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Dating Antarctic ice sheet collapse: proposing a molecular genetic approach

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Abstract

Sea levels at the end of this century are projected to be 0.26–0.98 m higher than today. The upper end of this range, and even higher estimates, cannot be ruled out because of major uncertainties in the dynamic response of polar ice sheets to a warming climate. Here, we propose an ecological genetics approach that can provide insight into the past stability and configuration of the West Antarctic Ice Sheet (WAIS). We propose independent testing of the hypothesis that a trans-Antarctic seaway occurred at the last interglacial. Examination of the genomic signatures of bottom-dwelling marine species using the latest methods can provide an independent window into the integrity of the WAIS more than 100,000 years ago. Periods of connectivity facilitated by trans-Antarctic seaways could be revealed by dating coalescent events recorded in DNA. These methods allow alternative scenarios to be tested against a fit to genomic data. Ideal candidate taxa for this work would need to possess a circumpolar distribution, a benthic habitat, and some level of genetic structure indicated by phylogeographical investigation. The purpose of this perspective piece is to set out an ecological genetics method to help resolve when the West Antarctic Ice Shelf last collapsed.

Keywords: Antarctic; West Antarctic Ice Sheet; Marine Ice Sheet Instability; interglacial; Eemian; genetic

Introduction

The West Antarctic Ice Sheet (WAIS) lies on bedrock that is mostly below sea level and that slopes downward in the inland direction (Fig. 1) (Fretwell et al., 2013). Mercer (1978) warned that this 'marine ice sheet' configuration may be inherently unstable in a warming climate, with severe consequences: complete melt (collapse) of the marine component of the WAIS would raise global sea level by over 3 m (Bamber et al., 2009). There is not yet a consensus on how quickly such a collapse could occur in response to future global warming scenarios, or on the ocean and atmosphere temperature thresholds required to trigger it (Church et al., 2013; Ritz et al., 2015; DeConto and Pollard, 2016). Determining how the ice sheet responded to past warmer than present climate states can provide an important test for climate and ice sheet models and inform ongoing debate.

Marine diatoms found in sediment samples from beneath the WAIS indicate that major retreat has occurred during the Pleistocene but the dating is insufficient to resolve exactly when (Scherer et al. 1998). Offshore marine records are similarly inconclusive (Scherer et al., 2008; Naish et al., 2009). In particular, it is not known if the WAIS collapsed during the Last Interglacial (LIG; 130,000-116,000 years ago), when global temperatures were around 2°C warmer and sea levels 5.5–9 m higher than today (Dutton and Lambeck, 2012; Otto-Bliesner et al., 2013). To reach the upper bound of the LIG sea level rise estimate a complete WAIS collapse would be required, however the lower end could be accounted for by loss of the Greenland ice sheet (2 – 4m, [NEEM Community Members, 2013]), ocean thermal expansion and loss of small ice caps and glaciers (<1 m) (Dutton and Lambeck, 2012). Attempts to resolve the LIG configuration of the WAIS based on water isotope signals in Antarctic ice cores have so far also failed to resolve the question, with one recent study supporting collapse (Steig et al., 2015) and another arguing that the isotope signal is more readily explained by major sea ice retreat (Holloway et al., 2016). Constraining the magnitude of Antarctic ice mass loss during the LIG has important implications for understanding its contribution to future sea level rise.

Retreat of the WAIS would open seaways (Fig. 2), initially between the Weddell and Amundsen Seas, and in the case of a full collapse, between the Weddell, Amundsen and Ross Seas (Vaughan et al., 2011). In this perspective we argue that genetic exchange through such ancient seaways will be recorded in the genomes of benthic marine species and that genomic techniques therefore offer an independent method to constrain past WAIS configuration.

Marine ice sheet instabilities

Dynamic flow of ice from the WAIS into the ocean is largely controlled by the buttressing effect of extensive floating ice shelves in the Ross and Weddell Seas and smaller ice shelves in the Amundsen and Bellingshausen seas. Ice shelf thinning, caused by warm ocean water melting the ice from below (Shepard et al., 2004), or by surface melt and meltwater percolation from above (Scambos et al., 2000), reduces the back-stress that the ice shelves apply to land ice. A marine ice shelf instability is triggered where the reduced back-stress and resulting increase in the flux of ice from inland causes thinning of the ice at the point at which it begins to float (the grounding line), in turn setting up a runaway process in which the grounding line retreats back inland (Mercer, 1978). An additional destabilising mechanism involves the mechanical collapse of ice cliffs (Bassis and Walker, 2012; DeConto and Pollard, 2016). In regions where fringing ice shelves have been lost and where the grounding line thicknesses exceeds around 800 m, the resulting ice cliff faces cannot be supported by the yield strength of the ice and will collapse, driving ice retreat yet further inland. Meltwater produced by surface melt or rainfall further enhances (through hydrofracturing) both the marine ice sheet and marine ice cliff instabilities (De Conto and Pollard, 2016).

A recent simulation of the Antarctic response to LIG climate conditions finds that the WAIS is highly sensitive to marine ice cliff instability and ocean warming (DeConto and Pollard, 2016). When the model is run with 3°C subsurface ocean warming and the physics of marine ice sheet instability the WAIS remains largely intact and the seaways remain closed (Fig. 2a). When the model is run with the same ocean warming and including the physics of marine ice sheet instability, marine ice cliff instability and hydrofracturing, the WAIS collapses early in the LIG, opening seaways between the Weddell, Amundsen and Ross Seas (Fig. 2c). The dominant factor in WAIS collapse under the revised physics is marine ice cliff instability, which erodes the >1000 m thick marine ice sheets that currently block these seaways. Hydrofracturing is not important during the LIG since temperatures are too low. An intermediate state in which a seaway opens between the Weddell and Amundsen Sea but not through to the Ross Sea is also plausible (Fig. 2b, Vaughan et al., 2011; De Conto and Pollard, 2016). Constraining the configuration of previous WAIS seaways therefore provides a crucial test of ice sheet model physics and assumptions on sub-surface ocean warming relevant to both the past and future WAIS stability.

Current biological evidence for a trans-Antarctic seaway

Collapse of the WAIS has primarily been investigated using geological data and ice sheet modelling, however support also exists for a historic trans-Antarctic seaway from biological data. The community composition of extant bryozoan (Barnes and Hillenbrand, 2010; Vaughan et al., 2011) and gastropod and bivalve (Linse et al., 2006) assemblages have been shown to be more similar between the Weddell Sea and the Ross Sea than other regions around the Antarctic shelf including those in close proximity to these locations that also possess similar ecological conditions. However these studies were limited by small sample sizes and low spatial coverage. In addition, macroevolutionary signals can be misleading in an area such as Antarctica where true distributional data is often obscured by the presence of cryptic species, (i.e. distinct species that unable to be distinguished using morphological characters).

Two early genetic studies revealed hints that there were greater levels of similarity between Weddell Sea and Ross Sea populations, compared to other locations (isopod *Glyptonotus*, Held & Wagele 2005; bivalve *Lissarca*, Linse et al., 2007). However, both studies lacked robust spatial and sample representation, which is necessary to determine whether similar genetic signatures in the Ross and Weddell Seas simply reflect a pattern present throughout East Antarctica (versus maritime Antarctic Peninsula), or rather, are indicative of an historic seaway. A later study that did include samples from East Antarctica identified similar genetic signatures between Weddell Sea, Ross Sea and Amundsen Sea populations of the octopod, *Pareledone* *turqueti*, (Strugnell et al., 2012) with contrasting genetic patterns present at the Antarctic Peninsula region and the Scotia Arc. Although the population genetic signature present from Prydz Bay, East Antarctica, differed from that which was dominant in the Weddell Sea/Ross Sea/Amundsen Sea populations, the sample size (n =3) from this region was too small to be conclusive. Due to limitations in samples size and marker choice, none of these studies have been able to use their data in a hypothesis testing framework to investigate or date historic trans-Antarctic connectivity. Recently, a hypothesis testing framework (Approximate Bayesian Computation) was employed to compare seven historical scenarios of the evolution of the brittle star, *Ophionotus victoriae*, however this study likely included several cryptic species in a single data set, thus lowering their power of detection, and also lacked samples from East Antarctica (Galaska et al., 2016). To date, robust attempts at testing for a trans-Antarctic seaway using molecular genetic methods have not been carried out.

Genomics as a tool for investigating the most recent opening of the trans-Antarctic seaway

Genomic data in extant species contains a record of population genetic processes, past migration patterns and demographic history. Improvements in sequencing technology (massively parallel sequencing) has meant that our ability to sequence genomic data has increased dramatically and the costs of doing so have correspondingly decreased. Recent development in molecular laboratory techniques now allow the same sections of the genome to be sequenced across large numbers of individuals within a population (e.g. RAD-seq, ddRAD-seq, Genotyping by Sequencing [GBS], exon capture etc.) allowing substantial datasets to be constructed that are representative of evolution across the entire genome. These developments, in conjunction with corresponding advances in statistical methods, can now provide powerful insight into the demographic history of species including processes such as migration, population divergence and changes in effective population size.

A range of different approaches have been developed whereby the user can build complex demographic models and provide estimates of parameters within the context of the model in order to investigate demographic histories (Gutenkunst et al. 2009; Excoffier et al. 2013). Several of these methods take advantage of the site frequency spectrum (SFS) which is a useful summary of population genomic data. The SFS is a histogram which shows the distribution of allele frequencies across polymorphic sites. The shape of this histogram, which reflects the proportion of low, medium and high-frequency alleles, can indicate different demographic processes including population bottlenecks, population subdivision and population growth.

Initial methods incorporating the SFS to investigate demographic history were limited to three populations (*dadi*, Gutenkunst et al., 2009) but more recently developed methods using coalescent simulation (e.g. *Fastsimcoal2*, Excoffier et al., 2013) have been developed which enable investigation of a larger number of populations and more complex scenarios. Importantly, these methods permit estimation of divergence of more than three populations and also historical migration. Therefore contrasting evolutionary scenarios that may have given rise to observed patterns of genetic diversity (i.e. SFS) can be compared. The likelihood of alternative models can be compared based using the Akaike Information Criterion (AIC).

The SFS approach has been used to compare complex alternative scenarios incorporating population divergence, expansion and contraction and asymmetric historical migration that have led to present day patterns of genetic diversity in humans (Excoffier et al., 2013; Malaspinas et al 2015), American Aspens (Wang et al., 2016), Lake Victoria cichlids (Meier et al., 2016) and the Hispaniolan solenodon (Turvey et al., 2016) over time frames of a few thousand years to up to 10 million years.

This approach could be used to test alternative scenarios that have led to the patterns of genetic diversity that are present in populations of Southern Ocean marine animals today, including historical connectivity across a West Antarctic seaway (Fig. 1). It is highly likely that a trans-Antarctic seaway occurred ~3 mya in the Pliocene (Naish et al. 2009, Dutton et al., 2015, Pollard and de Conto, 2009) and according to geological data also one or more times during the Pleistocene (Scherer 1998, Scherer 2008, McKay et al. 2012). It remains unclear if a trans-Antarctic seaway existed during the last interglacial period (LIG; 130,000 to 116,000 years ago).

The Fig 2. schematic shows how the demographic approach can be applied to test the last time a trans-Antarctic seaway has opened since the Pliocene (Fig 2a), including whether the opening was during the LIG, and if so it's most likely configuration; Weddell Sea to Amundsen Sea (Fig 2b) or full connectivity between the Weddell Sea, Amundsen Sea and Ross Sea. The genetic approach is powerful because every species investigated represents an independent test of the alternative scenarios. Asymmetric migration could also be incorporated into such models.

The significance of such testing is underlined by recent Antarctic ice sheet modeling of DeConto and Pollard (2016). Their modelling suggests significant ocean warming driving marine ice cliff instability in addition to marine ice sheet instability is required to collapse the WAIS ice sheet during the LIG. Demographic support for connectivity between the Amundsen Sea, Weddell Sea and Ross Sea during the LIG would provide an important test of that model result with implications for the centennial-scale stability and vulnerability to ice shelf and ice cliff instabilities of the WAIS in the future.

Selecting the right experimental design

Not all of the thousands of Southern Ocean species (De Broyer et al., 2011) are suitable for investigating the last date of the WAIS collapse. Appropriate taxa must show a truly circumpolar distribution without any indication of cryptic species, which has been an increasing issue for determining accurate species distributions (Strugnell and Allcock, 2013). To ensure enough power, some degree of phylogeographic structure is required, and panmictic species (i.e. those in which all individuals are potential partners) need to be excluded outright. Initial detection of phylogeographic structure (and also confirmation of a single target species) should be tested via preliminary screening using mitochondrial markers which have been shown to provide a strong indication of species boundaries (e.g. Allcock et al. 2011).

Ideally samples would be obtained from the Weddell Sea, Ross Sea, Amundsen sea and multiple locations from around the Antarctic Peninsula and across East Antarctica. Multiple sample locations either side of the Weddell and Ross Seas are essential in order to be certain that any genetic similarity does not simply reflect present day connectivity.

Reduced representative genomic methods (e.g. ddRAD-seq, GBS) would allow large amounts of data to be obtained. Specifically, target capture based approaches may be advantageous as they provide greater reproducibility across studies and enable the use of samples with degraded DNA (e.g. museum samples). Whole genome resequencing offers even greater power for inferring demographic parameters, (e.g. Li and Durbin 2011; Palamara and Pe'er 2013) but is currently limited in practice by sequencing costs and the need for further theoretical development to take full advantage of the information encoded within this data.

In order to investigate absolute time scales, selected species would require a known generation time and also an estimate of mutation rate (μ). Although the use of outgroup species with fixed divergence times can be used to help calibrate mutation rates, it is understood that substitution rates measured at a phylogenetic time scales can be up to an order of magnitude slower than those estimated at population genetic/phylogeographic time scales (Ho et al., 2005). Therefore caution must be exercised to ensure that mutational rates are assigned at the correct level.

It is worth briefly mentioning approaches with terrestrial taxa. Like marine taxa, determining the dispersal ability of the taxonomic group is challenging and under sampling remains an issue, with many of the relatively small ice-free areas unsurveyed (Convey et al., 2009). The relationship between the underlying physical attributes of the environment and the observed patterns of biodiversity (Terauds et al., 2012; Terauds & Lee, 2016) resulted in the designation of distinct Antarctic Conservation Biogeographic Regions. Although the relationships among those regions are unknown, there is a strong biogeographic discontinuity between the Antarctic Peninsula and continental Antarctica (Gressitt Line, Chown & Convey 2007). For many higher taxonomic groups there is no overlap in species across these two regions, so it is likely that there are few widespread terrestrial candidates to test demographic models.

As with many grand challenges, interdisciplinary and international collaboration will be needed to obtain sample numbers from required locations for target species. However such an approach will provide an independent test of ice sheet models and insights into the sensitivity of the Antarctic ice sheet to past and future climate change.

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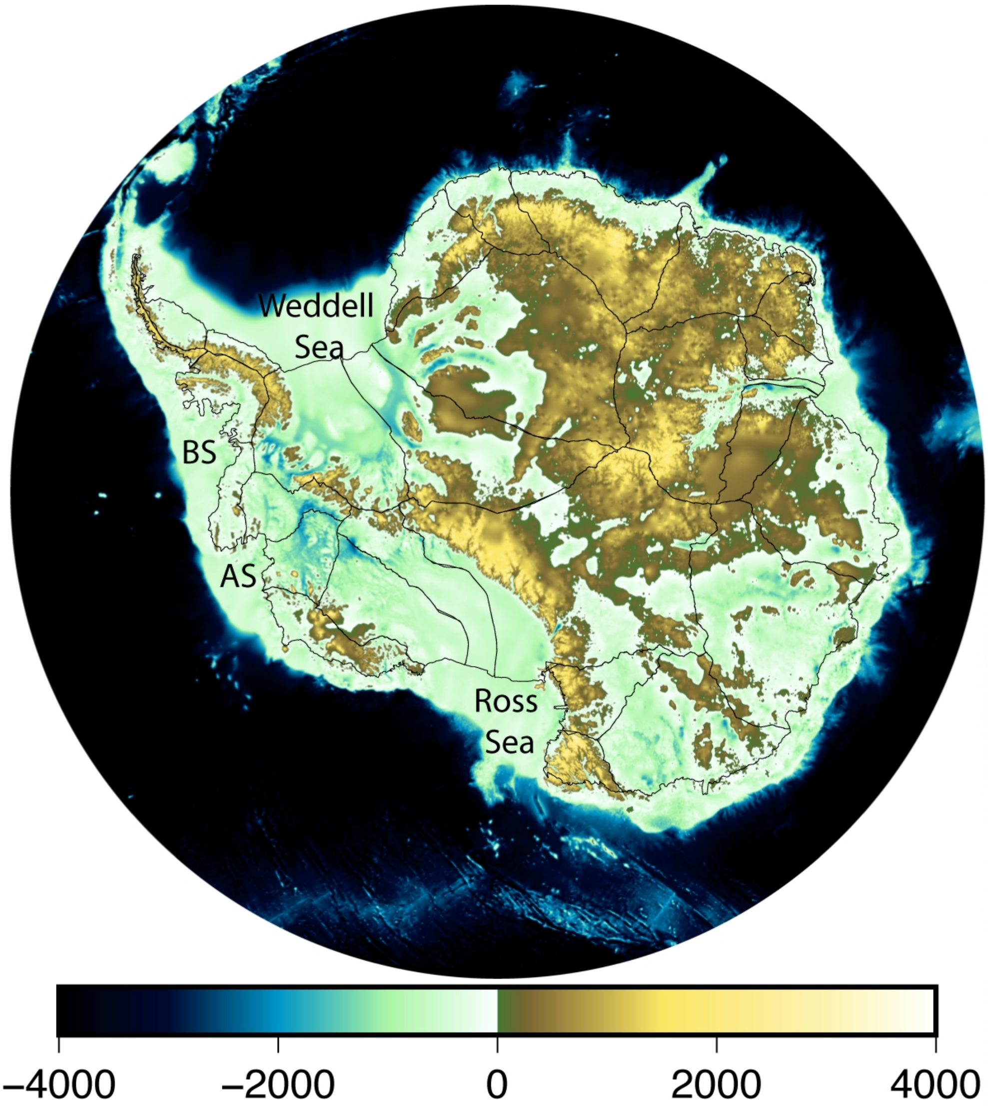
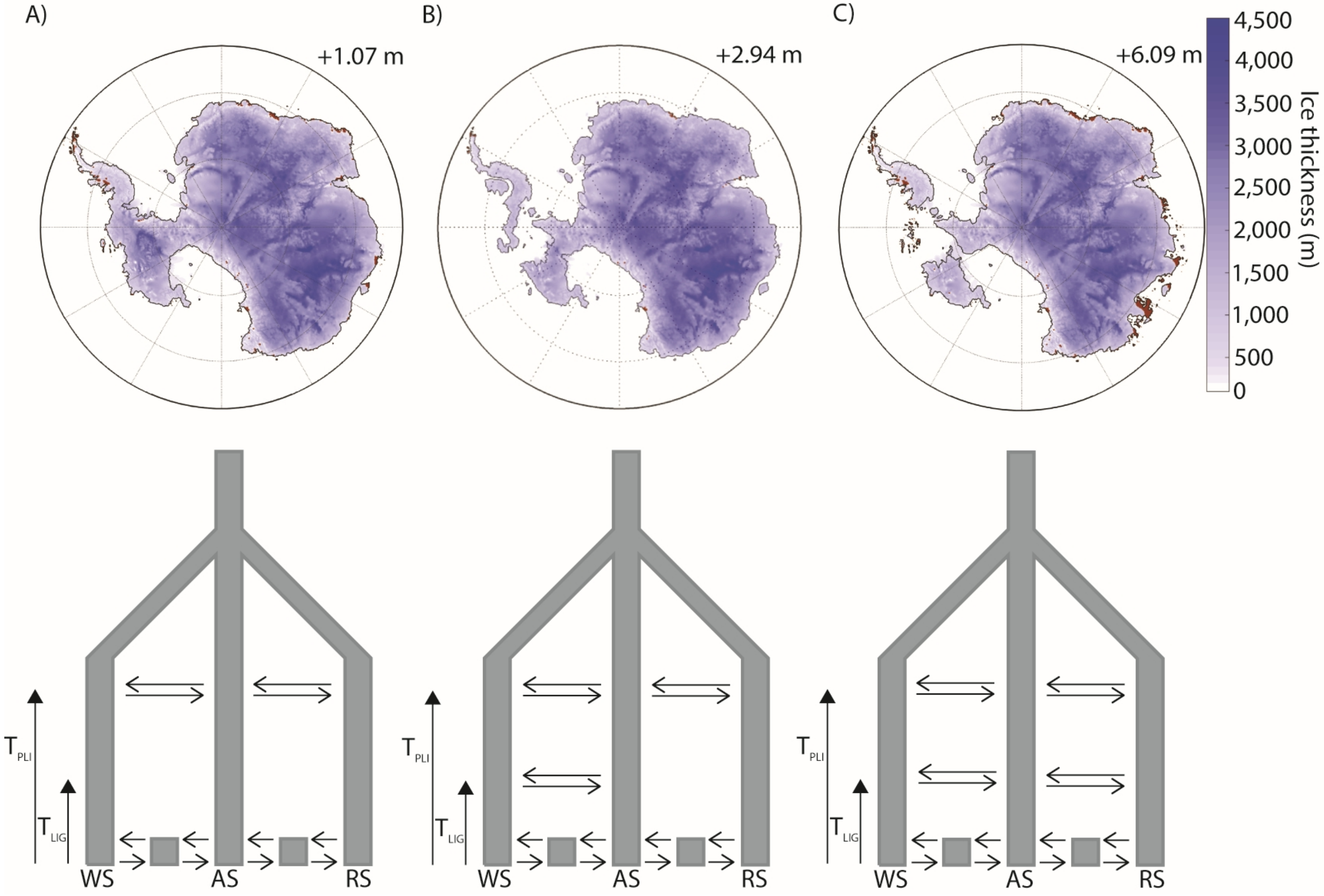
Figures

Figure 1. Antarctic sub-glacial bed elevation (m), from Bedmap2 (Fretwell et al., 2013). Place names mentioned in the text are marked: Amundsen Sea (AS) and Bellingshausen Sea (BS). Figure adapted from Graham et al., (2017).

Figure 2. Possible Last Interglacial (LIG) Antarctic ice sheet configurations (top) and associated demographic models of genetic connectivity through the resulting trans-Antarctic seaways (bottom). All genetic models presented assume WAIS collapsed and trans-Antarctic seaways (two-way arrows) opened between the Weddell Sea (WS), Amundsen Sea (AS) and Ross Sea (RS) during the Pliocene (PLI). Demographic model a) does not allow the seaways to reopen after the Pliocene. Demographic model b) assumes that the most recent opening of trans-Antarctic seaway occurred during the LIG and connected the WS and AS. Demographic model c) as for b) but connecting the WS, AS and RS. The ice thickness maps are adapted from LIG Antarctic Ice Sheet simulations of DeConto and Pollard (2016). Adapted by permission from Macmillan Publishers Ltd: Nature (De Conto, R., Pollard, D., 2016. Contribution of Antarctica to past and future sea-level rise. Nature 531, 591-597), copyright (2016). Map a) shows the maximum LIG ice retreat for a simulation that includes the physics of marine ice sheet instability but excludes the physics of marine ice cliff instability and meltwater enhanced calving. Map c) shows same, but for a simulation including all three of these instability mechanisms. Scenario b) is from a control simulation forced by a 5°C sub-surface ocean warming felt only by the ice sheet. Numbers at the top left of the maps show the change in global mean sea level in response to the ice retreat (including contributions from WAIS and the East Antarctic Ice Sheet).


Weddell
Sea
BS
AS
Ross
Sea
−4000
−2000
0
2000
4000


A)
B)
C)
+1.07 m
+2.94 m
+6.09 m
Ice thickness (m)
4,500
4,000
3,500
3,000
2,500
2,000
1,500
1,000
500
0
T_{PLI}
T_{LIG}
WS
AS
RS