *B. poppei* resting stages could have been rapidly transported and colonized new suitable environments. If so, after establishment, populations of *B. poppei* would have expanded across Signy Island without genetic structure. Alternatively, if colonization occurred through founding events and resource monopolization then limited further gene flow, local populations of *B. poppei* may exhibit patterns of genetic differentiation (De Meester et al. 2002). All things considered, *B. poppei* provides a suitable model to infer how historical and contemporary processes have affected the distribution of intraspecific genetic diversity and structure.

The primary aim of this study was to evaluate the mechanisms of small-scale dispersal and colonization success in an Antarctic freshwater species from a phylogeographic and population genetic perspective using samples collected from lakes distributed across multiple water catchments in Signy Island. Additionally, we examined possible drivers shaping the genetic architecture of *B. poppei* across the island and evaluated the possible scenarios of colonization or persistence in refugia in situ during Quaternary glaciation.

## Methods

### Sampling

Individuals were sampled from seven lakes in four valleys on Signy Island (South Orkney Islands, maritime Antarctic; Fig. 2) during the austral summer of 2012/2013. Individuals were collected in shallow water close to the shoreline from eastern lakes: (1) Three Lakes Valley: Pumphouse Lake (S60°42.01, W45°36.78), Heywood Lake (S60°41.57, W45°36.56); (2) Paternoster Valley: Sombre Lake (S60°41.27, W45°36.86), Changing Lake (S60°41.48, W45°37.15); and from western lakes: (3) Tranquil Valley: Light Lake (S60°41.95, W45°38.87), Tranquil Lake (S60°42.20, W45°38.81); and (4) Cummins Valley (unofficial name): Twisted Lake (S60°43.29, W45°39.76).

The area of these lakes ranges between 5,000 $m^2$ (Pumphouse and Light lakes) and 41,000 $m^2$ (Heywood lake); their depth typically ranges between 3 and 8 m, with Sombre Lake being the deepest with a maximum depth of 12 m. The range of maximum summer temperature recorded is 1–6°C with constant water temperature throughout the ice-free period (Heywood et al. 1980; Butler et al. 2000). Snow cover is a key factor, since all lakes can freeze to depths of 1–2 m for 8–11 months each year, limiting the level of visible light at the ice–water interface (0.1–20% irradiance) (Heywood et al. 1980). Continuous monitoring of several physicochemical parameters in these lakes has revealed considerable differences in nutrient concentration and phytoplankton abundance related to moss stands, and the presence of birds or seals which enrich their catchment areas and affect the thickness of ice cover throughout the year (Hawes 1983; Butler 1999; Butler et al. 2000). It is worth noting that the topography is particularly

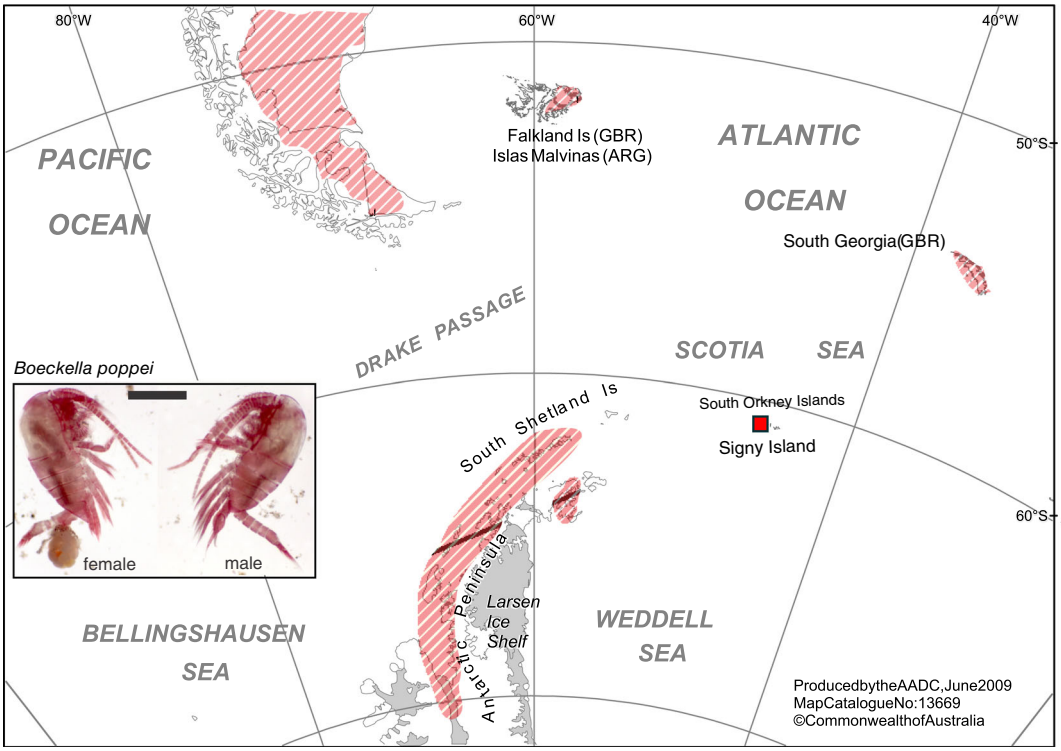


**Fig. 1** Distribution map of *Boeckella poppei* in the maritime Antarctic, sub-Antarctic islands and South America. The geographic position of Signy Island is shown on the scotia ridge map with reference to the wider *B. poppei* distribution (red dashed area). Inset: Photographs of male and female specimens from Antarctica under a stereoscope lens (×3.5). Scale bar represents 0.5 mm.

elevated in Signy Island (up to 278 m) between the eastern and the western lakes, separating these areas by a partially glaciated mountain ridge (McLeod Glacier, Fig. 2).

Whole crustacean specimens were immediately preserved in ethanol (96%) for subsequent morphological and molecular analyses. For taxonomic identification to species level, we observed the diagnostic character in the fifth leg from male specimens (Bayly 1992) under an inverted microscope at ×10 and ×20 magnification. As *B. poppei* is the only species of *Boeckella* in these lakes and females of this genus are structurally very similar (Bayly 1964), females were presumed to be the same species as the males that were identified.

### DNA preparation and sequence editing

DNA was extracted from entire individual specimens using a modification of the DNAeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) protocol for small tissue samples (see Supporting Information Appendix S1). Three DNA loci were amplified, one segment of the fast-evolving mitochondrial cytochrome c oxidase subunit I (*cox*1), and two slower-evolving segments of the 28SrRNA gene and the Internal Transcribed Spacers (*ITS*) 1 and 2. We amplified nuclear genes using previously reported primers for 28SrRNA (Littlewood et al. 2000; Olson et al. 2003) and *ITS* (Presa et al. 2002). Polymerase Chain Reaction (PCR) amplifications were performed separately following each cited reference for thermal cycle and mix protocols. The mitochondrial *cox*1 gene was amplified using specific *Boeckella* primers modified from universal primers LCO1490 and HCO2918 (Folmer et al. 1994), 43F_Boeck 5′-CGAATAGAATTAGGTCAAGC-3′ and 485R_Boeck 5′-GCAAATAAAGGTATTCGATCT-3′. The 25-μL PCRs consisted of 1X reaction buffer (50 mM KCl, 10 mM Tris–HCl, pH 8.0), 1.8 mM $MgCl_2$, 200 mM of each deoxyribonucleotide triphosphate (dNTP), 0.4 mM of each primer, 60 μg $mL^{-1}$ bovine serum albumin (BSA), 1 U Taq polymerase (Invitrogen), 4 μL DNA, and double-distilled water. Thermal cycling parameters used were an initial denaturation step at 94°C for 1 min, followed by 10 cycles at 94°C for 1 min, 40°C for 90 s and 72°C for 1 min, followed by 30 cycles at 94°C for 1 min, 46°C for 90 s and 72°C for 90 s, and a final 10 min extension at 72°C. Sequences were manually quality controlled, examined, assembled, and edited using GENEIOUS 10.2.2 (Kearse et al. 2012). Multiple alignments were obtained using MUSCLE (Edgar 2004) with standard settings. For *cox1*, codon usage was determined using the effective number of codons value (ENC, Wright 1990) from DNASP 5.0 (Librado and Rozas 2009). This statistic has a value between 20 (extremely biased codon usage) and 61 (totally random codon usage). *Cox*1, 28S rRNA, and *ITS* sequences of *Boeckella* were deposited in GenBank under the following accession numbers: *cox*1 (MN087317 to MN087400), 28S (MN088122), and *ITS* (MN088371).

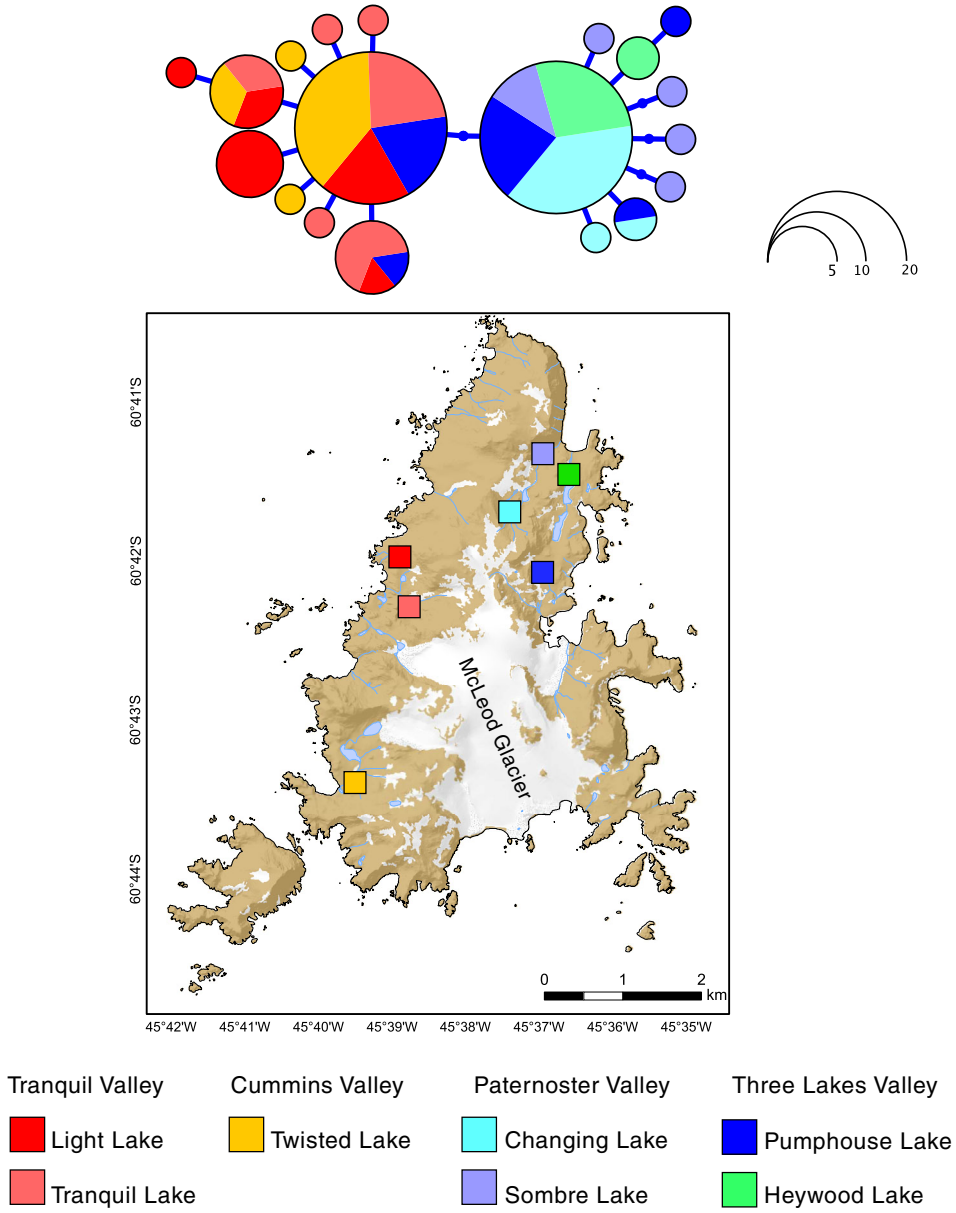


**Fig. 2** Haplotype network in *Boeckella poppei*, including 84 mtDNA *cox*1 across the seven Signy Island lakes. Neighbor-joining network illustrating the distribution of haplotypes in each surveyed lake in Signy Island, South Orkney Islands. Each type of sequence (haplotype) is represented by circles whose sizes are proportional to the frequency of the haplotype in the entire sample. The color key indicates the lake of collection. The map illustrates the geographic positions of the seven lakes across Signy Island. The reference of the size of each circle and their frequencies in the sample size (5, 10, 20) is displayed on the right.

### Genetic diversity and genealogical relationships in *B. poppei*

We characterized genealogical relationships using a neighbor-joining haplotype network with 28S, *ITS*, and *cox*1 data sets in MEGAX (Kumar et al. 2018) and visualized them in Hapview http://www.cibiv.at/~greg/haploviewer. Levels of genetic polymorphism for Signy Island and for each lake were determined using standard diversity indices with the *cox*1 data set, including number of haplotypes ($k$), number of segregation sites ($S$), haplotype diversity ($Hd$), average number of pairwise differences ($\Pi$), and nucleotide diversity ($\pi$). Statistical tests for neutrality (Tajima's $D$ and Fu's $F_S$) were performed for the whole *cox*1 data set using DNASP v5.10.01 (Librado and Rozas 2009). Although we have unbalanced samples from the lakes, we used Contrib v1.02 (Petit et al. 1998) to obtain the allelic richness (hereafter called R) after rarefaction.

**Spatial genetic structure and gene flow**

We estimated the levels of genetic differentiation between the localities analyzed using mean pairwise differences ($\Phi_{ST}$) and haplotype frequencies ($F_{ST}$) using the *cox*1 data set in ARLEQUIN v3.5.2.2 (Excoffier and Heckel 2006). We also measured genetic differentiation using the nearest-neighbor statistic ($S_{nn}$) in DNASP v5.10.01 (Librado and Rozas 2009). This statistic is a measure of how often the "nearest neighbors" (the most genetically similar sequences) are from the same locality in geographic space (Hudson 2000). To test statistical significance of differentiation, we performed a permutation test (20,000 iterations). The $p$ value for pairwise $\Phi_{ST}$ and $F_{ST}$ between populations was corrected using false discovery rate (FDR) correction (Benjamini et al. 2005). Two different clustering methods were used to determine the spatial genetic structure of *B. poppei* in *cox1*. First we estimated the number and the composition of genetic units and the spatial boundaries among them using GENELAND (Guillot et al. 2005), a Bayesian model in the R environment (R version 3.3.4). The geographic information is considered a prior, so clusters that are spatially structured are considered more likely than clusters randomly distributed in space. Analyses were run using $50 \times 10^6$ Markov chain Monte Carlo (MCMC) iterations sampled every 1000 steps. The initial 10% of parameter values were discarded as burn-in. A maximum number of clusters ($K = 7$) was run to estimate the parameters of the model and posterior probabilities of belonging to a specific group. Second, we conducted an analysis of molecular variance (AMOVA) in Arlequin v3.5 (Excoffier et al. 2005) to estimate the proportion of genetic variation explained by partitioning lakes into western and eastern groups. This analysis characterizes spatial genetic structure by partitioning the variance within populations, among populations within groups and among groups.

While $F_{ST}$ can provide information regarding the distribution of current alleles within and among populations, it ignores the underlying gene genealogy and assumes that sharing of alleles is caused exclusively by recurrent gene flow (i.e., gene-flow and genetic drift equilibrium assumption; Marko and Hart 2011). We used the nonequilibrium population genetic approach to evaluate intensity and direction of migration, analyzing *cox1* using the coalescent-based method implemented in $IM_A2$ software v.3.5 (Hey and Nielsen 2007). To estimate the best set of priors that ensure mixing and convergence of parameters, we carried out several preliminary runs in the MCMC mode of $IM_A2$. All analyses were run using the Hasegawa-Kishino-Yano (HKY) substitution model previously estimated by jModeltest v2 (Darriba et al. 2012). Chain length ranged from 50,000,000 to 150,000,000 generations, until convergence was achieved. Chains were sampled every 100 generations with the first 10% discarded as burn-in. After reaching convergence, we used the same simulated genealogies in the L-mode (Load Tree Mode) of the full isolation-with-migration model to calculate the log maximum-likelihood and credibility intervals based on the 95% highest posterior density (95% HPD) for each of the six demographic parameters. The significance of the migration pattern was estimated using a likelihood ratio test (LRT; Nielsen and Wakeley 2001). To rescale the splitting time of east and west haplogroups into years, we calculated $t/\mu$ ($\mu$ as substitution rate). We also explored the impact of using two different substitution rates on the estimated historical divergence time. First, we used a conservative phylogenetic substitution rate estimate reported for crustaceans ($\mu$ = 1.5% per million years; Lessios 2008; Knowlton and Weight 1998; Schubart et al. 1998) and, second, we assumed that this substitution rate was 10 times faster ($\mu$ = 15% per million years), considering the correction for time dependence of molecular

**Table 1** Diversity indices and neutrality tests for *Boeckella poppei* sampled across Signy Island. Hd, haplotype diversity; *K*, number of haplotypes; *n*, number of sequences; S, segregation sites; Π, mean number of pairwise differences; $\pi$, nucleotide diversity; p.a., private alleles; *R*, allelic richness after rarefaction. *$p < 0.0001$.

| Sampling site | *n* | S | Π | Hd | *K* | *R* | $\pi$ | p.a | Tajima's *D* | Fu's $F_S$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Changing | 12 | 2 | 0.333 | 0.318 | 3 | 2.167 | 0.001 | | | |
| Heywood | 8 | 1 | 0.389 | 0.389 | 2 | 1.972 | 0.001 | | | |
| Pumphouse | 14 | 5 | 1.604 | 0.725 | 5 | 3.748 | 0.004 | | | |
| Sombre | 7 | 7 | 2 | 0.857 | 5 | 5 | 0.005 | | | |
| *Eastern lakes* | **41** | **12** | **1.197** | **0.609** | **11** | | **0.003** | **8** | **−1.741** | **−6.169*** |
| Light | 14 | 4 | 1.143 | 0.769 | 5 | 3.748 | 0.003 | | | |
| Tranquil | 15 | 5 | 1.067 | 0.790 | 6 | 4.076 | 0.003 | | | |
| Twisted | 14 | 3 | 0.549 | 0.495 | 4 | 2.769 | 0.001 | | | |
| *Western lakes* | **43** | **9** | **0.979** | **0.729** | **10** | | **0.002** | **8** | **−1.525** | **−5.933*** |
| Total | **84** | **17** | **1.836** | **0.806** | **19** | **4.3495** | **0.004** | - | **−1.323** | **−10.794*** |

*Segregation sites* (S): polymorphic sites. *Mean number of pairwise differences* (Π): mean number of differences between all pairs of sequences in the sample. *Nucleotide diversity* ($\pi$): mean number of nucleotide differences per site between two sequences. *Haplotype Diversity* (Hd): probability that two randomly sampled alleles are different. *Number of Haplotypes* (*K*): number of sequence types in the sample. *Allelic Richness* (*R*): number of alleles after rarefaction.

rate at the population level proposed by Ho et al. (2011). Even though time dependence is still controversial (Emerson and Hickerson 2015; Ho et al. 2015), several studies have provided empirical evidence that phylogenetic mutation rates overestimate the date of recent biogeographic events (Burridge et al. 2008; Ney et al. 2018). For example, in katydid insects the intraspecific calculated mutation rate calibrated with a post-Pleistocene event resulted in a rate of 14.4–17.3% per million years, 13 times the phylogenetic mutation rate (Ney et al. 2018). Such correction has already been implemented in population-based studies of Antarctic organisms (limpets, González-Wevar et al. 2011; algae, Billard et al. 2015; gentoo penguins, Vianna et al. 2017; sea urchins, Diaz et al. 2018).

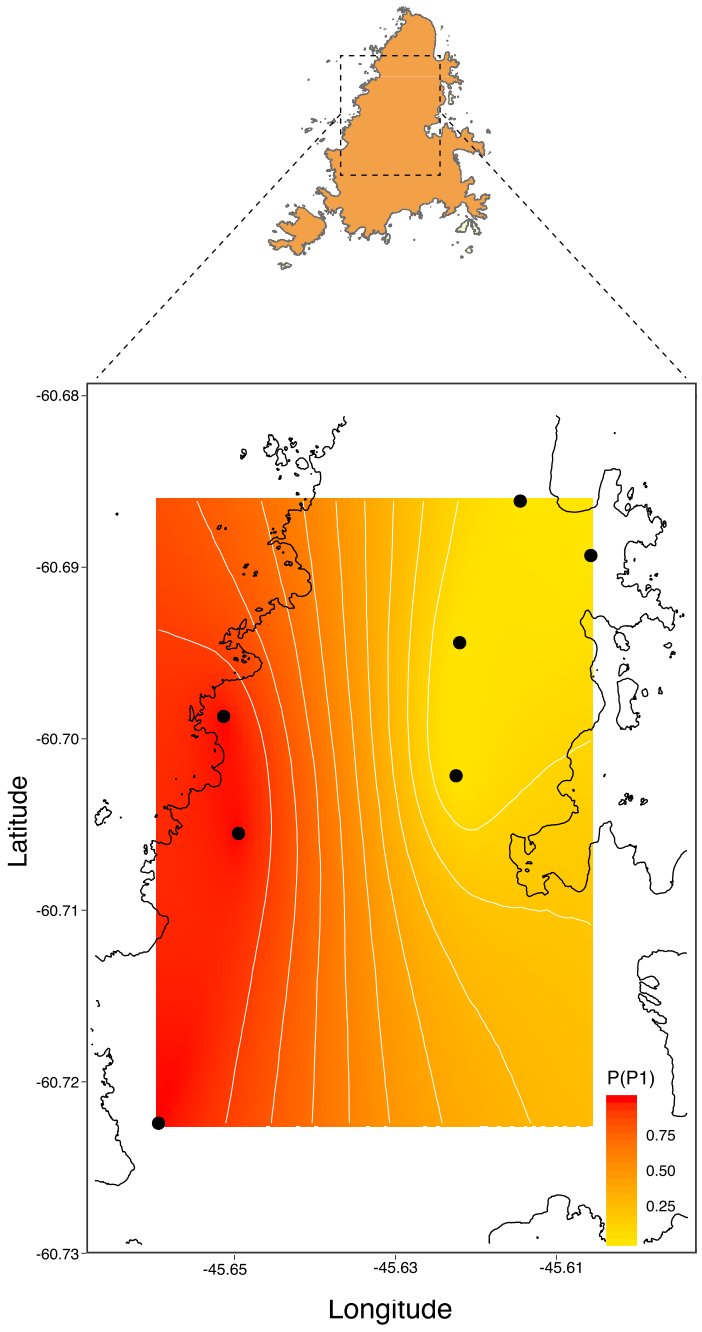


**Fig. 3** Spatial genetic structure from the spatial model in Geneland across the lakes on Signy Island. Higher posterior probabilities of population membership are indicated in red. Black circles indicate the relative position of the sampling localities. Posterior probabilities of membership were plotted with the *shapefiles* of the Signy Island coastline available in the repository in the Antarctic digital database from British Antarctic survey (BAS). https://add.data.bas.ac.uk/

## *Results*

A total of 84 individuals of *B. poppei* were included in our analyses, obtained from seven lakes across Signy Island. The *cox*1 sequence data identified 19 distinct haplotypes and had a total length of 424 bp without insertion/deletion or stop codons. There were 17 variable sites (4%), with 7 (1.7%) being parsimony informative. No evidence for codon bias was detected (ENC = 44.180). Global haplotype diversity (Hd) was 0.806, with substantial variation among both the individual lakes and the different valleys (Table 1). In Three Lakes Valley, Heywood Lake exhibited the lowest diversity in terms of haplotype diversity (Hd) and allelic richness (R) (Hd = 0.389, $R$ = 1.972, $n$ = 8), while Pumphouse Lake showed the greatest diversity (Hd = 0.464, $R$ = 3.748, $n$ = 14), with five haplotypes (Table 1). In Paternoster Valley, Sombre Lake exhibited the highest genetic diversity (Hd = 0.857, $R$ = 5, $n$ = 7 individuals), while the allelic richness in Changing Lake was half of that (Hd = 0.318, $R$ = 2.167, $n$ = 12), despite double the number of sequences being available (Table 1). In Tranquil Valley, genetic diversity was more homogeneous between the two sampled lakes (Light and Tranquil Lakes), while Twisted Lake (Cummings Valley) was less diverse ($R$ = 2.769, $n$ = 14, Table 1).

Median-joining and maximum-likelihood networks of *B. poppei* constructed using the *cox*1 data set identified two haplogroups separated by two mutation steps. The first haplogroup included haplotypes only found in eastern lakes from Three Lakes and Paternoster Valleys (i.e., Changing, Heywood, Pumphouse, and Sombre), while the second haplogroup included individuals carrying haplotypes from western valleys (i.e., Light, Tranquil, and Twisted), but also from Pumphouse Lake from the eastern valley system. Each haplogroup (henceforth referred to as East and West haplogroups) showed well-defined geographic ranges and a typical star-like topology (Fig. 2) with a central haplotype distributed in all the lakes where the respective haplogroup was detected.

For the 28S rRNA (685 bp) and *ITS* (690 bp) dataset, we were able to amplify 50 and 59 individuals, respectively. We did not detect any variation in the studied individuals at those loci, obtaining a single haplotype across Signy Island.

**Table 2** *B. poppei* pairwise difference values calculated among the Signy Island lakes. $F_{ST}$ below the diagonal and $\Phi_{ST}$ above the diagonal. Significant values after multiple comparison testing (FDR) are in bold.

| | | Eastern lakes | | | | Western Lakes | | |
|---|---|---|---|---|---|---|---|---|
| | | **Changing** | **Heywood** | **Pumphouse** | **Sombre** | **Light** | **Tranquil** | **Twisted** |
| Eastern lakes | Changing | – | 0.074 | **0.239** | **0.054** | **0.735** | **0.734** | **0.817** |
| | Heywood | –0.002 | – | 0.197 | 0.049 | **0.713** | **0.705** | **0.807** |
| | Pumphouse | **0.173** | **0.147** | – | **0.162** | **0.337** | **0.315** | **0.372** |
| | Sombre | **0.124** | 0.081 | 0.038 | – | **0.595** | **0.610** | **0.670** |
| Western lakes | Light | **0.446** | **0.398** | **0.138** | **0.193** | – | **0.094** | 0.099 |
| | Tranquil | **0.431** | **0.384** | **0.095** | **0.181** | **0.048** | – | 0.045 |
| | Twisted | **0.589** | **0.550** | **0.181** | **0.357** | **0.128** | 0.074 | – |

**Spatial genetic structure and gene flow**

The Bayesian clustering algorithm detected two main clusters ($K$ = 2). The first cluster included the three lakes from the western valley, while the second cluster included the four lakes from the eastern valley (Fig. Fig. 3). Values of cluster membership were high for all localities (ca. $p$ = 0.99). Mean probability values ($p$ = 0.5) corresponded to the boundary between the East and West clusters, matching the island's ice cap and north–south central ridge that separates these sectors. *B. poppei* displayed strong genetic and phylogeographic structure on Signy Island. The nearest-neighbor statistic ($S_{nn}$) among all localities showed medium to high significance in terms of levels of phylogeographic signal ($S_{nn}$ = 0.3108; $p < 0.0001$). However, when this analysis was performed considering eastern and western lakes, $S_{nn}$ became very high ($S_{nn}$ = 0.866), confirming the strong differentiation between these two areas. Pairwise comparison based on two statistics related to $F_{ST}$ (Table 2) detected significant genetic differentiation ($\Phi_{ST}$ = 0.561, $p < 0.00001$ vs. $F_{ST}$ = 0.269, $p < 0.00001$). Similarly, AMOVA and comparison of pairwise differences also revealed the greatest differentiation between eastern and western lakes (56.06%, $F_{CT}$: 0.561), while differentiation within groups only explained 5.72% ($F_{SC}$: 0.130, $p < 0.0001$) of the total genetic variance.

There are six demographic parameters in the coalescent approach of isolation-with-migration of two populations implemented in $IM_A2$. With these parameters, we can capture many of the phenomena that can occur when one population splits into two (henceforth referred to as splitting event): (1) the timing of the splitting event ($t$); (2) the population size of the ancestral and the two descendant populations ($N_{Anc}$, $N_W$, and $N_E$, respectively); (3) the gene flow during the time since population splitting ($m_E$, $m_W$); and (4) the direction of gene exchange (Hey and Nielsen 2004, Fig. 4). First, the timing of the splitting event for *B. poppei* across Signy Island was estimated at ~ 10,220 years ago (95% HPD 4913–23,484) with 10-fold correction of substitution rate. Using the phylogenetic substitution rate, the splitting time was ~ 102,200 years ago (95% HPD 49,135–235,849). Second, the effective population sizes were estimated for east ($N_E$ = 9,900; range 2,357–29,700), west ($N_W$ = 25,000; range 7390–220,597), and ancestral populations ($N_{ANC}$ = 1572; range 15.72–211,670). Finally, there was evidence of asymmetric dispersal event(s) detected by a low but significant (LRT 5.0, $p < 0.05$) level of migration across Signy Island ($IM_A2$, Fig. 4). Dispersal event(s) would have occurred more from west to east, rather than the other direction, as indicated by the estimation of the number of immigrants per generation ($m_{W\to E}$ = 0.388, $p < 0.05$ vs. $m_{E\to W}$ = 0.003, ns). We note that confidence intervals on all parameter estimates are very broad, reflecting the relatively low genetic variation in the *cox*1 data set.

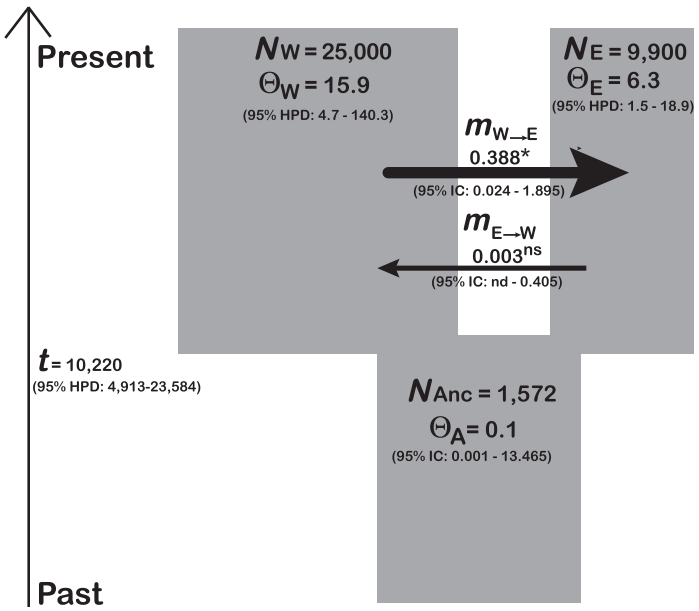


**Fig. 4** Estimated migration rates ($m$) in each direction, effective population size ($N$), and splitting time ($t$) of eastern and western lakes based on the isolation-with-migration model implemented in IMa2. For each parameter, the high point (HP) and 95% HPD of the marginal posterior probabilities are shown. Splitting time was calculated using the corrected substitution rate by ×10 the standard estimate. Significant $m$ values of the LRT are indicated with an asterisk: *$p < 0.05$. ns, nonsignificant; nd, not determined.

## *Discussion*

It is clear that the extent of ice along the Antarctica Peninsula and Scotia Arc was much greater during the LGM and previous maxima than at present (Convey et al. 2008). The impact of these repeated cycles of ice-sheet waxing and waning are expected to be that low-altitude terrestrial and freshwater habitats were periodically displaced (at best) or completely erased (at worst) by covering ice. Possible consequences of these processes include the periodic local and temporal extinction of the associated fauna of these ecosystems, allowing the later colonization of vacant niches, as well as creating opportunities for geographic isolation, genetic structuring, and speciation (Marko et al. 2010; Allcock and Strugnell 2012). Evidence supporting these processes has been shown in studies of Antarctic marine benthic invertebrates (Linse et al. 2006; Allcock and Strugnell 2012), fish (Near et al. 2011), freshwater tardigrades (Cesari et al. 2016), and terrestrial invertebrates (McGaughran et al. 2010; Allegrucci et al. 2012). However, until now, this hypothesis has not been tested in Antarctic freshwater crustaceans.

### Postglacial history of *B. poppei* at Signy Island

*B. poppei* did not exhibit any genetic diversity within either nuclear marker (28S and *ITS*) across Signy island. For mDNA *cox*1, a faster evolving marker, *B. poppei* showed overall low genetic diversity in terms of number of haplotypes and nucleotide diversity, and strong genetic and phylogeographic structure within Signy Island. Such low nucleotide diversity, network star-like pattern, and significant negative Fu's $F_S$ index may reflect recent demographic population growth after either (1) a strong genetic bottleneck due to a reduction in population size during the last glacial period, and/or (2) a founder effect associated with a postglacial recolonization of Signy Island from elsewhere (Taberlet et al. 1998; Provan and Bennett 2008; Marko et al. 2010).

A bottleneck scenario would imply that *B. poppei* survived in refugia in Signy Island, at least during the last glacial cycle. However, lakes on Signy Island are considered relatively young ($\sim$ 7000 YBP), since most of the island was presumably covered by the South Orkney ice cap (Sudgen and Clapperton 1977; Smith 1990; Laybourn-Parry and Wadham 2014). Such a glacial landscape may have restricted the persistence of freshwater ecosystems, and also reduced the possibility that *B. poppei* populations survived the harsh environmental conditions in situ. However, there is evidence that such survival is possible; the freshwater cladoceran *Daphniopsis studeri* survived multiple glacial periods in Lake Reid, East Antarctica, including the LGM (Cromer et al. 2006), with faunal microfossils of dormant or resistant eggs (ephippia) found in a sediment core extending back to ca. 130,000 YBP. Nonetheless, no evidence of *B. poppei* has been recovered in pre-LGM Antarctic lake sediments to date; the species does not occur in the precise location of Cromer et al.'s (2006) study, and pre-LGM sediments are yet to be analyzed elsewhere in the species' range. Further sediment core investigations are required to better understand the survival capacity of this species during glacial periods. A further possibility is that refugial survival could have occurred in epishelf lakes. Studies of the biogeography and morphology of *B. poppei* populations in East Antarctica have provided indirect evidence of long-term presence in situ in epishelf lakes (Bayly et al. 2003; Cromer et al. 2006; Gibson and Bayly 2007). These unusual freshwater lakes lie between the ice shelves and the land mass (Laybourn-Parry and Pearce 2007) and could potentially have provided glacial in situ refugia in the South Orkney Islands, although there is no explicit evidence for this. One of the most plausible aquatic refugia for *B. poppei* in Antarctica suggested to date is Beaver Lake, one of the largest epishelf lakes in East Antarctica (Bayly and Burton 1993; Bayly et al. 2003).

Another—probably more accountable scenario—is the postglacial recolonization of freshwater lakes on Signy Island from less impacted regions within *B. poppei*'s overall geographic distribution (e.g., southern South America) during the Holocene. Under this scenario, long-distance dispersal (LDD) would have played a significant role in shaping patterns of genetic diversity in *B. poppei*. LDD has been described—in particular for terrestrial ecosystems—as resulting from two primary vectors, wind, and seabirds, and its occurrence has been increasingly supported by phylogeographic patterns (Gillespie et al. 2012; Biersma et al. 2017). Intrinsic physiological features of propagules (e.g., resistance to desiccation, salinity, and/or temperature tolerance) contribute to the effectiveness of these vectors as dispersal agents over distances required for such dispersal (e.g., Drake Passage). LDD has been previously suggested for various Antarctic terrestrial invertebrates and plants (Greenslade et al. 1999; Mortimer et al. 2011; Biersma et al. 2018*a*). However, which of these scenarios is the most likely remains to be elucidated, and ongoing phylogeographic analyses across the complete distribution of *B. poppei* will be required to differentiate between these hypotheses.

The phylogeographic pattern of *B. poppei* is strongly structured within Signy Island, with separate clusters in geographically distinct areas explaining almost 60% of the total genetic variation. Even though there is not an "official consensus" for a frame of reference, $F_{ST}$ values above 0.3 are usually interpreted as moderate population structuring (Hartl et al. 1997). Moreover, this population of *B. poppei* displayed disparities between the global differentiation indices measured ($\Phi_{ST} > F_{ST}$), indicating that the differentiation between the eastern and western lake groups has been due mainly to evolutionary divergence between the haplotypes in each region. Following Posada and Crandall (2001), the dominant haplotype is most likely to be the ancestral haplotype. In the case of the western lakes, the ancestral haplotype is also present in individuals from Pumphouse Lake (an eastern lake). Such a genetic pattern may reflect a founder effect from west to east, without any subsequent gene flow after colonization event(s). Alternatively, the

high levels of differentiation could point to two independent colonization events into the eastern and western lakes of Signy Island, with subsequent asymmetrical and occasional dispersal event(s) from west to east. This latter scenario is also supported by demographic analyses, since both east and west clusters showed similar star-like topologies (Fig. 2), suggesting recent (separate) population expansion events in both regions. Bayesian coalescent analyses performed by $IM_A2$ using the 10× corrected substitution rate estimated dates of the divergence between the east and west haplogroups ($t$) matching with the post-LGM deglaciation process on Signy Island ($\sim$ 10,000 y). The analysis also detected significant population growth processes in both areas ($N_W$ and $N_E$) and effectively distinguished low but significant gene flow from west to east ($m_E$, $m_W$, Fig. 4). If the crustacean-derived substitution rate is used, the estimation dates of splitting time will be higher, occurring within the last interglacial ($\sim$ 100,000 y). However, as noted above, the use of phylogenetic mutation rate may overestimate the dates of biogeographic events (Burridge et al. 2008).

**Historical vs. recent dispersal events**

*B. poppei* showed marked genetic structure between eastern and western valleys only separated by a few kilometers. Moreover, there was low, but significant, genetic structure (Table 2) between the lakes within the same valley (e.g., Pumphouse and Heywood Lakes from Three Lakes Valley and Light and Tranquil Lakes from Tranquil Valley) and even within the same catchment (e.g., Changing and Sombre Lakes from Paternoster Valley). This was corroborated by significant differentiation among lakes within valleys (AMOVA, $F_{SC} = 0.130$, $p < 0.0001$). Several other studies (Ellis-Evans and Walton 1990; Gomez et al. 2000; Caceres and Soluk 2002; Hebert et al. 2003; Ishida and Taylor 2007; Thielsch et al. 2009; Xu et al. 2009; Marrone et al. 2013; Tonkin et al. 2014) also recognize the significant role of ecological requirements and recent dispersal in shaping the local/regional distribution pattern of some species. In other members of *Boeckella* from Western Australia (*B. fluvialis*, *B. triarticulata*, *B. minuta*, and *B. symmetrica*), there is evidence of recent dispersal and the colonization of new bodies of water within their geographical range within weeks to a few years after their formation (Maly and Bayly 1991). Analyses of *cox*1 sequences at a broader geographic scale in terrestrial invertebrates have also highlighted strong genetic structure ($F_{ST} = 0.959$, $p < 0.001$) in maritime Antarctic and sub-Antarctic populations in midges (Allegrucci et al. 2012) and in the Antarctic Peninsula and Victoria Land in springtails (Stevens and Hogg 2003; Torricelli et al. 2010; Collins et al. 2019). These studies concluded that this general pattern has been determined by historical dispersal and colonization events over Pliocene and Pleistocene timescales.

To understand the pattern of distribution within a species, it is necessary to consider the extent of historical events, dispersal, and current ecological requirements that have molded them (Endler 1977). Ponds represent naturally fragmented ecosystems, and dispersal between sites is an important process in the dynamics of the freshwater community (Briers and Biggs 2005). There is little evidence to support the idea that the distribution of freshwater invertebrates can be explained by contemporary dispersal at a large biogeographic scale, suggesting that historical dispersal events or survival in refugia are the primary determinants of present distribution in rotifers (Gomez et al. 2000), *Boeckella* (Maly and Bayly 1991) and *Daphnia* species (Hebert et al. 2003; De Gelas and De Meester 2005). In continental Antarctica, the ice-free areas—where most of the lakes are formed—contribute only 0.18% (Burton-Johnson et al. 2016) to 0.44% (Brooks et al. 2019) and are particularly patchy or "island like" (Bergstrom and Chown 1999). Consequently, studies increasingly support the hypothesis of isolation in local long-term refugia coupled with only occasional dispersal events (Allegrucci et al. 2012; Biersma et al. 2018*b*; Collins et al. 2019; McGaughran et al. 2019).

The low (but significant, Fig. 4) and asymmetrical gene flow detected in this study could be the consequence of (1) rare dispersal events within the island, or (2) barriers against the establishment of newly invading individuals in the lake. A literature review indicates that bird-mediated passive transport of propagules of aquatic invertebrates is a frequent process in the field (Figuerola and Green 2002). Signy Island hosts at least 16 breeding species of birds and 21 visitors and vagrants (Rootes 1988). Of the common breeding species, the sheathbills (*Chionis alba*), skuas (*Catharacta* spp.), and gulls (*Larus dominicanus*) are potential transportation vectors since they are very common and spend the most time within the island. Adults skuas nest very close to the freshwater bodies on Signy Island (Rootes 1988), and regularly use the lakes for washing (CM personal observations). Nonetheless, the strong genetic structure detected in our study clearly suggests that birds are not effective vectors for *B. poppei*, and at most may be involved in exceptional dispersal events rather than in the establishment of regular gene flow across Signy Island. Another plausible explanation for the current dispersal pattern, is aerial-mediated transport guided by wind patterns and geographic location (Muñoz et al. 2004; Cowie and Holland 2006; McGaughran et al. 2019; Vega et al. 2019). Wind has been documented or inferred as an effective vector for terrestrial biota in the Antarctic (lichens, Galloway 1987; moss propagules, Marshall and Convey 1997; bryophytes, Biersma et al. 2017, 2018*a*; collembola, McGaughran et al. 2019), and freshwater invertebrates (Rivas et al. 2018). It may also aid the transfer of larger organisms, like moths, from Australia to Macquarie Island (Greenslade et al. 1999) and from South America to South Georgia (Convey 2005). Marshall (1996) documented a dramatic influx event of biological material into the South Orkney Islands from South America, suggesting one possible mechanism of immigration of organisms from more northerly land masses by long-distance dispersal. The prevailing westerly wind at higher southern latitudes, moving from west to east, could therefore underlie the asymmetry of dispersal events on

Signy Island. Finally, exceptional dispersal events may also occur by accidental transport mediated by humans. Human presence has been documented in Signy Island since the early 20th century, when the whaling industry built facilities around Factory Cove (60°43′0″S, 45°36′0″W). The current (originally year-round but now summer-only) research station operated by the British Antarctic Survey (Signy Station) was established in 1947 in the same area. Since then, over the past ~ 70 years researchers studying marine, terrestrial, and limnological ecosystems on Signy Island may have accidentally transported *Boeckella* individuals or eggs in sampling devices or even in personal clothing and effects (Hughes and Convey 2014). Records of *B. poppei* in McMurdo Dry Valleys, Victoria Land (Hansson et al. 2011) and Beaver Lake, East Antarctica (Pugh et al. 2002) have also been suggested as a result of human introduction. However, the harsh conditions and the very strong restrictions for entering the area and visiting these lakes reduce the possibility for invading species to enter the area through human assistance and become established. Additionally, morphological (Bayly et al. 2003) and paleolimnological (Bissett et al. 2005) studies in East Antarctica have shown that *B. poppei* has been present in that area for at least 9000 y.

A further alternative hypothesis explaining postdispersal challenge is the monopolization hypothesis (De Meester et al. 2002). This postulates that a combination of founder effect, rapid local adaptation, and resilience due to large, resting propagule banks derived from local populations buffer against the establishment of newly invading genotypes, thus restricting the extent of gene flow in the face of dispersal events (the "dispersal-gene flow paradox"). This idea provides a theoretical basis to explain the high genetic structure observed between geographically close populations despite the potential for passive dispersal (Gomez et al. 2002; Xu et al. 2009; Marrone et al. 2013; Ventura et al. 2014). Under this hypothesis, the allopatric distribution of the two distinct haplogroups (east and west valley) in *B. poppei* within Signy Island could be explained by colonization of newly available habitat after LGM, combined with rapid local adaptation and monopolization of available resources. Although this hypothesis has been frequently cited, suggesting that monopolization should occur in the field (Loeuille and Leibold 2008; Urban et al. 2008; Urban and De Meester 2009; Vanoverbeke et al. 2016), clear empirical tests are rare (De Meester et al. 2016). However, in this case the physical proximity of lakes and differentiation even within catchments, point to the possibility that this effect may be in play for *Boeckella*.

### Concluding remarks

Our results clearly emphasize the complexity of historical and recent processes, which have molded the genetic architecture of *B. poppei* within Signy Island. The assembly patterns of local genetic diversity in *B. poppei* on the island suggest that successful dispersal between and—in some cases within—the western and eastern lakes are rare events. We also evaluate the potential mechanisms of dispersal and small-scale colonization, and challenge the traditional view of frequent and recurrent passive dispersal for freshwater invertebrates.

Ongoing phylogeographic analyses will be required to delineate the historical biogeography of *B. poppei* across the species' entire distribution and evaluate the alternative scenarios of in situ refugia vs. post-LGM recolonization proposed here. Additionally, parallel genetic studies including more rapidly evolving nuclear markers (e.g., using Restriction site Associated DNA markers sequencing) of the other components of the freshwater crustacean community present in the sub-Antarctic islands and maritime Antarctica (e.g., *Branchinecta gaini*, *Parabroteas sarsi*), will be useful in order to elucidate further the role of Quaternary glaciations in shaping the distribution of the freshwater biota at higher latitudes.

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## Conflict of Interest

None declared.

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