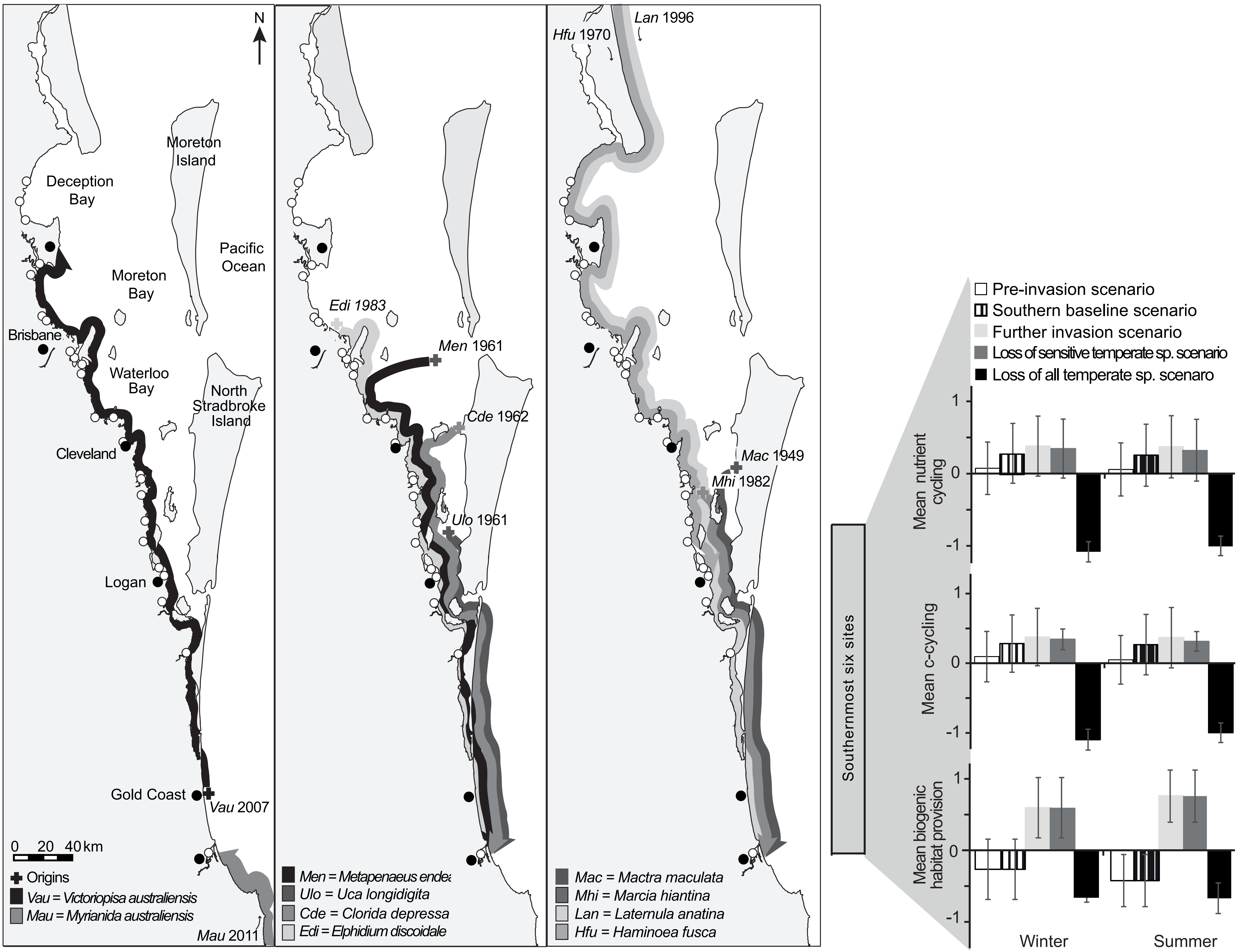

Caswell et al. 2019 Graphical abstract

Influence of climate-induced biogeographic range shifts on mudflat ecological functioning in the subtropics

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Abstract

A growing volume of evidence shows that the broad-scale biogeographic redistribution of species is occurring in response to increasing global temperatures. The present study documents poleward movements of up to eight species of nominally 'tropical' macroinvertebrates (molluscs, polychaetes, crustaceans and foraminifera) from intertidal mudflats on the south east coast of Australia. The speed of movement was comparable with that for Australian marine fauna generally, but was particularly fast for worms and molluscs (~70–300 km decade^{-1}) and may be facilitated by the southward flowing East Australia Current. Further, two temperate taxa appear to have extended their ranges northwards. Changes in species biogeographic ranges raises questions surrounding the response of ecological processes within the altered and novel species combinations, including processes that underpin valuable ecosystem services. Using biological traits analysis to investigate how the observed species range changes might have impacted mudflat ecosystem functioning, and to predict the possible impacts of further poleward movements of tropical taxa. Our models suggest the changes to date, and those likely to occur in the near future, are within the envelope whereby ecological functioning is maintained by functional compensation and redundancy within the mudflat assemblage. However, in the most extreme scenario the replacement of temperate by tropical taxa resulted in major changes in ecological functioning with potential impacts on nutrient cycling and C-cycling, undermining the potential of these mudflats to continue to deliver critical ecosystem services. The widespread nature of biogeographic range shifts and the value of coastal systems should add further weight to calls for global action to mitigate global temperature change.

Keywords: climate change; ecosystem services; infauna; functional compensation, biological traits; novel assemblages

1. Introduction

Global average temperatures have risen > 1°C since the 1900s and are predicted to rise a further 1.1–4.8°C under most climate scenarios (RCP4.5 and above) by the end of the century (IPCC, 2014). Forecasting the responses of marine ecosystems to these changes is limited not only by uncertainties surrounding such predictions, but also by regional variations in environmental changes and ecological responses (IPCC, 2014; Poloczanska et al., 2013), differences in species biology and behaviour (Deutsch et al., 2015; Nagelkerken et al., 2016; Poloczanska et al., 2013; Wethey et al., 2011) and synergies between the effects of different anthropogenic pressures (e.g. fishing and pollution; Deutsch et al., 2015; Nagelkerken et al., 2016; Rijnsdorp et al., 2009). One consequence of warming is the global redistribution of taxa, with some displacement, contraction and expansion of species biogeographic ranges (Pecl et al., 2017; Poloczanska et al., 2016) leading to the formation of 'novel species combinations'. That is assemblages which comprise, as yet, unobserved combinations of taxa (Alexander et al., 2015). For marine taxa the reported rates of biogeographic shifts are highly variable (~10–400 km decade^{-1}) (Parmesan and Yohe, 2003; Poloczanska et al., 2016; Sorte et al., 2010). A recent meta-analysis found rates of 72 ± 13.5 km decade^{-1} for 360 marine species across a range of taxonomic groups at the poleward or 'leading' edge of their biogeographic distributions (Poloczanska et al., 2013). This is compared with 6.1 ± 2.4 km decade^{-1} (Poloczanska et al., 2013) to 17.6 ± 2.9 km decade^{-1} for terrestrial taxa (Chen et al., 2011). Przeslawski et al. (2012) assessed 311 marine invertebrates using rigorous criteria and found 37% had robust evidence for poleward shifts of 3.8–8.9 km decade^{-1}. Variations in the reported rates probably result from differing physiology and dispersal abilities of taxa, regional environmental variations and the more restrictive criteria used by Przeslawski et al. (2012).

Whatever the mechanism driving species range shifts these taxa can have significant, positive and negative, impacts on the recipient marine communities that are similar to those for introduced non-native invasive species (Pecl et al., 2017; Sorte et al., 2010). Species arrivals may have no detectable impacts on the established assemblages (Zwerschke et al., 2018) or change may be catastrophic (Katsanevakis et al., 2014; Ling, 2008; Scheffer et al., 2001) for example the decline or extirpation of native species (Cheung et al., 2009; Landschoff et al., 2013; Pereira et al., 2010). The recipient communities are also subjected to changing temperatures, which may alter their abundance or distribution. Species vary in their thermal tolerance (Sunday et al., 2012) and it is likely that sensitive taxa will be lost first from an established community while the assemblage is being colonised by incoming taxa with higher thermal tolerances. The dynamics of species interactions, e.g. competition and predation (Alexander et al., 2015; Poloczanska et al., 2013), within novel assemblages may differ and so too might ecological functioning and service delivery. Sorte et al. (2010) identified eight biogeographic shifts which affected marine ecosystem processes including nutrient cycling, competition, herbivory, predation and disease dynamics. For example, the sea urchin *Centrostephanus rodgersii* extended its range from temperate New South Wales to eastern Tasmania where its intensive grazing negatively impacted the macroalgal communities. This loss of biogenic habitat contributed to declines in macrofaunal diversity (Ling, 2008). Poleward shifts, of 57–801 km, for > 30 species of tropical reef fish are impacting functional dynamics on temperate reefs by grazing important habitat-forming kelp species in New South Wales (Fowler et al., 2017; Vergés et al., 2016). Northward shifts of boreal fish are changing food-web dynamics in the Barents Sea, benthic-pelagic coupling has strengthened and competition with resident taxa has led to declines in fish and mammal abundance and body condition (Bonebrake et al., 2018; Kortsch et al., 2015). Similar changes are predicted for Arctic benthos due to shifts in larger, faster-growing molluscs from the Bering Sea (Vermeij and Roopnarine, 2008). The formation of novel assemblages and changes in species interactions will ultimately lead to changes in the ecosystem functioning (Alexander et al., 2015). The biological traits of species can be used to better anticipate functional changes which seem to be critical predictors of system responses to ‘invasion’ (Alexander et al., 2015; Kortsch et al., 2015; Kristensen et al., 2014).

Intertidal soft sediment habitats such as mudflats deliver a range of ecosystem services (Crowe and Frid, 2015), including the production of food, fuel and construction materials, and the protection of coastal communities from storm surges and flooding (Barbier et al., 2011; Himes-Cornell et al., 2018). The ecosystem services provided by intertidal systems such as estuaries and mudflats are estimated to be US\$ 5.2 x 10^{12} y^{-1} (in 2007) globally, with a further US\$24.8 x 10^{12} y^{-1} (in 2007) from tidal marshes and mangroves (Costanza et al., 2014). Macrofaunal communities inhabiting soft sediments make important contributions to the ecological functions that underpin these ecosystem services, e.g.

facilitating effluxes of nutrients from sediments that support primary production or sequestering carbon and so mitigating ocean acidification and anthropogenic warming. Therefore, future changes in species biogeographic distributions that impact ecological functioning as a result of warming may have major impacts on the livelihood and economies of coastal communities.

Subtropical regions are a key area of focus for identifying changes in species distributions, where the arrival of tropical taxa and/or loss of temperate taxa become apparent as their ranges expand or contract (Bonada et al., 2007; Davie and Phillips, 2010; Endean et al., 1956). The present study examined changes in the distribution of macroinvertebrates in subtropical mudflats throughout SE Queensland. Generally, information on the biodiversity and taxonomic composition of soft-sediment invertebrate assemblages in SE Queensland are sparse (Davie and Phillips, 2010) with work focussing on sandy shores (Barnes and Hamylton, 2016), northern Queensland (Dittmann, 1996, 2002; Inglis and Kross, 2000) or subtidal benthos (Eertman and Hailstone, 1988; Poiner, 1977; Young and Wadley, 1979). This study provides new data on mudflat macrofaunal assemblages in Moreton Bay, and considers changes in species distributions, and the implications of the observed and future variations for the traits, and so ecological functioning, of these economically important habitats.

2. Materials and Methods

2.1 Field site and macrofaunal sampling

A total of 24 intertidal mudflats (comprising > 10% silt and clay) were sampled throughout SE Queensland from Deception Bay (27.15°S) in the north to Tallebudgera Creek (28.11°S) in the south (Fig. 1A-B, Appendix Table A.1)(Dissanayake et al. 2019). All mudflats were bordered by mangroves and showed little evidence of direct anthropogenic impact. This region (referred to herein as SE Queensland) is of recognised ecological value, being designated a RAMSAR wetland (Department of Environment and Science, 2019). The sampling sites occupy the northern part of the 'Tweed Moreton ecoregion' and so are near to the boundary (at 25°N) between the Temperate Australasian and Central Indo-Pacific biogeographic marine realms (Spalding et al., 2007). As such it represents an important faunal transition between tropical and temperate latitudes (Davie and Phillips, 2010; McPhee, 2017). The southern boundary of the 'Tweed Moreton ecoregion' (Spalding et al., 2007) is delimited by the point where the southward flowing East Australia Current meets the northward Tasman Sea Current (between 30–32°S) and is deflected offshore (Dambacher et al., 2012).

Sampling was conducted once in winter (July–August 2016) and once in summer (January–February 2017). At each site, five box cores (25 * 25 cm to 11 cm sediment depth) were collected from the mid-shore (approx. 2–5 cm above port datum) for infauna. A minimum of 2 m distance was maintained between box core samples. Sediments were sieved *in situ* over 0.5 mm mesh and the residues were preserved in 90% ethanol containing Rose Bengal stain. Samples were kept at 4°C and returned to the laboratory for identification and enumeration. Given the lower density, mobility and heterogeneous distribution of large epifauna, they were not expected to be adequately represented within the box core samples. Thus, epifauna were collected, adjacent to the infaunal sampling locations, from the upper 20 cm of sediment within three 0.5 x 0.5 m quadrats (with raised sides providing a barrier against fast-moving animals), and were sieved over 2 mm mesh. The retained fauna were preserved in 90 % ethanol. Scientific names were verified using the World Register of Marine Species (WoRMS Editorial Board, 2019).

2.2 Biological traits analysis

Biological trait analysis (BTA) was used (Bremner et al., 2003, 2006) to identify the potential contribution of macrofauna to the ecological functioning of the mudflats. Eleven traits were selected to represent a range of morphologies, life histories and behaviours. Each biological trait was characterised by 3–5 trait modalities (Table 1), giving a total of 45 trait modalities. The affinity of each taxon to each trait modality was assigned using fuzzy coding such that the ‘total’ affinity for each trait summed to 1. Using this approach the score may be split across the modalities within a single trait (Chevene et al., 1994) allowing both diversity/plasticity in the biology or behaviour of an organism to be captured, and/or any uncertainty surrounding its behaviour. Information on the biological traits of taxa was obtained from sources including the Biological Traits Information Catalogue (MarLIN, 2006), the Marine Species Identification Portal (ETI Bioinformatics, 2018), BOLD systems (Ratnasingham and Hebert, 2007), Polytraits (Faulwetter et al., 2014) and selected papers (e.g. Kristensen et al., 2012; Macdonald et al., 2010; Queirós et al., 2013).

2.3 Biogeographic distribution of macrofaunal assemblages

To explore biogeographic patterns in species and trait composition the 24 sampling sites were grouped according to three criteria (Fig. 1); (i) sites to the north and south of Cleveland, (ii) four equal-sized groups ordered north to south, and (iii) the northernmost and the southernmost six sites. Differences between water circulation patterns to the north (open bay) and south of Cleveland (many large islands inhibit water flow) provided a rationale for the latitudinal subdivision of mudflats (McPhee, 2017). Site groupings (ii) and (iii) were objectively divided based on latitude, with classification (iii) representing the two ends of the latitudinal gradient. Given the potential for complex environmental gradients in Moreton Bay, we carefully examined the ordinations for potential patterns in the species composition that would not be detected by statistical comparisons between the selected geographic groupings (i-iii). We concluded that no such patterns existed (Appendix Fig. B2).

The published biogeographic ranges of each of the taxa sampled were obtained from the Atlas of Living Australia (ALA, 2018) and the Ocean Biogeographic Information Systems (OBIS, 2018), these databases contain information from a series of museum records. For each species the apparent range change between the most recently documented occurrence (ALA, 2018; OBIS, 2018) and the most northerly or southerly sampled occurrences were estimated using the difference in degrees of latitude (1° latitude = 110 km) between the two. Subsequently each taxon was classified based on their published biogeographic ranges (ALA, 2018; OBIS, 2018) as either tropical, temperate or cosmopolitan. The taxa were assigned to one of six categories (A–F) based on their historic distribution or that recorded in this study. **A**. Tropical species that have extended their range to the southernmost six mudflats sampled in SE Queensland (range shifters, Fig. 1C–D). **B**. Tropical species that occur throughout SE Queensland. **C**. Tropical species that currently only occur in the northernmost sites of SE Queensland. **D**. 'Robust' temperate species whose current range extends throughout SE Queensland, and **E** temperate species that are sensitive to temperature change (i.e. did not occur in the northernmost six mudflats). The 'cosmopolitan taxa' formed group **F**. For the purposes of this study cosmopolitan taxa are those that were distributed throughout tropical, temperate and subtropical climatic zones along Australian coastlines only (cf. Hutchings and Kupriyanova, 2018). This restricted definition is used because these records have been confirmed by Australian taxonomists and so are not confounded with other morphologically similar taxa (Przeslawski et al., 2012). Based on their biogeographic distribution three species and the polygeneric taxa (Nematoda and Nemertina) were characterised as cosmopolitan.

2.4 Effects of climate change on the ecological functioning of mudflats: Simulating taxonomic and trait change

The observed changes in species biogeographic ranges were used as the basis for simulating five scenarios of changes in species composition of the mudflat fauna. The implications of past and further climate induced range shifts on mudflat ecosystem functioning were explored using biological traits analysis. Each scenario was derived from the macrofaunal assemblages at the southernmost six mudflats, with scenario 1 being the present or '*baseline'* state (1), and for the remaining four scenarios (Table 2) taxonomic composition was manipulated as follows.

- 1. *Southern baseline:* the present assemblage from the southernmost six mudflats.
- 2. *Pre-invasion*: the tropical range shifting species (observed in the 24 mudflats sampled in the present study) were removed from the baseline community.
- 3. *Further invasion*: Tropical taxa that were absent from the southernmost six assemblages were added to the baseline at their mean densities found at the northernmost six sites.
- 4. *Loss of sensitive temperate taxa:* The most sensitive temperate taxa i.e. those absent from the northernmost six sites (suggesting they had reached the physiological limits of their distribution) were removed from the scenario 3 assemblage.
- 5. *Loss of all temperate taxa*: All temperate taxa were removed from the scenario 3 assemblage.

Analyses were performed on both unconstrained and constrained data. In the latter case all of the simulated assemblage data were standardised to the same total density to aid comparisons between scenarios. This emphasises the influence of changing species compliment rather than the size of the assemblage (Table 2). For each simulated assemblage the corresponding biological trait matrices were multiplied by the constrained and unconstrained densities to generate the biological trait composition for each scenario.

The impacts of climate-induced biogeographic range shifts on three ecological functions were investigated: nutrient cycling, C-cycling (food web dynamics) and biogenic habitat provision. In coastal seas nutrient cycling is strongly coupled with benthic processes that regenerate nitrogen compounds from sediments, this can provide 20–100% of the annual N requirements for water column primary production (Blackburn, 1986; Heinen and McManus, 2004). Macrofaunal communities also transport, transform and store carbon within an ecosystem, and may contribute 11–43% of total benthic community respiration (Hyndes et al., 2014; Piepenburg et al., 1995; Van Oevelen et al., 2006). This organic C-cycling is driven by food-web dynamics (ingestion, respiration, production) and reproductive processes. Infaunal and epifaunal macrofauna also provide structures (e.g. emergent tubes, mussel/oyster beds) creating habitat for species that require hard substrates, and they provide physical protection and refugia (Buhl-Mortensen et al., 2010). Further discussion of these processes and rationale for the determination of these indices (Table 1) is addressed in Appendix B.

Two models were used to explore the implications of species losses and gains from the southernmost mudflat assemblages. Model A included only those trait modalities thought to make meaningful contributions to each of the functions, and these were assigned a weighting of 1 (Frid and Caswell, 2016; Table 1). An additional model (Model B) employing differential weightings, to better reflect our, partial, understanding of the contribution of different trait modalities to particular functions, was also developed although it is not considered further herein (Appendix Tables A.2 and B.10, Fig. B.6).

2.5 Data analyses

Firstly, the abundances for all infaunal and epifaunal samples were converted to density per m^2. The epifaunal and infaunal data were combined, and in instances where epifaunal taxa occurred in both box cores and the 0.5 x 0.5m quadrats the mean densities from the quadrats were used as they were more reliable for mobile epifauna. The mean and median number of individuals, species richness, Shannon-Weiner diversity and Pielou's evenness were calculated for each site for the two seasons separately, and for the three biogeographic groups (i)–(iii). Median values were compared between sites and groups using the Mann-Whitney *U* test or Kruskal-Wallis test (SPSS v.25, IBM).

Bray Curtis similarities were calculated from log (x+1) transformed pooled species densities (per m^2) from each site (for the replicate box cores and quadrats, as described above). For biological trait composition the species-traits (determined as described in Section 2.2) were multiplied by the species densities to produce a trait modality by site matrix. Bray-Curtis similarities were calculated on untransformed biological traits data. Differences in species and biological trait composition were explored between seasons, biogeographic groups (Section 2.3), and range shift scenarios (Section 2.4) using non-metric multidimensional scaling (nMDS), Analysis of Similarities (ANOSIM) and the similarity percentage routine (SIMPER). The delivery of ecological functioning under the five range shift scenarios were compared using one-way ANOVA, and differences in trait modalities were compared using t-tests. Differences in the trait profiles of the taxa were compared between climatic zones, based on their distribution (A to F, Table 2), using ordination (nMDS and ANOSIM). The similarity percentage (SIMPER) routine was used to identify the trait modalities that contributed to the dissimilarities between groups, and the abundances of the modalities were compared using t-tests. Multivariate analyses were completed using Primer 6 Beta (Plymouth Routines in Multivariate Ecology Research Ltd).

3. Results

3.1 Macrofaunal assemblages of mudflats in southeast Queensland

A total of 3047 individuals were retrieved in the summer and 1800 were observed in winter across the 24 sites sampled in SE Queensland (from 120 box core samples; Mann-Whitney *U* test, $Z = -3.629$, $p<0.001$, Fig. 2A). In the summer 50 taxa were recorded while in the winter there were 46, with the polychaete *Platynereis antipoda*, the bivalve *Paratapes undulatus* and the gastropods *Recluzia johnii* and *Nassarius coronatus* being absent during the winter. In both seasons 10 taxa contributed to ~70% of the cumulative macrofaunal density in the assemblage (Appendix Table B.1). In summer the suspension feeding bivalve *Hiatula alba* dominated, followed by the polychaetes *Barantolla lepte* and *Aglaophamus australiensis*. Whereas in winter the crabs *Mictyris longicarpus* and *Macrophthalmus setosus* dominated. Mudflat assemblage species composition significantly differed between winter 2016 and summer 2017 (ANOSIM, global $R = 0.076$, $p = 0.004$, Fig. 2B) with an average SIMPER dissimilarity of ~52%. Given the marked seasonal differences in the mudflat assemblages, for the remainder of the analyses the summer and winter assemblages were considered separately.

3.2 Biogeographic variations in the species composition of mudflat assemblages

Overall, northern mudflats appeared to have higher macrofaunal densities, diversity and evenness than those to the south, however they did not significantly differ between mudflats in any of the three biogeographic comparisons (i–iii; Fig. 1B) in either season (Kruskal Wallis test, $p < 0.05$ in all cases; Appendix Fig. B1). Macrofaunal species composition did not significantly differ between mudflats north and south of Cleveland (one way ANOSIM; winter global $R = -0.001$, $p > 0.05$; summer global $R = 0.011$, $p > 0.05$) nor between the four groups of mudflats on a north-south gradient (ANOSIM, winter global $R = -0.035$, $p > 0.05$; summer, global $R = 0.057$, $p > 0.05$) (Appendix B). Despite the lack of significant differences in macrofaunal densities and diversity between the northernmost and southernmost six mudflats (comparison iii), species composition significantly differed between these mudflats in summer (ANOSIM, global $R = 0.272$, $p = 0.015$, 55% dissimilar, Fig. 3B), but not winter (global $R = 0.065$, $p > 0.05$, Fig. 3A). Five taxa, the polychaetes *A. australiensis* and *M. dakini*, the bivalves *H. alba*, *M. hiantina* and the gastropod *H. fusca* each contributed > 4% to the SIMPER dissimilarity between the northernmost and southernmost six sites (Fig. 3).

In summer, the assemblage at the southernmost sites was comprised mostly of taxa with temperate affinities and were dominated by the bivalve *H. alba* and the polychaete *A. australiensis*, but only *A. australiensis* occurred in significantly higher densities in the south compared to the north (t-test, t(10) = 0.923, p = 0.017, Fig. 3E). *M. dakini* also occurred in higher densities in the south although it did not significantly differ (t-test, p > 0.05; Table 3, Fig. 3E). Four temperate taxa, the shrimp *Alpheus richardsoni*, the polychaetes *Trypaea australiensis*, *Sthenelais boa* and *Helograpsus haswellianus*, and three tropical taxa the stomatopod *Clorida depressa*, the gastropod *R. johnii* and the decapod *Uca longidigita* were present in the southernmost mudflats but were absent from the northernmost sites. The northernmost assemblage was dominated by the tropical bivalve *M. hiantina* which occurred at significantly higher density than in the south (t-test, t(10) = -1.991, p = 0.040). Density of the tropical gastropod *H. fusca* was five-fold higher in the north (Fig. 3E), although it did not significantly differ (t-test, p > 0.05; Table 3, Fig. 3E). Five tropical taxa the bivalves *Mactra maculata*, *P. undulatus*, *Lutraria impar*, the brachiopod *Lingula anatina* and the decapod *Tubuca polita* occurred in the northernmost assemblages, but were absent from the southernmost mudflats.

Of the total pool of 50 taxa recorded in SE Queensland mudflats 50% were classified as temperate, 40% were tropical and 10% were ‘cosmopolitan’ taxa (i.e. widely distributed in both zones) based on their known occurrences (ALA, 2018). According to the documented species distributions (ALA, 2018; OBIS, 2018), five taxa the polychaetes *H. fusca*, *Prionospio queenslandica*, *Eurysyllis tuberculata*, *Sternaspis scutata*, and the bivalve *Laternula anatina* had previously only been recorded once in the greater SE Queensland region (ALA, 2018; OBIS, 2018; Table 3). Three species had previously only been recorded once in the study area (Table 3).

Ten taxa had wider biogeographic distributions throughout SE Queensland than had previously been documented (Table 3). Up to eight tropical taxa exhibited range shifts, the gastropod *H. fusca*, the bivalves *L. anatina*, *M. maculata*, *M. hiantina*, and the crustaceans *Metapenaeus endeavouri*, *C. depressa* and *U. longidigita*, and the foraminifera *Elphidium discoidale* extended their ranges southwards shifting on average 146 ± 66 km (Table 3, Fig. 1B). The relatively small difference in the biogeographic range of the stomatopod *Clorida depressa* since 1998 (Table 3) may simply result from new records due to greater sampling effort. The foraminifera *Elphidium discoidale* may exhibit a shift of 381 km since 1983, but this is also uncertain, as it may be confounded by subspecies *Elphidium discoidale* var. *multiloculum* (Narayan and Pandolfi 2010). Two temperate taxa also changed distribution, the polychaetes *V. australiensis*, and *M. australiensis* which shifted 85 km and 374 km northwards (Table 3), respectively. The shifts ranged from 6 km up to 477 km, and the fastest shifters were *H. fusca*, *L. anatina* and *M. australiensis* which have all shifted > 100 km decade^{-1} (Table 3).

3.3 Biogeographic differences in macrofaunal trait composition

Trait modality richness of the macrofaunal assemblage did not significantly differ (Appendix Table B.4) between the mudflats; (i) north and south of Cleveland, (ii) in the four groups along the north to south gradient or (iii) at the northernmost and southernmost six sites. Overall, most macrofaunal taxa were short lived (1–2 years), intermediate sized (> 5 cm), unattached, free moving, habitat modifiers which made burrows, and had planktotrophic larval development (Appendix Fig. B.4). Although taxa composition significantly differed between the northernmost and southernmost six sites in winter or summer the trait composition did not differ (ANOSIM, winter global R = 0.004, summer global R = 0.091, p > 0.05, Fig. 3C–D). Assemblages from mudflats north and south of Cleveland (ANOSIM, winter global R = 0.026, summer global R = -0.042, p > 0.05) and the four groups along a north-south gradient did not have different trait compositions (ANOSIM, winter global R = 0.013, summer global R = 0.073, p > 0.05; Appendix B).

3.4 Taxa trait modality profiles

The trait modality profiles for taxa with tropical, temperate and cosmopolitan geographic distributions significantly differed (ANOSIM, global R = 0.143, p = 0.002, Fig. 4A), with those for tropical taxa differing from those for temperate taxa (R = 0.149, p = 0.003; average SIMPER dissimilarity ~60%). More temperate taxa had body-sizes > 50 mm, and vermiform body shapes with no exoskeleton, contrastingly tropical taxa typically had more rectangular–subrectangular body shapes and were generally smaller and had exoskeletons. The trait profiles of cosmopolitan taxa did not differ from the tropical or temperate taxa (pairwise ANOSIM, p > 0.05).

To explore these differences in greater detail the taxa were further categorised based on their occurrences within the 24 mudflats sampled and their reported biogeographic range. The trait profiles of macrofauna significantly differed between the six biogeographic (A–F, Table 3) categories of taxa (ANOSIM, global R = 0.223, p = 0.001, Fig. 4B). Pairwise ANOSIM showed the trait profiles of temperate taxa occurring across all 24 mudflats significantly differed from those of: tropical species occurring across all 24 sites (pairwise ANOSIM, R = 0.199, p = 0.012), tropical species present at all but the southernmost 6 sites (R = 0.518, p = 0.003) and tropical range shifters (R = 0.299, p = 0.003). A total of 18 trait modalities contributed to > 50% of the cumulative SIMPER dissimilarity between the trait profiles of taxa in these four categories (Fig. 4C). The main differences between the trait profiles of temperate species (D) and those from the other three categories (A–C) was the greater incidence of vermiform body shapes and lack of body armour (Mann-Whitney U test, p < 0.05; > 50% contribution to dissimilarity; Fig. 4C, Appendix B). Whereas, tropical taxa (B–C) had more rectangular shaped bodies, and tropical taxa absent from the southernmost sites had more 0.5–1 mm thick body armour (p < 0.05). Tropical species which occurred throughout SE Queensland were typically 10–30 mm body size whereas the other three groups (A, C, E) were comprised of taxa > 50 mm body size. Significantly less of the temperate taxa were suspension feeders (Mann-Whitney U test, p<0.05) and significantly more were deposit feeders (p < 0.05) compared to the tropical range shifters. There were also significantly more deposit feeding temperate taxa (Mann-Whitney U test, p < 0.05) than tropical taxa absent from the southernmost sites (Fig. 4C, Appendix Table B.5). These differences in trait profiles are consistent with those between all tropical and all temperate taxa.

3.5 Simulations of species, traits and functional change

ANOSIM identified significant differences in the taxonomic composition of the simulated assemblages (or ‘scenarios’) using unconstrained species abundances during both seasons (ANOSIM, winter global R = 0.362, p = 0.001; summer global R = 0.401, p = 0.001, Fig. 5A-B). Pairwise ANOSIM showed both the winter and summer taxonomic composition of scenario 5 significantly differed from all other scenarios (SIMPER dissimilarity 61–81%); and, in summer scenario 1 differed from scenario 4, and scenario 2 differed from scenarios 3 and 4 (SIMPER 47–49% dissimilar; Appendix Table B.7). The biological trait composition significantly differed in winter (ANOSIM, global R = 0.127, p = 0.05, Fig. 5A) and summer (ANOSIM, global R = 0.187, p = 0.004, Fig. 5B), and similar to taxonomic composition the traits of the scenario 5 assemblage significantly differed from all other scenarios (pairwise ANOSIM, p <0.01; Appendix B). Fourteen to seventeen of the 45 trait modalities contributed to 70% of the cumulative SIMPER dissimilarity between the trait composition for scenario 5 and all of the other scenarios in both winter and summer ($p<0.05$). All modalities except one were significantly more abundant in scenarios 1–4 (Appendix Table B.8). Thus, despite the changed density of 4–8 taxa in scenarios 1–4 (Table 2) only scenario 5 consistently differed in species and trait composition across both seasons (Appendix Table B.8 and B.9).

The estimates for nutrient cycling significantly differed between the winter scenarios (ANOVA, winter: F = 2.868, p = 0.04), however post-hoc Tukey tests failed to identify pairwise differences. Pairwise Mann-Whitney U tests (with sequential Bonferroni correction, Rice 1989, Appendix Table B.10) showed scenario 5 significantly differed from scenarios 1–4 only ($p<0.05$; Appendix Table B.10) and delivered three-fold lower mean functioning (Fig. 6A). Scenarios 1–4 contained more taxa with the following traits compared to scenario 5; medium and large body sizes (> 30 mm), showing free movement, bioturbate by biodiffusion, deposit feeders and deep sediment dwellers (> 50 mm). Therefore, a correspondence existed between the trait composition, functional estimates (Table 1, Appendix Fig. B.4A) and the elimination of all temperate taxa from the scenario 5 assemblage, the latter being typified by trait profiles with larger body sizes and deposit feeding modes.

Estimates for C-cycling were significantly higher in scenarios 1–4 than scenario 5 in the winter (ANOVA, F = 2.956, p = 0.04; Mann-Whitney U test, $p < 0.05$; Fig. 6B, Appendix Table B.10). Higher C-cycling was provided by taxa with medium and large body sizes (> 30 mm), a lack of armour, < 2 years longevity and planktotrophic larvae (Table 1, Appendix Fig. B.4A and Table B.10). In the summer estimates for biogenic habitat provision were higher in scenarios 3 and 4 compared with scenario 5 (ANOVA, F = 4.240, $p < 0.001$; Appendix B). However, the trait modalities included in the functional estimates (Table 1) represented a small proportion of the total density (and < 10% of the cumulative SIMPER dissimilarity) between the trait composition of the different scenarios (Appendix Table B.10).

For the constrained data the trait composition of the assemblage representing scenario 5 differed from all of the other scenarios (Appendix Table B.7), and for the three constrained functional estimates (Table 1) only biogenic habitat significantly differed between assemblages. The nature of the differences was consistent with that for the unconstrained estimates (Appendix Table B.6).

4. Discussion

Using new data on mudflat macrofaunal communities together with historic biogeographic datasets poleward biogeographic range expansions were identified for up to eight typically tropical species, representing 14% of the 50 taxa recorded from mudflats. To date this is the most comprehensive survey of mudflat macrofauna in SE Queensland, with most past work focussing on macrofauna within intertidal seagrass meadows (38%), mangroves (9%) and sandflats (16%) with mudflats forming only ~10% of the published work within the region. The SE Queensland assemblages were typical for the subtropics (Davie and Phillips, 2010; Dissanayake et al., 2018; Dissanayake et al. 2019; Johnson, 2010) having a mixture of species with tropical and temperate affinities, in the mudflats 50% of species were temperate and 40% tropical (ALA, 2018; OBIS, 2018). Similar patterns are observed for rocky shore invertebrates (Endean et al., 1956) and fish (Johnson, 2010) in Moreton Bay reflecting the transition from the Temperate Australasian to Central Indo-Pacific biogeographic realms at 25°S (Spalding et al., 2007). However, biogeographic shifts are apparent for fish (Fowler et al., 2017; Sunday et al., 2015), rocky shore (Poloczanska et al., 2011) and mudflat species (the present study) and further climatic warming may cause the biogeographic boundaries to move.

The documented shifts of mudflat macroinvertebrates are consistent with the widely reported movements of marine and terrestrial species towards the poles as a result of anthropogenic warming (Freeman et al., 2018; Poloczanska et al., 2016), and prompted us to ask how will the ecological functioning of marine ecosystems be affected by this restructuring of macrofaunal assemblages? Simulations were used to explore how macrofaunal assemblages formed by past, present and future biogeographic shifts will impact mudflat community structure and functioning. Our results suggest that even quite severe changes in species composition will not fundamentally alter the ecological functioning or the delivery of ecosystem services, initially because species with similar traits will compensate for the species lost. However, as the severity of the perturbation increase a sudden collapse in functioning may occur. This pattern of compensation followed by a catastrophic failure has previously been reported for hypoxia in ancient oceans (Caswell and Frid, 2017), and those experiencing high levels of anthropogenic organic enrichment (Caswell et al., 2018).

4.1 Biogeographic range expansions of macrofaunal taxa

Changes in biogeographic ranges have been documented for 54 species in the SW Pacific and more than 360 marine species globally, across most taxonomic groups and ocean regions, at a mean rate of 72 km decade^{-1} at the leading edge (Poloczanska et al., 2013; Poloczanska et al., 2016). For most of these range shifts increases in average global surface air and seawater temperatures since the start of the 20th century (IPCC 2014) have been implemented as the primary driver (Poloczanska et al., 2016; Sorte et al., 2010). Generally, leading edge expansion rates are fastest for taxonomic groups with high dispersal abilities e.g. phytoplankton (469.9 ± 115.3 km decade^{-1}), zooplankton (142.1 ± 27.8 km decade^{-1}) or bony fish (277.5 ± 76.9 km decade^{-1})(Poloczanska et al. (2013). In this study up to eight usually tropical taxa appear to have shifted on average 145 km south over the last 20–60 years (Fig. 1). The poleward movements of these species are probably also symptomatic of ocean warming. The tropical mudflat species moved on average 34 km decade^{-1} towards the poles and so shifted approximately four times faster than the 6.8 km decade^{-1} for intertidal invertebrates reported by Przeslawski et al. (2012), but slower than reported for subtidal macroinvertebrates in the N Atlantic (Hale et al. 2017). The subtropical mudflat macrofauna shifted at approximately half the global rates reported across all marine taxa (Poloczanska et al., 2013), but were comparable with the average rate (29 km decade^{-1}) reported for Australian marine invertebrates and fish (Champion et al., 2018; Fowler et al., 2017; Hobday, 2010; Ramos and Pecl, 2015; Sunday et al., 2015). The rate of crustacean shifts were within the range already reported for the taxon, whereas the molluscs and polychaetes shifted ~70–300 km decade^{-1} which is faster than the rates reported for these taxonomic groups in recent global meta-analyses (Poloczanska et al., 2016). *L. anatina* was the fastest moving taxon which is shifting ~220 km decade^{-1}, a very high rate for a benthic mollusc, and is comparable with that for zooplankton (Poloczanska et al., 2016).

Species traits that may facilitate biogeographic range shifts include large existing geographic ranges (and so thermal tolerances) and wide dispersal abilities, these taxa are more likely to successfully colonise new habitats (Cheung et al., 2009; Cowen and Sponaugle, 2009). Sunday et al. (2015) showed that this was the case for pelagic fish in SE Australia and that many of the fish species were omnivorous meaning they could exploit a greater range of resources. However, to date predictions based on these traits have had limited power to explain the pattern of marine species range shifts (Angert et al., 2011; Pinsky et al., 2013; Przeslawski et al., 2012). The tropical range shifters documented in the present study did not differ from any of the non-shifting taxa with respect to these traits, similar results have been found for range shifters in the temperate Atlantic benthos (Hale et al., 2017). The faster rates of expansion for benthic invertebrates reported in the present study might be facilitated by oceanographic features such as the strong (up to 1.3 ms^{-1}) southward flowing East Australia Current which promotes larval and juvenile dispersal (Booth et al., 2007), which has strengthened with climate change and now penetrates further south than prior to the 1940s (Ridgway, 2007). A further complicating factor may be the nature of the intertidal environment which is subject to warming as a result of both rising sea and air temperatures and while broadly correlated, the detailed changes will vary between sites and different species may be more sensitive to one or another causing further variations in the response.

Species distributional responses to increasing SST are mixed, in addition to shifts at the leading edge of species biogeographic ranges some taxa lag or do not respond, and equatorward shifts such as those documented herein have been observed in response to complex regional phenomena (i.e., where seawater temperatures may vary locally or geographical barriers exist; Burrows et al., 2014; Pinsky et al., 2013) or due to differences in species biology or ecology (Poloczanska et al., 2013). For instance, in subtidal benthic communities along the Atlantic coast of USA between 1990 and 2010 60% of species shifted north (poleward) by on average 181 km and 23% shifted ~65 km southward (equatorward) (Hale et al., 2017). Of the two species of temperate taxa that seem to have expanded their geographic ranges towards the tropics in the present study, *M. australiensis* moved the furthest (368 km in 5 years). This rate is at the upper end of estimates for natural range expansions, and could indicate an introduction, for example on ship hulls or in ballast water (e.g. Ricciardi, 2016). None of the range shifting taxa were documented in the global non-native invasive species database (Invasive Species Specialist Group ISSG, 2015), however species introductions have been observed for *Laternula anatina* (Pagad et al., 2018) and the congenerics *Clorida albolitura* (Galil et al., 2009), *Haminoea japonica* (Hanson et al., 2013) and *M. pentadentata* (Nygren, 2004). Some of the equatorward shifts may simply result from the higher sampling intensity used in this study and so may represent new records and not biogeographic range shifts (e.g. McPhee, 2017). However, regional environmental variations may also contribute, for instance, within Australia the fastest warming (~30% faster than in Queensland) is occurring in a ‘hotspot’ on the south western and south eastern coasts (CSIRO and Bureau of Meteorology, 2015; Hobday and Pecl, 2014).

Reporting range shifts can be fraught with difficulties (Przeslawski et al., 2012), but our range shift data conform to the rigorous criteria employed by other studies (Parmesan and Yohe, 2003; Przeslawski et al., 2012; Sorte et al., 2010) for identifying range shifts, e.g. the data are based on species occurrences, not abundances, and are collected from assemblages not individual species. Further, all species were found at > 4 mudflats and were abundant in the majority of the mudflats sampled. However, it is not possible to determine when the range shifts occurred nor when they achieved their current southerly limits, except to say that they shifted sometime between their most recent record in ALA or OBIS and our 2016-2017 sampling. Thus, the estimated rates of range shifts are maximums and assume movement spanned the entire time period between the two records. Given the paucity of studies in SE Queensland mudflats, some of these range expansions could simply result from new records due to greater sampling effort. Therefore, the findings of this study need to be further validated by conducting more extensive benthic sampling programs in this and other ‘biogeographic boundary zones’.

4.2 Changes in macrofaunal traits and ecological functioning

Whilst the species within assemblages have differing identities, they often share traits (e.g. morphology, life history and behavioural characteristics; Bremner et al., 2006; Peres and Dolman, 2000) usually resulting in less variation in traits than taxa between assemblages (Bremner, 2008; Törnroos et al., 2013). For instance, the trait composition of subtidal benthos around the UK does not differ regionally between the southern North Sea and eastern English Channel unlike the taxonomic composition (Bremner et al., 2003). At the global scale this may also be true: clear latitudinal differences exist in the taxa that dominate marine systems e.g. the proportions of decapods and bivalves are higher in tropical mudflats (Boschi, 2000; Crame, 2000; Dissanayake et al., 2018). Therefore, it is likely that shifts in functioning will occur that are associated with the differing biology of these taxonomic groups when temperate species are replaced by tropical ones. Similar to the previously documented regional (Bremner et al., 2003; Hemingson and Bellwood, 2018; Toussaint et al., 2016) and global trends (e.g. Dissanayake et al., 2018; Safi et al., 2011), spatial differences in the taxa present but not their traits suggest conservation of the macrofaunal contribution to mudflat functioning within SE Queensland. The assemblages seemed to perform similar functional roles at the northernmost and southernmost (Fig. 1) ends of the biogeographic gradient. Therefore, turnover of species in these assemblages will not necessarily result in changes in trait composition or functioning.

Up to eight tropical macroinvertebrate species were identified that have moved on average 145 km southwards in the last 60 years, and it is likely that these changes were driven by increasing SST on the SE Queensland coast. Mean SST in Queensland is predicted to increase 0.6–0.8°C by 2030 and 0.8–2.9°C by 2090 (IPCC scenarios RCP2.6, RCP4.5 and RCP8.5) above the 1986–2005 baseline (CSIRO and Bureau of Meteorology, 2015; IPCC, 2014). Given future forecasts, it is highly likely that further shifts will occur leading to a restructuring of macrofaunal assemblages. Such changes may include alterations to the biological traits and ecological functioning of macrofaunal assemblages. In the present study biogeographic range shifts were simulated to produce five novel species compositions for mudflats. By altering species composition, changes in the associated traits of macrofauna that mediate a range of benthic functions were also simulated. Specific biological trait modalities were mapped onto functions and it was assumed that all modalities contributed equally to functioning. This assumption was tested using an alternative model, and the functional estimates were found to be insensitive to the differential trait weighting (Frid and Caswell, 2016) and so the, unweighted, results presented here are conservative in describing functional change. This is consistent with other studies using this approach (Clare et al., 2015; Frid and Caswell, 2016). However, note these estimates describe 'potential' and relative levels of functioning only rather than actual values that might drive ecosystem or economic models (Bateman et al., 2013; Culhane et al., 2018; Pereira et al., 2010).

Experimental studies are of limited utility for anticipating complex changes in ecosystem dynamics, therefore to predict ecosystem responses models are needed that explore hypothetical scenarios of species movements. In the present study, models of changing assemblage composition were based on three main assumptions. Firstly, species sharing physiological characteristics were assumed to move together rather than individually. Uncertainty regarding the species-specific relative rates of movement made it difficult to determine exactly where and when taxa will arrive. Secondly, species are assumed to function similarly within the new and existing assemblages, however this is unlikely to always be the case (Alexander et al., 2015). For instance, the feeding (Cesar and Frid, 2012) or burrowing behaviour (Olafsson, 1986) of taxa may vary between sediments with differing properties, and so the expression of their traits and the delivery of functioning may also differ. Thirdly, species relative abundances were assumed to be either: equivalent to the areas in which they presently reside (unconstrained total abundance; Table 2, Fig. 5); or, the total carrying capacity of the system was constrained whilst the relative proportions of taxa remained the same. The functioning estimates derived from these constrained and unconstrained formulations of the model followed similar trends. This suggests that while the abundance effect was clearly present in setting the quanta of the function predicted by the model, the pattern of functional change was robust under the different model formulations. This supports interpretations of a period of consistent functioning, driven by species replacements, followed by collapse as previously reported for contemporary systems subject to anthropogenic pressures (Caswell et al., 2018; Clare et al., 2015).

The transition from a 'pre-invasion' to the present-day scenario considers the arrival of up to eight taxa that have shifted southwards by 6–447 km over 23–70 years. These shifts are commensurate with a ~1°C increase in air and seawater surface temperatures (above the 1961-1990 average; CSIRO and Bureau of Meteorology, 2015, 2018; IPCC, 2014). In the 'further invasion' scenario tropical taxa moved 84 km south from Nudgee Beach to the mudflats between Redland Bay and Tallebudgera at on average 49 km decade^{-1}. If the rate of SST increase remained constant these taxa would reach Tallebudgera by ~2036. Our comparison of hypothetical scenarios shows that biological traits, and therefore also functioning, were initially conserved followed by a potential threshold when 10–50% of macrofaunal species were lost. This is seen in the shift between 'further invasion by tropical taxa sensitive to SST' (4 taxa, scenario 4) and subsequent loss of the temperate component of the assemblage (24 taxa, scenario 5). To date most marine species shifts have produced changes in trophic dynamics e.g. predator-prey dynamics or grazing patterns (e.g. Fowler et al., 2017; Ling, 2008; Vergés et al., 2016), but there are comparatively few identifying changes in nutrient or C-cycling within marine (but see Pessarrodona et al., 2019) or terrestrial systems (Collins et al., 2016; Pureswaran et al., 2015; Zhao et al., 2019). In the present study, estimates for nutrient cycling, C-cycling and biogenic habitat provision were three-fold lower after the *loss of all temperate taxa* compared with any other scenario (including the current scenario). Although the differences in emergent biogenic habitat provision were a small proportion of total functioning.

An increasing number of marine species are exhibiting changes in their biogeographic distributions, and these shifts are predicted to continue leading to elevated local extinctions in tropical and sub-polar regions (Cheung et al. 2009). Thus, novel species compositions will continue to form, however, considerable uncertainty remains regarding which species move and how the recipient communities will respond to the new arrivals. Experimental simulations have shown that differences in species interactions based on their traits can be more important predictors of ecosystem responses to 'invasion' than their physiological limits (Alexander et al., 2015). Forecasts of the possible impacts therefore could be improved by greater understanding of the functional dynamics of marine ecosystems. In this study it was only under the most extreme scenarios of species shifts that functioning differed from the *southern baseline* assemblage. These changes were primarily driven by the loss of the temperate species, for which the invading tropical species, which had a different mix of traits, were unable to fully compensate. Arrival of novel species can also strongly undermine the performance of stressed communities through competition and predation. Functional dissimilarity between the incoming 'novel competitors' and 'resident competitors' has a greater impact at the trailing compared with the leading edges of species ranges (Alexander et al., 2015). Thus, the impacts of changes in trait composition presented in this study are likely to be more moderate than in mudflats at the trailing edges. The vulnerability of ecosystem service delivery in coastal areas to climate-induced species redistribution needs to be considered within climate change resilience and mitigation planning. This study shows that these impacts could occur suddenly, associated with thresholds making collapses challenging to predict. Managers, fisheries and aquaculture sectors and others concerned with healthy functioning ecosystems in coastal systems need to be aware of these risks.

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Figure captions

Fig. 1. Spatial distribution of the sites sampled, groupings for the biogeographic analyses and apparent range shifts. (A) Map of Australia with study region indicated. (B) The 24 mudflats (Appendix Table A.1) sampled (open circles) along the SE Queensland coast in 2016-17. The sites are numbered 1-24 from north to south, and for the purpose of biogeographic analyses are grouped into; (i) those to the north (1–14) and south (15–24) of Cleveland, (ii) into four equal-sized groups from north to south, (iii) the northernmost six (1-6) and southernmost six sites (19-24). (C) The northward biogeographic range shifts for the three temperate taxa. (D) Southward range shifts for crustaceans and foraminifera, and (E) molluscs. The distance and direction shifted is illustrated by grey arrows with the origin and year of most recent record in the Australian Living Atlas (ALA, 2018) and the Ocean Biogeographic Information System (OBIS, 2018). For distances moved (km) see Table 3. For three species (*Myrianida australiensis*, *Laternula anatina* and *Haminoea fusca*) only the current location is provided because the origin falls outside of the sampled area.

Fig. 2. (A) Mean (±SE) macrofaunal density (number of individuals m^{-2}), from the 24 mudflats sampled in SE Queensland, Australia (Fig. 1) in winter 2016 (black) and summer 2017 (white). Means are based on five $0.0625m^2$ box cores at each site. (B) nMDS ordination of the Bray-Curtis similarity of the macrofaunal species composition (log X+1 transformed) in each season.

Fig. 3. nMDS ordination of the Bray-Curtis similarity of the mudflat macrofaunal assemblage taxonomic composition (log X+1 transformed density) for mudflats in the northernmost (between Deception Bay and northern Moreton Bay) and southernmost six sites (between Redland Bay and Tallebudgera) sampled in SE Queensland (Fig. 1A), (A) in summer and (B) in winter. Macrofaunal trait composition, weighted by density, (C) in winter and (D) in summer. (E) The mean densities (± SE) of the five taxa contributing most to the SIMPER dissimilarity between the northernmost and southernmost six sites in summer in SE Queensland. *Indicates significance difference.

Fig. 4. (A) The trait modality profiles of taxa based on their typical biogeographic occurrences e.g. tropical, temperate or cosmopolitan. (B) Trait modality profiles of taxa based on the biogeographic occurrences throughout the sampled area (including identified range shifters) in SE Queensland. The species that were absent from the winter assemblage are indicated in ‘W’. (C) The trait modalities

contributed to > 50% cumulative differences between the trait profiles of temperate taxa that occurred throughout SE Queensland (Qld) and tropical range shifters, tropical species that occurred throughout SE Queensland, tropical species that were absent from the southernmost 6 sites. The traits modalities that differed significantly (Mann-Whitney *U* test) between three pairs were illustrated in bold, 2 pairs as underlined and an * was added to represent one significant pair.

Fig. 5. nMDS ordination of the Bray-Curtis similarity of the simulated mudflat macrofaunal assemblage trait composition in 24 SE Queensland mudflats under five scenarios of species compositional change (e.g. pre-invasion, baseline, further invasion, loss of sensitive temperate species and loss of all temperate species scenarios) (A) in winter, and (B) in summer.

Fig. 6. Estimates for three ecological functions (mean ± SE) within SE Queensland mudflats under five scenarios of species compositional change (e.g. pre-invasion, baseline, further invasion, loss of sensitive temperate species and loss of all temperate species scenarios). Data are standardised to zero mean and unit variance. (A) Nutrient cycling, (B) C-cycling, and (C) biogenic habitat provision in model A in both winter and summer.

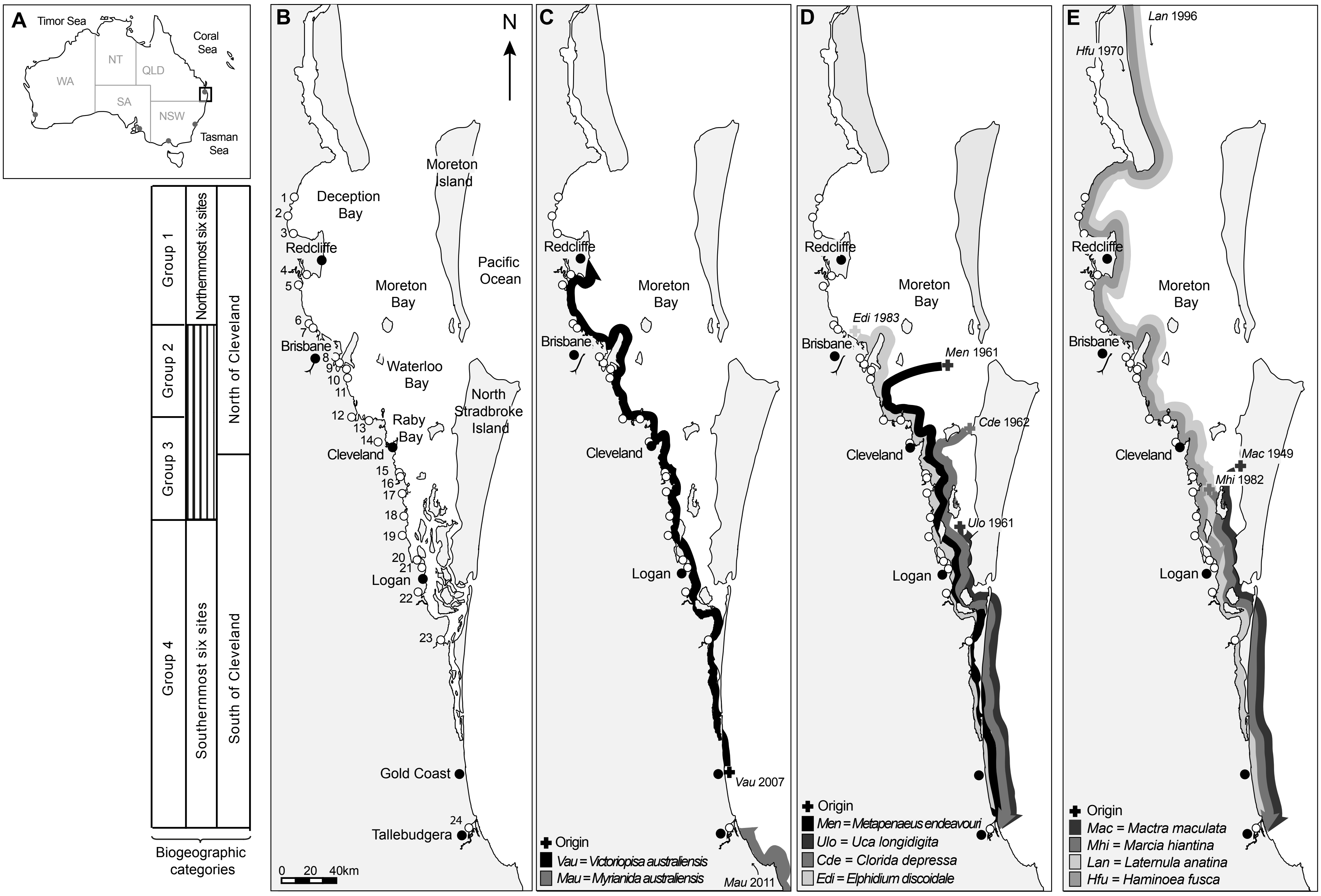


Figure 1 Caswell et al. 2019

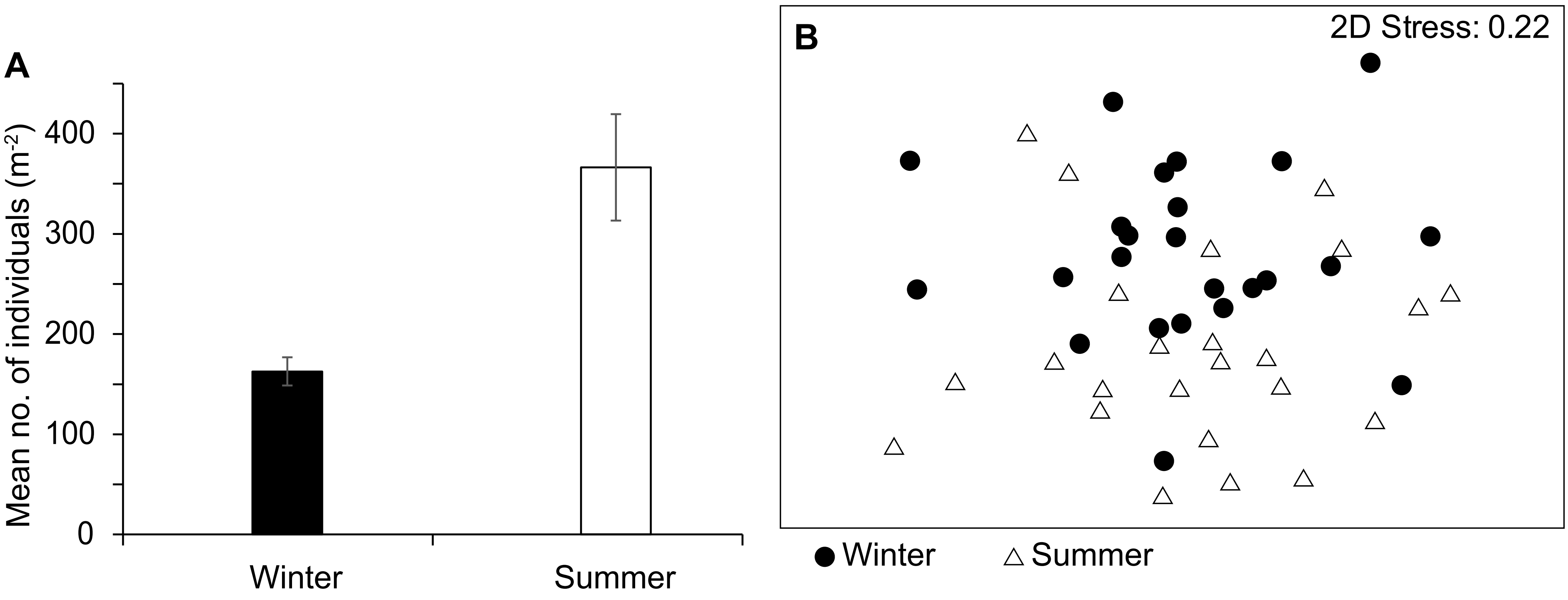


Fig. 2 Caswell et al. 2019

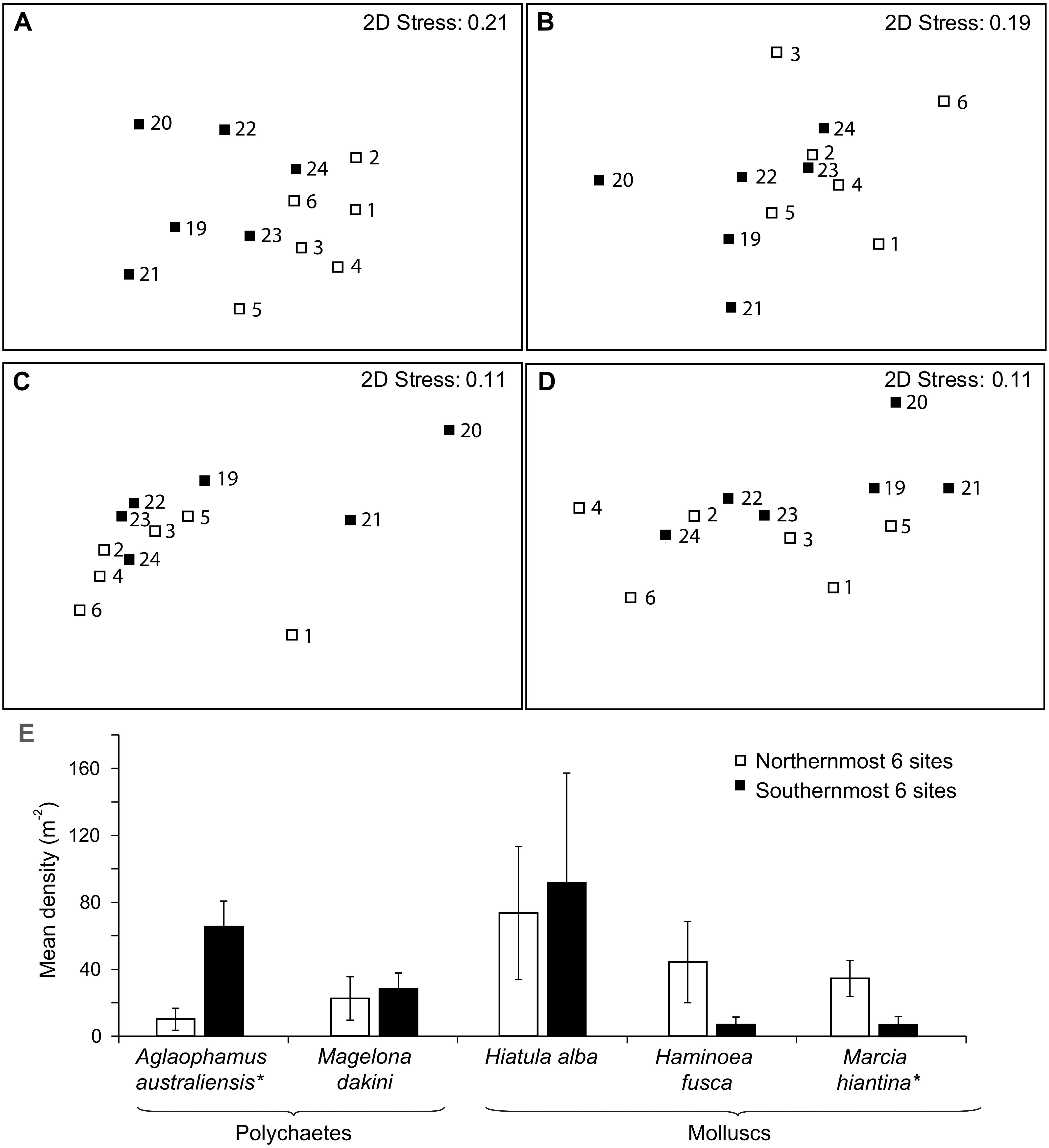
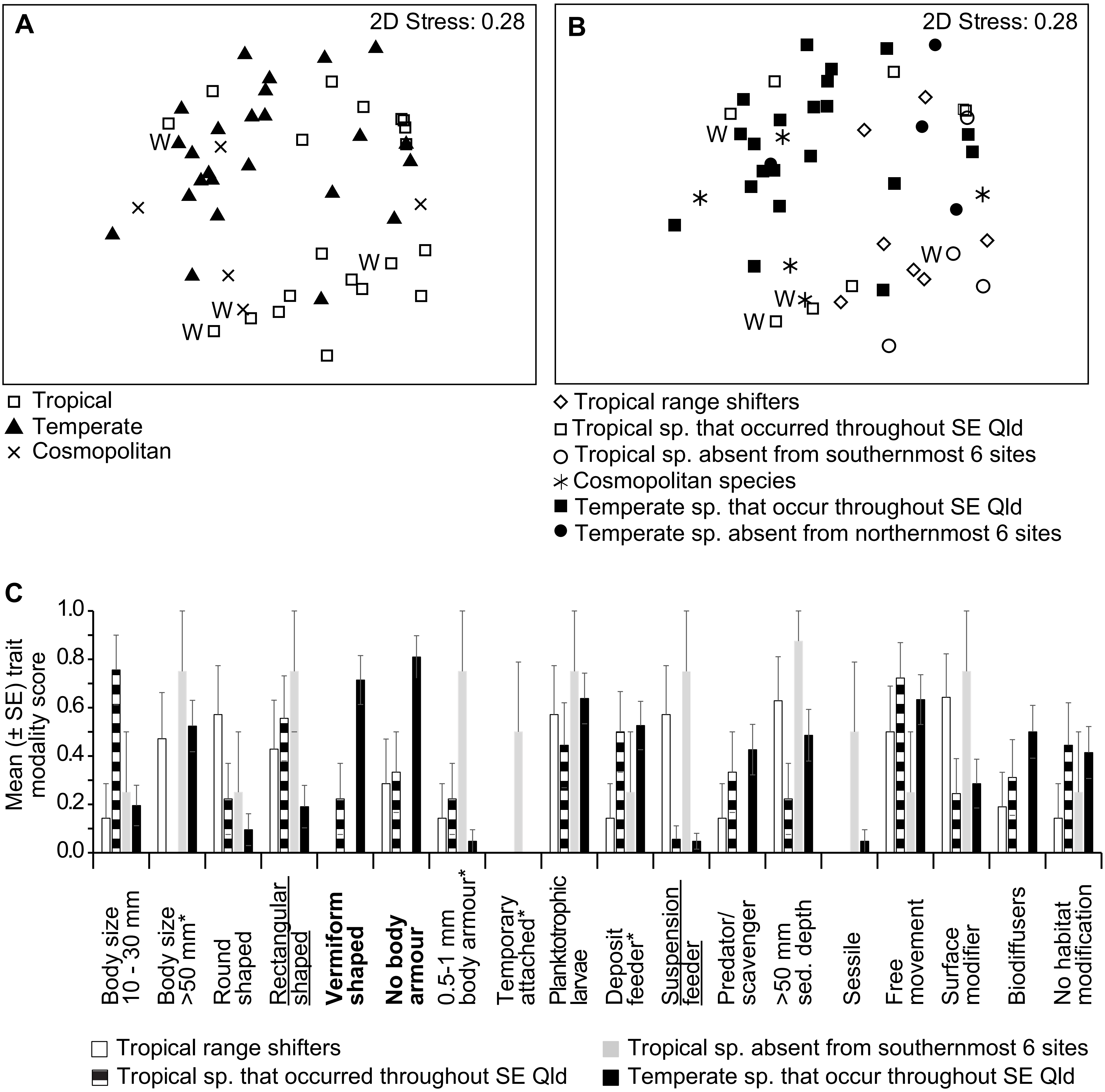


Fig. 3 Caswell et al. 2019



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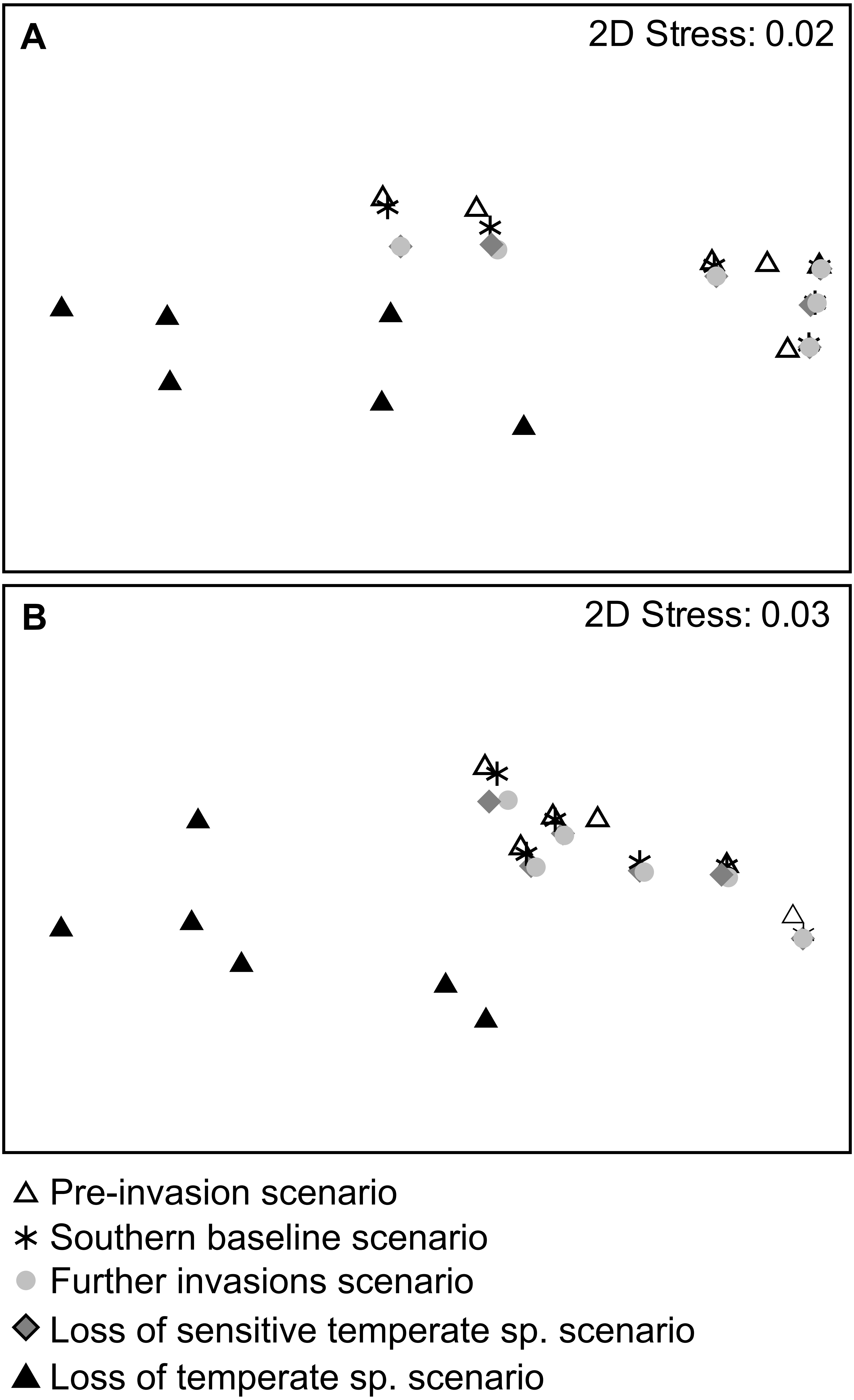


Fig. 5 Caswell et al. 2020

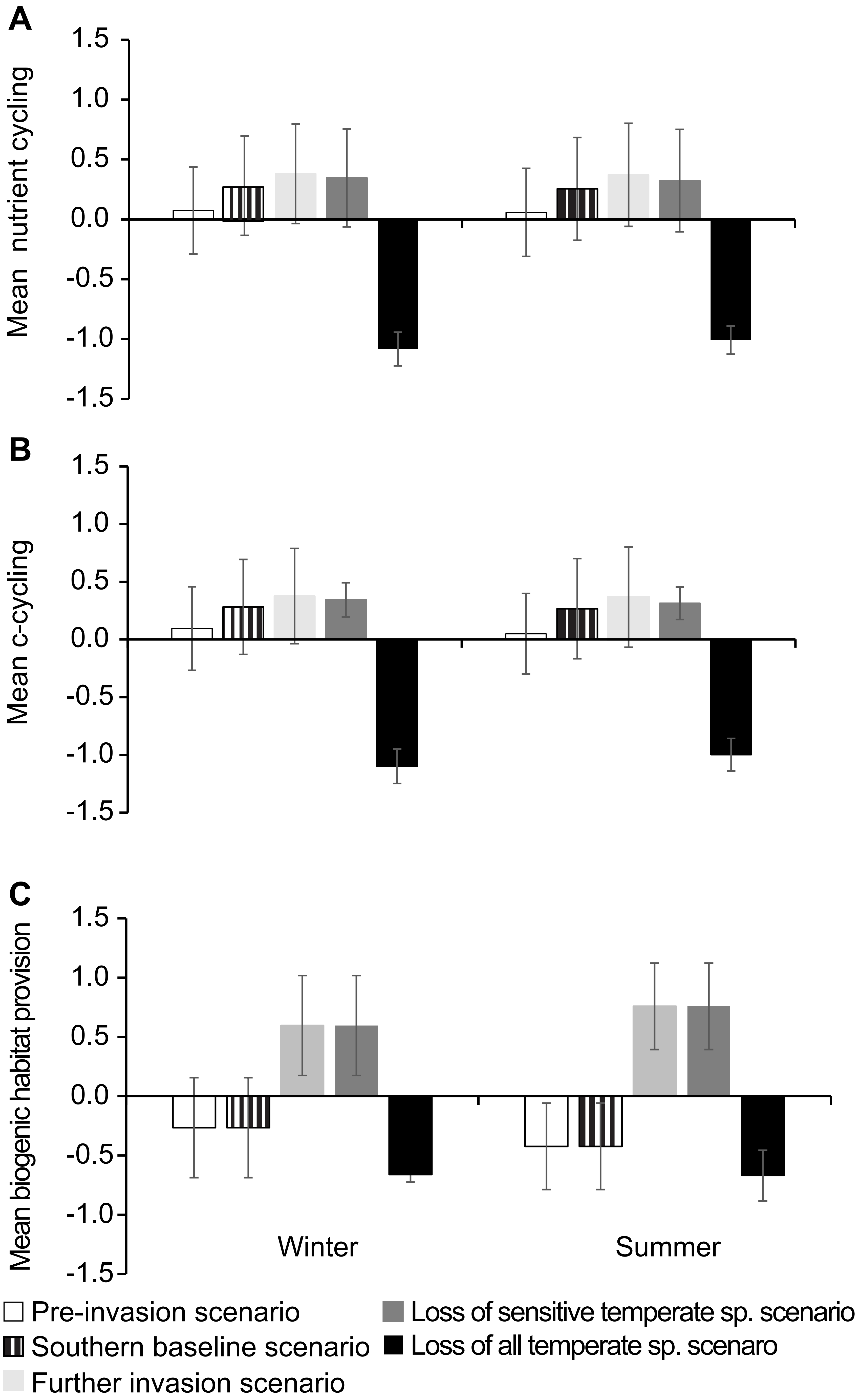


Fig. 6 Caswell et al. 2020

Table 1. The eleven biological traits and 45 trait modalities used to characterise the mudflat macrofaunal taxa, and the three ecological functions investigated (and the trait modalities used to index them). Traits were selected to represent a range of morphologies, life histories and behaviours and because they are thought to be important contributors to the three ecological functions (see detailed scientific rationale in Appendix A2). Two models were employed, for model A the value of 1 was assigned for trait modalities with highest affinity to functions and 0 for the lowest contribution. A differentially weighted model (B). was developed where trait modalities varied in their contribution to each function (see Appendix Table A.2).

Traits	**Trait modalities**
Morphological traits	
A. Maximum adult body size[1]	(1) <10 mm; (2) 10–30 mm; (3) 30–50 mm; (4) >50 mm
B. Body shape[2]	(1) Round-oval; (2) rectangular-sub-rectangular; (3) vermiform
C. Body armour thickness	(1) None; (2) 0.1–0.5 mm; (3) 0.5–1 mm; (4) 1–5 mm; (5) >5 mm
Life history traits	
D. Degree of attachment[3]	(1) None; (2) temporary; (3) permanent
E. Longevity	(1) <1 yr; (2) 1–2 yr; (3) 3–5 yr; (4) 5–10 yr; (5) >10 yr
F. Larval development	(1) Direct; (2) planktotrophic; (3) lecithotrophic
Behavioural traits	
G. Feeding	(1) Deposit feeder; (2) suspension/filter feeder; (3) predator/scavenger; (4) grazer
H. Sediment dwelling depth	(1) Epifauna; (2) 2–20 mm; (3) 20–50 mm; (4) >50 mm
I. Adult mobility	(1) Sessile/sedentary; (2) limited movement; (3) free movement; (4) swimming
J. Sediment reworking[4]	(1) None; (2) surface modifiers; (3) biodiffuser/diffusive mixing; (4) regenerators; (5) upward / downward conveyors
K. Habitat modification[5]	(1) No modification; (2) cast or mound; (3) burrow ditch/hollow; (4) biogenic tubes (5) emergent structures

Ecological Function	**Models**
<u>Nutrient cycling</u>	
Maximum adult body size >10 mm[5,6,7] (A2-A4) + rounded or rectangular body shapes (B1-B2) + deposit or suspension/filter feeders[11] (G1-G2) + sediment dwelling depths >2 mm[10] (H2-H4) + taxa with adult mobility[10] (I3) + all sediment reworking modes[8, 9] (J2-J5) + taxa that modify habitat by burrowing (K3)[10]	**Model A:** (A2*1) + (A3*1) + (A4*1) + (H3*1) + (H4*1) + (G1*1) + (G2*1) + (I3*1) + (J2*1) + (J3*1) + (J4*1) + (J5*1) + (H2*1) + (K3*1) + (B1*1) + (B2*1)
<u>Food web dynamics (C-cycling)</u>	
Taxa of all maximum adult body sizes[12] (A1-A4) + those with body armour <1 mm thick[14, 15] (C1-C3) +	**Model A:** (A1*1) + (A2*1) + (A3*1) + (A4*1) + (C1*1 + (C2*1) + (C3*1) + (E1*1) + (E2*1) + (F2*1) + (F3*1) + (G1*1) + (G2*1) + (G3*1) + (G4*1) + (H1*1) + (H2*1)

<2 year longevity (E1-E2) + all larval developmental modes[13] (F2-F3) + all feeding modes (G1-G4) + taxa dwelling at shallow sediment depths (H1-H2)	
Biogenic habitat provision	
Taxa that modify habitat by creating emergent structures (K5) + those that attach to substrates (D2-D3)	**Model A:** (K5*1) + (D2*1) + (D3*1)

[1] Largest dimension e.g. polychaetes body length, crab carapace width; [2] Length: width ratio of B1 = 1-2; B2 = 3 -10; B3 > 10; [3] D1 = highly mobile; D2= lives attached to substrate some of the time (e.g., via a weak byssus); D3 = lives permanently attached to hard substrates; [4] Sediment reworking includes: J1 = no bioturbation; J2 = surface modifiers bioturbate sediments near the surface; J3 = biodiffusors that constantly and randomly mix sediments; J4 = upward/downward conveyors that feed head up or down and transport sediment from depth to the surface or vice versa; J5 = regenerators that continuously excavate and maintaining burrows (Kristensen et al., 2012; Queirós et al., 2013). [5] Habitat modification K4: infaunal tubes. [5] Bolam et al. (2002); [6] Thrush et al. (2006); [7] Norkko et al. (2013); [8] Biles et al. (2003); [9] Kristensen et al. (2012); [10] Mermillod-Blondin et al. (2004); [11] Welsh (2003); [12] Zeuthen (1953); [13] Greve et al. (2004); [14] Mascaró and Seed (2001); [15] Boulding (1984)

Table 2. Five scenarios of changing macrofaunal assemblage composition at the southernmost mudflats (Appendix Fig. B.2) under continued anthropogenic warming in SE Queensland mudflats. The scenarios are based on changes in six categories of taxa in SE Queensland: (A) tropical species that have extended their distribution southwards over the last 20-60 years (tropical range shifters, Fig. 1C-D); (B) tropical species that occur throughout SE Queensland; (C) tropical species that currently <u>only</u> occur in the northern sites, but that could shift in the future; (D) robust temperate species whose current range extends throughout SE Queensland; (E) temperate species that are sensitive to temperature change (i.e. did not occur in the northernmost sites); and, (F) cosmopolitan species. Species that were eliminated from the observed baseline community are indicated by 'minus' and those that were added are indicated by 'plus'. Most species were present in both seasons, however for those where adjustments were made in only one season those changes are indicated.

Scenarios	Description	Density manipulations						
		Species categories						Species manipulated
		A	B	C	D	E	F	
1. Southern baseline *Describes the current functioning of mudflats*	The current community.	x	x		x	x	x	No manipulation
2. Pre-invasion *Describes functioning prior to the arrival of tropical range shifters.*	The baseline state **without** the tropical range shifters (A).		x		x	x	x	<u>Both seasons</u> • **Minus A:** *E. discoidale*, *H. fusca*, *M. hiantina*, *M. endeavouri*, *U. longidigita* <u>Winter</u> • **Minus A:** *M. maculata* <u>Summer</u> • **Minus A:** *C. depressa*, *La. anatina*
3. Further invasions *Describes functioning if more tropical species invaded.*	The baseline state **with the addition of** tropical species that might shift in the future (C).	x	x	**x**	x	x	x	<u>Both seasons</u> • **Plus C:** *L. impar*, *Li. anatina*, *T. polita* <u>Summer</u> • **Plus C:** *P. undulatus*,
4. Loss of sensitive temperate taxa *Describes functioning if more tropical species invaded AND sensitive temperate taxa were lost.*	Scenario 3 **without** sensitive temperate species (E).	x	x	x	x		x	<u>Both seasons</u> • **Plus C:** *Li. anatina*, *L. impar*, *T. polita* • **Minus E:** *A. sibogae*, *H. haswellianus*, *T. australiensis* <u>Summer</u> • **Minus E:** *S. boa* • **Plus C:** *P. undulata*
5. Loss of all temperate taxa Describes functioning if temperate species were lost and only tropical species remained.	Scenario 3 **without** any temperate species (D or E).	x	x	x			x	<u>Both seasons</u> • **Plus C:** *Li. anatina*, *L. impar*, *T. polita* • **Minus D:** *A. australiensis*, *A. richardsoni*, *A. intermedia*, *A. ehlersi*, *B. lepte*, *C. punctulatum*, *G. americana*, *H. alba*, *L. bifurcatus*, *L. tetraura*, *M. setosus*, *M. dakini*, *M. mullawa*, *M. australiensis*, *O. australis*, *P. novaehollandiae*, *V. australiensis* • **Minus E:** *A. sibogae*, *H. haswellianus*, *T. australiensis* <u>Summer</u> • **Plus C:** *P. undulata* • **Minus D:** *N. torquatus*, *P. antipoda*, *S. miersi* • **Minus E:** *S. boa*

Table 3: The biogeographic ranges of the 50 taxa (summer and winter combined) found in the 24 mudflats sampled during this study, and their known latitudinal ranges in Australia as documented from published databases (ALA, 2018; OBIS, 2018). (Globally documented latitudinal ranges are provided in Appendix B.3, NB: these do not affect the range shifts documented herein). These new data extended the ranges of 10 species (**bold rows**), and for these species the year (the latest date the shift could have begun), extent and direction of the expansion is provided. The 'typical' climatic zone of each species based on previous records is given using: the tropical climatic zones defined as 23° 27'S in Dissanayake et al. (2018), and the temperate climatic zone boundary (32.4° 00'S) was based on the southern boundary of Moreton-Tweed marine ecoregion described by Spalding et al. (2007) and the convergence of the Australian East Coast Current and the Tasman Sea Current (Cetina-Heredia et al., 2014). Abbreviations: Trop = Tropical, Temp = Temperate, N= number of sites/records.

Species	**Sp. zone**	**Max. documented latitudinal range (°) of taxa**			**Latitudinal range of taxa at 24 mudflats sampled**				**Distance & direction moved (km)**	**Rate (km decade^{-1})**
		Year	**North**	**South**	**N**	**North**	**South**	**N**		
Acetes sibogae[2]	Temp		-15.2250	-36.2070	174	-27.3436	-28.1069	12		
Aglaophamus australiensis	Temp		-17.0330	-43.0330	1093	-27.1464	-28.1069	23		
Alpheus richardsoni[2]	Temp		-16.7660	-41.4660	143	-27.1747	-28.1069	9		
Armandia intermedia[2]	Temp		-19.1160	-38.8500	285	-27.1747	-28.1069	16		
Australonereis ehlersi	Temp		-23.1830	-42.2752	566	-27.1464	-28.1069	12		
Australoplax tridentata	Trop		-10.7333	-36.2078	83	-27.1956	-28.1069	14		
Barantolla lepte	Temp		-22.3830	-38.8500	791	-27.1747	-27.8222	18		
Bulla vernicosa[2]	Trop		-23.9000	-34.7500	430	-27.2597	-28.1069	3		
Chaenostoma punctulatum	Temp		-10.7160	-36.0653	58	-27.1464	-28.1069	14		
Cirriformia tentaculata[2]	Temp		-22.3830	-42.8800	82	-27.1747	-27.6436	6		
Clorida depressa[2]	**Trop**	**1998**	-21.2350	**-27.6667**	**59**	**-27.1956**	**-27.7178**	**5**	**6 S**	**3**
Conuber sordidum[2]	All		-10.6000	-43.1179	544	-27.1464	-28.1069	21		
Elphidium discoidale [1]	**Trop**	**1983**	**-20.9000**	**-24.6814**	**2**	**-27.1747**	**-28.1069**	**7**	**381 S**	**112**
Eurysyllis tuberculata[2,4]	Trop		-14.5723	-34.7500	31	-27.1747	-27.7178	6		
Gelasimus vomeris[2]	Trop		-23.4122	-33.8083	145	-27.2775	-28.1069	10		
Glycera americana[2]	Temp		-22.3830	-41.1600	515	-27.1956	-27.8222	12		
Haminoea fusca[4]	**Trop**	**1970**	-14.6700	**-25.2500**	**16**	**-27.1747**	**-28.1069**	**16**	**317 S**	**68**
Helograpsus haswellianus[2]	Temp		-9.5833	-43.0300	207	-27.3436	-27.8222	10		
Hiatula alba	Temp		-26.7660	-43.4630	69	-27.1464	-28.1069	18		
Laternula anatina[2,4]	**Trop**	**1996**	-16.5500	**-23.4160**	**103**	**-27.1956**	**-27.7053**	**5**	**477 S**	**227**
Leitoscoloplos bifurcatus	Temp		-14.6794	-42.3902	489	-27.1464	-28.1069	12		
Lingula anatina	Trop		-20.4000	-27.9667	47	-27.2597	-27.5158	2		
Lumbrineris tetraura[2]	Temp		-28.1903	-38.7300	716	-27.1747	-28.1069	12		
Lutraria impar[2]	Trop		-23.2000	-28.3803	24	-27.1956	-27.4764	4		
Macrophthalmus setosus	Temp		-22.3833	-36.0612	133	-27.1747	-28.1069	21		
Mactra maculata[2, 3]	**Trop**	**1949**	-14.6600	**-27.5830**	**61**	**-27.1463**	**-28.1069**	**17**	**58 S**	**9**
Magelona dakini	Temp		-18.7330	-41.1612	371	-27.1464	-28.1069	19		
Marcia hiantina[2]	**Trop**	**1982**	-23.1827	**-27.6167**	**250**	**-27.1464**	**-28.1069**	**16**	**54 S**	**16**
Marphysa mullawa	Temp		-12.6660	-36.8917	122	-27.1747	-28.1069	9		
Metapenaeus endeavouri[2]	**Trop**	**1961**	-23.8450	**-27.4167**	**2395**	**-27.2775**	**-28.1069**	**8**	**77 S**	**14**
Mictyris longicarpus[2]	All		-11.9000	-38.4612	342	-27.1464	-28.1069	20		
Myrianida australiensis	**Temp**	**2011**	-30.5409	**-30.5409**	**1**	**-27.1747**	**-27.7503**	**11**	**374 N**	**623**
Nassarius coronatus[2]	Trop		-23.1300	-34.2544	299	-27.2597	-27.7503	4		
Nematoda[2]	All		-16.1333	-41.7339	30516	-27.1464	-28.1069	20		
Nemertea[2]	All		-14.5000	- 54.7083	3202	-27.1747	-28.1069	13		
Notomastus torquatus	Temp		-23.8160	-38.4889	493	-27.1464	-28.1069	21		
Owenia australis	Temp		-14.6700	-38.9000	248	-27.1464	-28.1069	21		
Paratapes undulatus[2]	Trop		-23.3330	-36.9033	230	-27.1956	-27.5158	2		
Phyllodoce novaehollandiae	Temp		19.8830	-38.7661	108	-27.1464	-28.1069	16		
Platynereis antipoda[2]	Temp		10.5863	-43.4350	385	-27.2775	-27.7178	6		
Prionospio queenslandica[4]	Trop		10.5861	-35.7461	17	-27.1463	-27.7178	11		
Pyrazus ebeninus	All		10.6830	-42.9111	380	-27.1464	-28.1069	22		
Recluzia johnii[3]	Trop		23.4167	-34.0583	11	-27.7178	-27.7503	2		
Stenothoe miersi	Temp		14.5719	-37.8898	48	-27.1747	-28.1069	8		

Sternaspis scutata[2, 4]	Trop		23.8500	-32.5000	3177	-27.3436	-27.7503	7		
Sthenelais boa[2]	Temp		27.1189	-34.0083	3971	-27.5158	-27.8222	4		
Trypaea australiensis	Temp		17.7833	-38.7000	651	-27.395	-28.1069	6		
Tubuca polita[2]	Trop		22.1167	-30.8830	102	-27.2775	-27.2775	1		
Uca longidigita	**Trop**	**1962**	21.1333	**-27.5000**	**27**	**-27.4222**	**-27.7503**	**4**	**28 S**	**5**
***Victoriopisa australiensis*[3]**	**Temp**	**2007**	27.9160	**-37.0963**	**186**	**-27.1464**	**-27.7503**	**11**	**85 N**	**86**

[1] The range given is for *E. discoidale*, however this record could potentially be confounded as subspecies *Elphidium discoidale* var. *multiloculum* was described from Moreton Bay (-27.1108 to -27.6583) by Narayan and Pandolfi (2010). If this ~~is~~ variety is confirmed as a distinct taxon then the record in the present study may not represent a range shift for the species. [2] Species that have different global ranges (see Appendix Table B.3). [3] Taxa previously recorded only once within the study area. [4] Taxa not previously recorded in the study area (and only once in greater SE Queensland).

We declare no conflict of interest

Bryony Caswell: Conceptualisation, methodology, Writing original draft preparation, Writing- review and editing, visualization, supervision
Navodha Dissanayake: Data curation, Writing original draft preparation, formal analysis, investigation, visualization
Chris Frid: Conceptualisation, methodology, Writing- review and editing, Resources, supervision, validation

Appendix A: Materials & methods

A.1 Geographic locations of the study site

Table A.1. The geographic coordinates of the 24 subtropical mudflats along the SE Queensland coast (negative latitudes indicate S of the equator) (Fig. 1).

Site no	Latitude (degrees)	Longitude (degrees)
1	-27.8222	153.0464
2	-27.1747	153.0319
3	-27.1956	153.0431
4	-27.2597	153.0747
5	-27.2775	153.0369
6	-27.3436	153.0933
7	-27.3425	153.1000
8	-27.3947	153.1391
9	-27.3950	153.1583
10	-27.3933	153.1689
11	-27.4222	153.1706
12	-27.4764	153.2033
13	-27.4808	153.2422
14	-27.5158	153.2622
15	-27.5739	153.3056
16	-27.5622	153.3003
17	-27.6019	153.3019
18	-27.6436	153.3119
19	-27.6589	153.3092
20	-27.7053	153.3239
21	-27.7178	153.3539
22	-27.7503	153.3511
23	-27.8222	153.3781
24	-28.1069	153.4464

A.2 Simulating species taxonomic and trait change and the effects on mudflat ecological functioning

Analyses were performed on both unconstrained and constrained data sets. In the latter case all of the simulated assemblage data were standardised to the same total density to aid comparisons between the five scenarios emphasising the influence of the changing species compliment rather than changes in the size of the assemblage (Table 2). This was prompted because biological traits analysis uses the total density of each trait modality to characterise an assemblage and so is sensitive to the total number of individuals within an assemblage. As we have no simple means of predicting changes in the relative densities of taxa, our constrained simulations capture changing species composition from the mean densities of the species within their observed range (i.e. the mean number of individuals/biomass recorded across the southernmost six sites during each season rounded to the nearest 10). The macrofaunal assemblages were standardised to a total of 390 individuals per m^2 in the summer and 160 individuals per m^2 in winter.

Two models (A and B) were used to explore the implications of species losses and gains from the macrofaunal assemblages of the southernmost SE Queensland mudflats sampled in this study. Model A included the trait modalities thought to make a contribution to each functions and these were effectively assigned a weighting of 1 (Frid and Caswell, 2016)(Table 1). An additional model (model B) employing differential weightings on these traits, to better reflect our, partial, understanding of the contribution of each trait modality to a particular function was also developed. For instance, macrofauna with large body sizes contribute proportionally more to some functions than smaller individuals (Norkko et al., 2013; Thrush et al., 2006). The differential weightings were derived based on known relationships between the biological traits of species and the level of ecological functioning delivered (see justification below). For both models the selected trait modalities, weighted by density, were summed separately for each function and each scenario.

Nutrient cycling. In coastal seas nutrient cycling is strongly coupled with benthic processes that regenerate nitrogen compounds from within intertidal and subtidal sediments and this can provide 20–100% of the annual N requirements for water column primary production (Welsh, 2003). Mudflats are recognised sources and sinks for organic matter and nutrients, with the direction and magnitude of these fluxes being determined by the resident macroinvertebrate, benthic primary producers and the microbial communities (D'Andrea and DeWitt, 2009). Microbes oxidise organic matter and transform elements through a series of oxidation and reduction reactions which in turn drive the biogeochemical cycling of nutrients in coastal waters facilitating pelagic primary production (Worden et al., 2015). The composition of the sedimentary microbial community and the rates of their metabolic processes are strongly influenced by local environmental conditions (Welsh 2003; Thrush et al. 2006), in particular the sediment redox state and availability of (labile) organic material (Piepenburg et al., 1995; Van Oevelen et al., 2006) (In coastal systems macrofauna facilitate the mineralization of sedimentary N and the efflux of the mineralization products into the water column. These fluxes are fourfold higher when macrobenthos are present compared with when they are not (Hansen and Blackburn, 1992; Kristensen and Blackburn, 1987; Welsh, 2003). Macrofauna facilitate nutrient cycling through a combination of biological traits such as sediment reworking which is mainly driven by the feeding, movement and behaviour of macroinvertebrates. These processes oxygenate the sediment, enhance the vertical transfer of organic matter, establish concentration gradients, increase the sediment surface area for chemical exchange with the water column (Fenchel, 1996) and influence the composition of meiofaunal and microbial communities (Fenchel and Finlay, 2008; Olafsson, 2003; Warwick and Clarke, 1984). Those with surface modifying and biodiffusive mixing traits perform constant and random local sediment mixing over short distances and make similar contributions to nutrient efflux. For instance, biodiffusive mixing by *Nereis diversicolor* and surface modifying behaviour of *Corophium volutator* and *Macoma balthica* contribute 21-38 NH_4-N µmol L^{-1} to nutrient effluxes (Biles et al., 2003). However, other bioturbatory modes such as sediment regenerators and upward/downward conveyors make greater contributions to sediment mixing and nutrient effluxes than surface modifiers or biodiffusors. The upward conveyors callianassid shrimps move deep sediment to the surface at a rate of 12 kg m^{-2} d^{-1} (Branch and Pringle, 1987) releasing 50-60 NH_4-N µmol L^{-1} (Nates and Felder, 1998). Whereas, regenerators continuously excavate sediment through digging and maintaining burrows (Kristensen et al., 2012) e.g. *Uca* sp. burrow >10 cm, excavating ~10g of sediment per day (Penha-Lopes et al., 2009) contributing between 650 and 800 NH_4-N µmol L^{-1} to the overlying waters. Thus, these traits were used to index nutrient cycling (Table 1) and included organisms with an adult body size >10 mm and more rounded/rectangular morphology that have the potential to overturn (or displace) larger amounts of sediment than those of smaller body size or more vermiform shape (Table 1, Norkko et al., 2013; Thrush et al., 2006). Similarly, mobile organisms and those that burrow have greater potential to disturb the sediment (Mermillod-Blondin et al., 2004), with some feeding and bioturbatory modes having greater influence upon sediment nutrient cycling and for this reason were weighted by their ability to disturb surface and subsurface sediments, irrigate their burrows (suspension feeders; Kristensen et al., 2012; Welsh, 2003) and mechanically degrade organic matter (Clare et al., 2015, Table 1; Welsh, 2003).

Food-web dynamics (C-cycling). The cycling of organic C in marine systems is driven by food-web dynamics (ingestion, respiration, production) and reproductive processes. Macrofaunal communities mediate the transport, transformation and storage of carbon within an ecosystem. Within sediments macrofauna may contribute between 11% and 43% of total benthic community respiration with the remainder being from bacteria and microbenthos (Piepenburg et al., 1995; Van Oevelen et al., 2006). Benthic macrofaunal C-cycling was therefore indexed by organisms of all body sizes, all feeding modes, and dispersive reproductive modes (these traits would move C around the wider ecosystem, and between the benthic and pelagic realm, more than direct developers where C from the adult is packaged into young and retained locally; Greve et al., 2004). In Model B this function was weighted towards larger-sized organisms (Table 2) that individually consume and respire more and thus cycle more C (Norkko et al., 2013; Zeuthen, 1953). A differential weighting was further applied to larger taxa that are more likely to be predated by higher trophic level consumers (Thrush et al., 2006) and so may contribute more towards wider ecosystem carbon cycling. Similarly, taxa that lack or have only a thin exoskeleton and those that only burrow to shallow sediment depths will be more regularly predated and so contribute more to C-cycling than those which have more substantial protection from, or more effectively avoid, predators. Deposit feeders ingest sediment containing organic matter that enters back into the environment through faeces recycling carbon (Wilson et al., 1993). Suspension feeders were weighted above the other feeding modes because they feed on suspended particulate organic carbon in the water column and so draw carbon into the benthic realm facilitating benthic-pelagic coupling (Smaal and Prins, 1993) compared with other feeding modes that cycle carbon within the sediment only. Species with shorter life-spans cycle more carbon through the food web (REF) as they are regularly consumed and decomposed. Whereas, longer-lived, usually larger organisms, retain organic carbon within their body tissues throughout their lives. and so shorter-lived taxa (<2 years) were included in estimates of C-cycling.

Biogenic habitat provision. Biological structures such as mussel beds, oyster reefs and kelp forests may have a substantial influence on local species diversity by increasing habitat heterogeneity (Bracken, 2018; Buhl-Mortensen et al., 2010) and providing important refuges and nursery habitat. For example, the polychaete *Diopatra cuprea* builds emergent leathery tubes incorporating fragmented bivalve shells, and so it provides hard substrates for the growth of macroalgae creating further habitat (Thomsen and McGlathery, 2005). In this way the biological activities of one organism e.g. the creation of casts, mounds or burrows can provide habitat or shelter from predators, and structures that emerge from the sediment may provide hard substrates for attachment. Taxa with such traits may act as ecosystem engineers whereby the biogenic tubes trap sediment and provide sediment stability (Rabaut et al., 2007) altering local sediment properties and organic content. Biogenic habitats are constructed by organisms that are sessile and have an attached epifaunal life habit and so this function was indexed by taxa that attach themselves to substrates and produce the emergent structures (Table 1).

Table A.1. The three ecological functions investigated (and the trait modalities used to index them) for the subtropical SE Queensland mudflats. Two models were employed an unweighted 'baseline' (model A), and a differentially weighted model (B) where trait modalities vary in their contribution to each function. Differential weightings were developed from Frid and Caswell (2016).

Ecological Function	**Models**
Nutrient cycling	
Maximum adult body size >10 mm [5, 6, 7] (A2-A4) + rounded or rectangular body shapes (B1-B2) + deposit or suspension/filter feeders[11] (G1-G2) + sediment dwelling depths >2 mm[10] (H2-H4) + taxa with adult mobility[10] (I3) + all sediment reworking modes[8, 9] (J2-J5) + taxa that modify habitat by burrowing (K3)[10]	Model A: (A2*1) + (A3*1) + (A4*1) + (H3*1) + (H4*1) + (G1*1) + (G2*1) + (I3*1) + (J2*1) + (J3*1) + (J4*1) + (J5*1) + (H2*1) + (K3*1) + (B1*1) + (B2*1) **Model B:** (A2*2) + (A3*4) + (A4*6) + (B1*1) + (B2*1) + (G1*1) + (G2*1) +(H2*2) + (H3*4) + (H4*6) + (I3*1) + (J2*1) + (J3*1) + (J4*2) + (J5*2) + (K3*3)
Food web dynamics (C-cycling)	
Taxa of all maximum adult body sizes[12] (A1-A4) + those with body armour <1 mm thick[14, 15] (C1-C3) + <2 year longevity (E1-E2) + all larval developmental modes[13] (F2-F3) + all feeding modes (G1-G4) + taxa dwelling at shallow sediment depths (H1-H2)	Model A: (A1*1) + (A2*1) + (A3*1) + (A4*1) + (C1*1 + (C2*1) + (C3*1) + (E1*1) + (E2*1) + (F2*1) + (F3*1) + (G1*1) + (G2*1) + (G3*1) + (G4*1) + (H1*1) + (H2*1) **Model B:** (A1*1) + (A2*2) + (A3*4) + (A4*6) + (C1*1) + (C2*1) + (C3*1) + (E1*1) + (E2*1) + (F2*1) + (F3*1) + (G1*1) + (G2*2) + (G3*1) + (G4*1) + (H1*1) + (H2*1)
Biogenic habitat provision	
Taxa that modify habitat by creating emergent structures (K5) + those that attach to substrates (D2-D3)	Model A: (K5*1) + (D2*1) + (D3*1) **Model B:** (K5*3) + (D2*1) + (D3*1)`

[5] Bolam et al. (2002); [6] Thrush et al. (2006); [7] Norkko et al. (2013); [8] Biles et al. (2003); [9] Kristensen et al. (2012); [10] Mermillod-Blondin et al. (2004); [11] Welsh (2003); [12] Zeuthen (1953); [13] Greve et al. (2004); [14] Mascaró and Seed (2001); [15] Boulding (1984)

Appendix B: Results

B.1 Macrofaunal assemblages of mudflats in SE Queensland

The total number of individuals recorded across the 24 sites were higher in summer (n = 3047) compared to winter (n = 1800). In both seasons 10 taxa contributed to ~70% of the cumulative macrofaunal density in the assemblage (Appendix Table B.1). In summer the suspension feeding bivalve *Hiatula alba* dominated, followed by the polychaetes *Barantolla lepte* and *Aglaophamus australiensis*. Whereas in winter the crabs *Mictyris longicarpus* and *Macrophthalmus setosus* dominated the assemblage.

Table B.1. The top 10 taxa (ranked by abundance) as a percentage of the total number of individuals retrieved in winter (2016) and summer (2017) from the 24 SE Queensland mudflats.

Summer 2017		**Winter 2016**	
Taxa	Abundance (%)	Taxa	Abundance (%)
Hiatula alba (bivalve)	14.8	*Mictyris longicarpus* (decapod)	10.4
Barantolla lepte (polychaete)	9.8	*Macrophthalmus setosus* (decapod)	10.1
Aglaophamus australiensis (polychaete)	9.7	*Barantolla lepte* (polychaete)	9.7
Elphidium discoidale multilocutum (foraminifera)	9.4	*Aglaophamus australiensis* (polychaete)	9.2
Macrophthalmus setosus (decapod)	5.5	*Hiatula alba* (bivalve)	8.2
Magelona dakini (polychaete)	4.5	*Pyrazus ebeninus* (gastropod)	6.8
Notomastus torquatus (polychaete)	3.8	*Magelona dakini* (polychaete)	4.3
Marcia hiantina (bivalve)	3.6	*Owenia australis* (polychaete)	4.1
Haminoea fusca (gastropod)	3.6	*Uca vomeris* (decapod)	4.0
Nematoda	3.4	*Notomastus torquatus* (polychaete)	3.9

B.2 Biogeographic variations in the species composition of mudflat assemblages

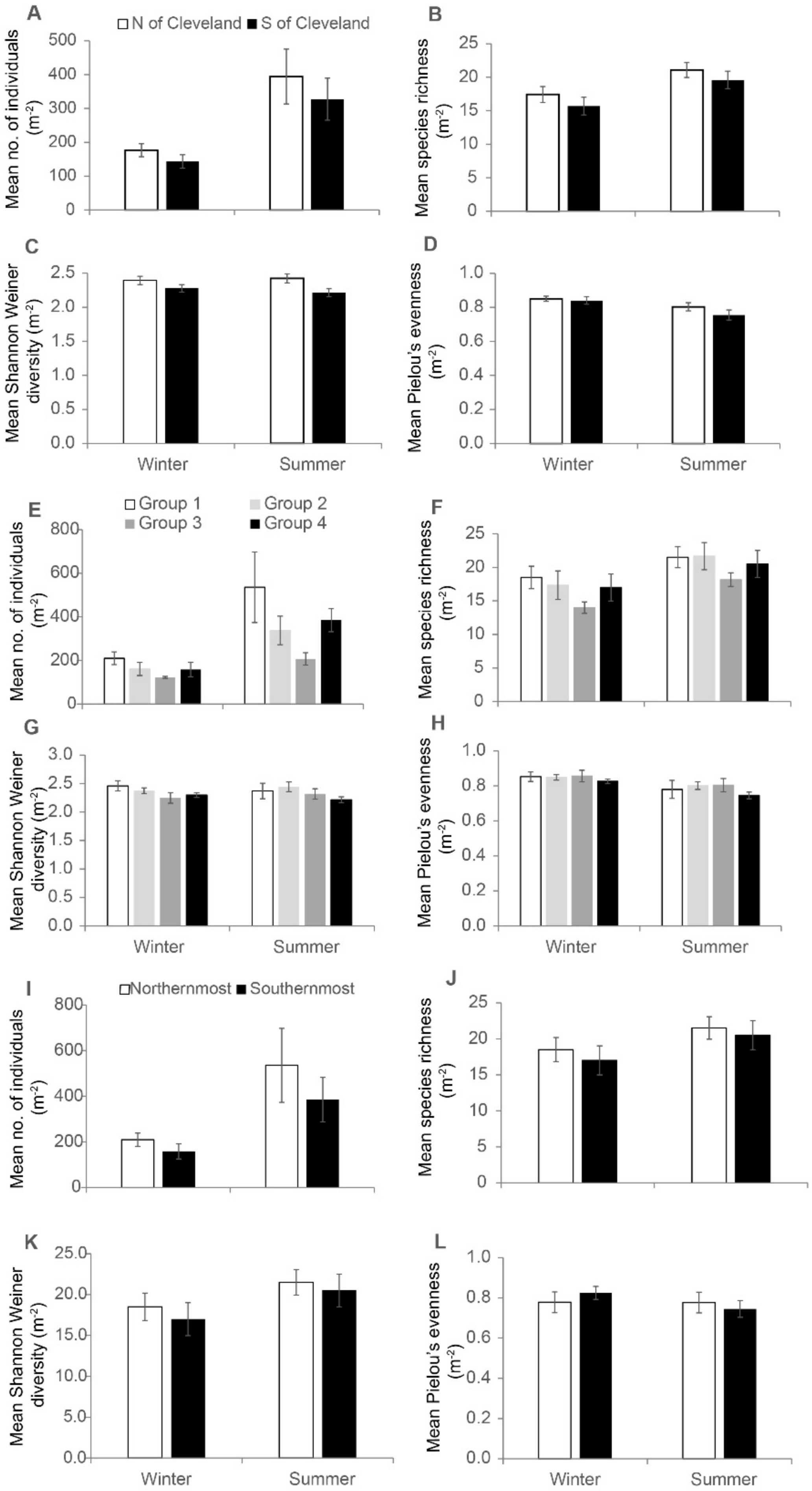


Fig. B.1. Mudflat macrofaunal assemblage (n=24) mean (±SE) density, species richness, Shannon Weiner diversity and Pielou's evenness across varying biogeographic conditions in SE Queensland, Australia in winter 2016 and summer 2017. Data are grouped: (A)-(D) north and south of Cleveland; (E)-(I) into four subgroups from north to south by latitude (group 1: mudflat 1-6; group 2: mudflats 7-12; group 3: mudflats 13-18; group 4: mudflats 19-24 most southern sites (Fig. 1); and (J)-(L) the northernmost and southernmost six sites.

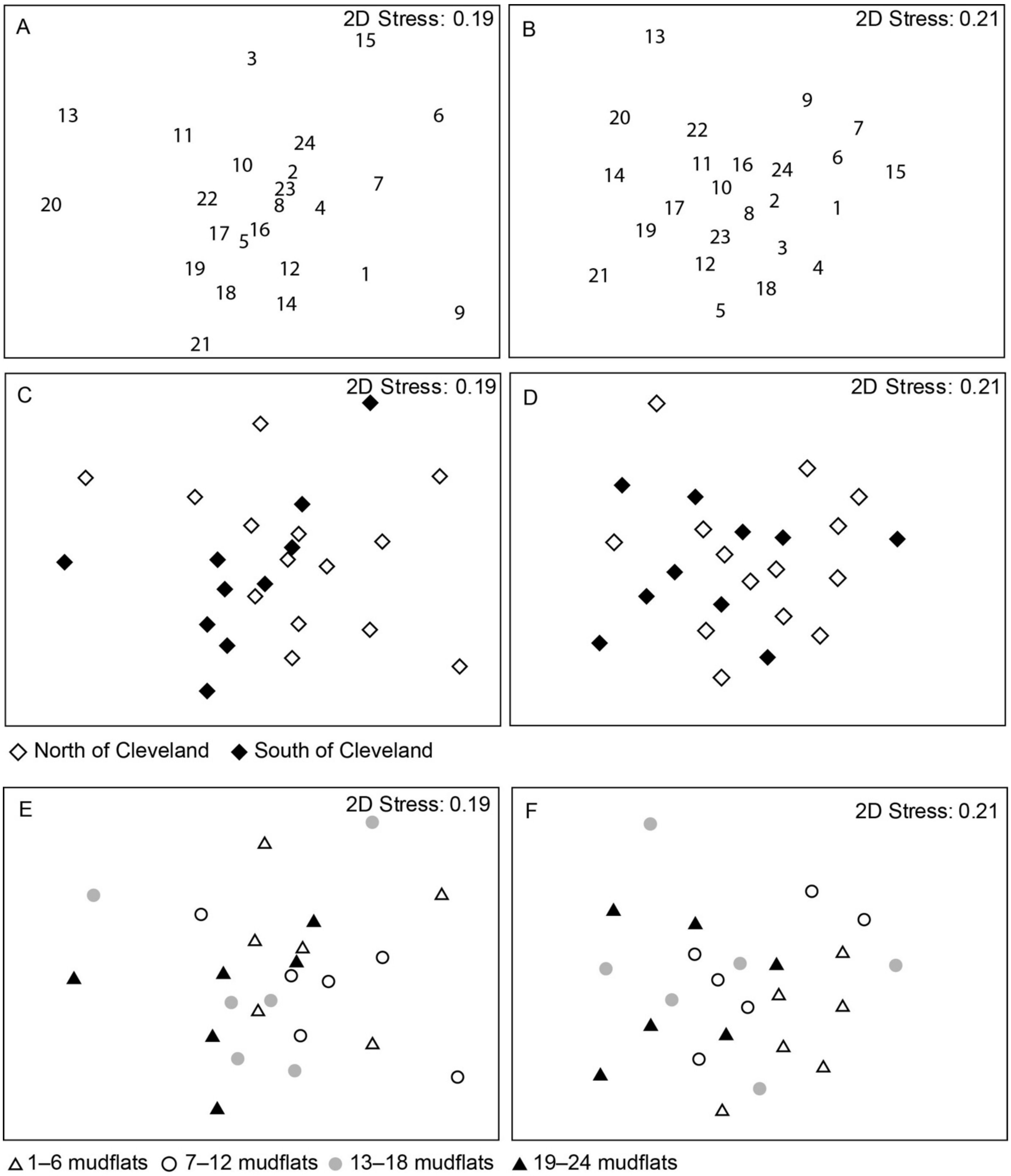


Fig. B.2 nMDS ordination of the Bray-Curtis similarity of the macrofaunal assemblage composition (log (X+1) transformed) in 24 mudflats in SE Queensland, Australia. The taxonomic composition of the mudflat assemblages (A) with site numbers for summer, (B) with site numbers for winter, (C) north and south of Cleveland in winter, and (D) summer; (E) between four groups of sites from north (sites 1-6) to south (sites 19-24) in winter, and (F) summer.

Table B.2. Kruskal-Wallis comparisons of the median number of individuals per m^2, species richness, Shannon Weiner diversity and Pielou's evenness of the macrofaunal assemblages from 24 mudflats in SE Queensland in winter 2016 and summer 2017. Three biogeographic comparisons are included (Fig. 1): (i) sites to the north and south of Cleveland, (ii) the 24 sites divided into 4 equal-sized groups proceeding from north to south, and (iii) the northernmost and southernmost six sites. *Indicates a significant difference.

Metric (m^{-2})	Winter 2016			Summer 2017		
	χ^2	df, n	p	χ^2	df, n	p
(i) North and south of Cleveland						
Total no. individuals	0.992	1, 24	0.319	0.014	1, 24	0.907
Species richness	0.679	1, 24	0.410	0.630	1, 24	0.427
Shannon Weiner	2.143	1, 24	0.143	5.488	1, 24	0.019*
Pielou's evenness	0.003	1, 24	0.953	1.895	1, 24	0.169
(ii) Four equal sized groups						
Total no. individuals	4.112	3, 6	0.250	4.780	3, 6	0.189
Species richness	2.934	3, 6	0.402	2.914	3, 6	0.405
Shannon Weiner	3.713	3, 6	0.294	3.527	3, 6	0.317
Pielou's evenness	0.420	3, 6	0.936	1.673	3, 6	0.643
(iii) Northernmost and southernmost six sites						
Total no. individuals	1.641	1, 6	0.200	0.641	1, 6	0.423
Species richness	0.105	1, 6	0.746	0.103	1, 6	0.748
Shannon Weiner	0.410	1, 6	0.522	1.641	1, 6	0.200
Pielou's evenness	0.316	1, 6	0.574	0.926	1, 6	0.336

Table B.3 The biogeographic ranges of the 50 taxa (summer and winter combined) found in the 24 mudflats sampled during this study, and their known **global** latitudinal ranges as documented from published databases (ALA, 2018; OBIS, 2018). (Australian documented latitudinal ranges in Australia are provided in the manuscript Table 3). These new records extended the ranges of 10 species (**bold rows**), and for these species the year (the latest date the shift could have begun), extent and direction of the expansion is provided. The 'typical' climatic zone of each species based on previous records is given using the tropical climatic zones defined as 23° 27'S (Dissanayake et al. (2018)), and the temperate climatic zone boundary (32.4° 00'S) was based on the southward boundary of Moreton-Tweed marine ecoregion described by Spalding et al. (2007) and the convergence of the Australian East Coast Current and westward Tasman Front (Cetina-Heredia et al., 2014). Abbreviations: Trop = Tropical, Temp = Temperate, N= number of sites/records.

Species	**Sp. zone**	**Max. documented latitudinal range (°) of taxa**				**Latitudinal range of taxa at 24 mudflats sampled**			**Dist. moved (km)**	**Rate (km decade^{-1})**
		Year	**North**	**South**	**N**	**North**	**South**	**N**		
Acetes sibogae^2	Temp		-5.0000	-36.2070	174	-27.3436	-28.1069	12		
Aglaophamus australiensis	Temp		-17.0330	-43.0330	1093	-27.1464	-28.1069	23		
Alpheus richardsoni^2	Temp		-9.5000	-41.4660	143	-27.1747	-28.1069	9		
Armandia intermedia^2	Temp		27.2355	-38.8500	285	-27.1747	-28.1069	16		
Australonereis ehlersi	Temp		-23.1830	-42.2752	566	-27.1464	-28.1069	12		
Australoplax tridentata	Trop		-10.7333	-36.2078	83	-27.1956	-28.1069	14		
Barantolla lepte	Temp		-22.3830	-38.8500	791	-27.1747	-27.8222	18		
Bulla vernicosa^2	Trop		26.5000	-34.7500	430	-27.2597	-28.1069	3		
Chaenostoma punctulatum	Temp		-10.7160	-36.0653	58	-27.1464	-28.1069	14		
Cirriformia tentaculata^2	Temp		60.4103	-42.8800	82	-27.1747	-27.6436	6		
Clorida depressa^2	**Trop**	**1998**	**-4.8172**	**-27.6667**	**59**	**-27.1956**	**-27.7178**	**5**	**6 S**	**3**
Conuber sordidum^2	All		-1.5000	-43.1179	544	-27.1464	-28.1069	21		

Elphidium discoidale[1, 2]	Trop		29.3800	-24.6814	48	-27.1747	-28.1069	7		
Eurysyllis tuberculata[2, 4]	Trop		60.4102	-34.7500	31	-27.1747	-27.7178	6		
Gelasimus vomeris[2]	Trop		11.6660	-33.8083	145	-27.2775	-28.1069	10		
Glycera americana[2]	Temp		54.9781	-41.1600	515	-27.1956	-27.8222	12		
Haminoea fusca[4]	**Trop**	**1970**	**-14.6700**	**-25.2500**	**16**	**-27.1747**	**-28.1069**	**16**	**317 S**	**68**
Helograpsus haswellianus[2]	Temp		34.6800	-43.0300	207	-27.3436	-27.8222	10		
Hiatula alba	Temp		-21.4592	-43.4630	69	-27.1464	-28.1069	18		
Laternula anatina[2, 4]	**Trop**	**1996**	**35.3317**	**-23.4160**	**103**	**-27.1956**	**-27.7053**	**5**	**477 S**	**227**
Leitoscoloplos bifurcatus	Temp		-12.4330	-42.3902	489	-27.1464	-28.1069	12		
Lingula anatina	Trop		-21.6786	-27.9667	47	-27.2597	-27.5158	2		
Lumbrineris tetraura[2]	Temp		60.4100	-38.7300	716	-27.1747	-28.1069	12		
Lutraria impar[2]	Trop		21.6788	-28.3803	24	-27.1956	-27.4764	4		
Macrophthalmus setosus	Temp		-22.3833	-36.0612	133	-27.1747	-28.1069	21		
Mactra maculata[2,3]	**Trop**	**1949**	**-9.9500**	**-27.5830**	**61**	**-27.1463**	**-28.1069**	**17**	**58 S**	**9**
Magelona dakini	Temp		-18.7330	-41.1612	371	-27.1464	-28.1069	19		
Marcia hiantina[2]	**Trop**	**1982**	**22.6252**	**-27.6167**	**250**	**-27.1464**	**-28.1069**	**16**	**54 S**	**16**
Marphysa mullawa	Temp		-12.6660	-36.8917	122	-27.1747	-28.1069	9		
Metapenaeus endeavouri[2]	**Trop**	**1961**	**-9.3100**	**-27.4167**	**2395**	**-27.2775**	**-28.1069**	**8**	**77 S**	**14**
Mictyris longicarpus[2]	All		24.1792	-38.4612	342	-27.1464	-28.1069	20		
Myrianida australiensis	**Temp**	**2011**	**-30.5409**	**-30.5409**	**1**	**-27.1747**	**-27.7503**	**11**	**374 N**	**623**
Nassarius coronatus[2]	Trop		28.9660	-34.2544	299	-27.2597	-27.7503	4		
Nematoda[2]	All		69.3539	-41.7339	30516	-27.1464	-28.1069	20		
Nemertea[2]	All		71.5508	- 75.0967	3202	-27.1747	-28.1069	13		
Notomastus torquatus	Temp		-23.8160	-38.4889	493	-27.1464	-28.1069	21		
Owenia australis	Temp		-12.0880	-38.9000	248	-27.1464	-28.1069	21		
Paratapes undulatus[2]	Trop		23.9850	-36.9033	230	-27.1956	-27.5158	2		
Phyllodoce novaehollandiae	Temp		-19.8830	-38.7661	108	-27.1464	-28.1069	16		
Platynereis antipoda[2]	Temp		21.4100	-43.4350	385	-27.2775	-27.7178	6		
Prionospio queenslandica[4]	Trop		-10.5861	-35.7461	17	-27.1463	-27.7178	11		
Pyrazus ebeninus	All		-10.6830	-42.9111	380	-27.1464	-28.1069	22		
Recluzia johnii[2]	Trop		-12.3500	-34.0583	11	-27.7178	-27.7503	2		
Stenothoe miersi	Temp		-14.5719	-37.8898	48	-27.1747	-28.1069	8		
Sternaspis scutata[2 ,4]	Trop		77.9983	-70.5000	3177	-27.3436	-27.7503	7		
Sthenelais boa[2]	Temp		69.9475	-34.0083	3971	-27.5158	-27.8222	4		
Trypaea australiensis	Temp		-12.8667	-38.7000	651	-27.395	-28.1069	6		
Tubuca polita[2]	Trop		-9.3830	-30.8830	102	-27.2775	-27.2775	1		
Uca longidigita	**Trop**	**1962**	**-21.1333**	**-27.5000**	**27**	**-27.4222**	**-27.7503**	**4**	**28 S**	**5**
Victoriopisa australiensis[3]	**Temp**	**2007**	**-27.9160**	**-37.0963**	**186**	**-27.1464**	**-27.7503**	**11**	**86 N**	**86**

[1]The range given is for *E. discoidale*, however this record could potentially be confounded as subspecies *Elphidium discoidale* var. *multiloculum* was described from Moreton Bay (-27.1108 to -27.6583) by Narayan and Pandolfi (2010). If this is variety is confirmed as a distinct taxon then the record in the present study may not represent a range shift for the species. [2]The global range of the species differed from the Australian range. [3]Taxa previously recorded only once within the study area. [4]Taxa not previously recorded in the study area (and only once in greater SE Queensland).

B.3. Biogeographic differences in macrofaunal trait composition

Similar to species compositional patterns, the trait diversity measures did not differ significantly between each biogeographic gradient (Table B.4) of the SE Queensland subtropical mudflat assemblages

Table B.4. Kruskal-Wallis comparisons of the median number of trait modality richness, Shannon Weiner diversity and Pielou's evenness for trait modalities of the macrofaunal assemblages found in mudflats from 24 sites in SE Queensland in the winter of 2016 and summer of 2017. Three comparisons are included (i) those sites to the north and south of Cleveland, (ii) the 24 sites divided into 4 groups (six sites each) proceeding from north to south, and (iii) the northernmost and southernmost six sites. *Indicates a significant difference

Metric (m^{-2})	Winter 2016			Summer 2017		
	χ^2	df, n	p	χ^2	df, n	p
(i) North and south of Cleveland						
Trait modality richness	0.468	1, 24	0.494	0.004	1, 24	0.951
Shannon Weiner	2.788	1, 24	0.095	4.443	1, 24	0.035*
Pielou's evenness	0.494	1, 24	0.492	3.295	1, 24	0.069
(ii) Four equal sized groups						
Trait modality richness	1.379	3, 6	0.711	3.729	3, 6	0.292
Shannon Weiner	3.980	3, 6	0.264	3.800	3, 6	0.284
Pielou's evenness	2.256	3, 6	0.521	2.993	3, 6	0.393
(iii) Northernmost and southernmost six sites						
Trait modality richness	0.061	1, 6	0.805	0.408	1, 6	0.523
Shannon Weiner	1.447	1, 6	0.229	1.256	1, 6	0.262
Pielou's evenness	0.231	1, 6	0.631	0.641	1, 6	0.423

B.4. Trait modality profiles

Table B.5. The trait modalities that contributed >50% cumulative dissimilarity between the trait profiles of temperate species that occurred throughout SE Queensland and (i) tropical range shifters, (ii) tropical species that occurred throughout SE Queensland, (iii) tropical species that were absent from southernmost 6 sites. The significant differences (*) of the trait modalities between the paired groups identified by Mann-Whitney *U* test are also represented.

Trait modalities	**Mann-Whitney U test to compare the differences between the groups**		
Temperate taxa vs	Tropical range shifters	Tropical sp. occurred throughout SE Qld	Tropical sp. that were absent in SE Qld
10-30 mm body size	Z = -0.445, p = 0.657	Z = -2.912, p = 0.004*	Z = -0.149, p = 0.882
>50 mm body size	Z = -0.176, p = 0.861	Z = -2.8276, p = 0.005*	Z = -0.872, p = 0.383
Round shaped	Z = -2.611, p = 0.009*	Z = -0.922, p = 0.357	Z = -0.855, p = 0.392
Rectangular shaped	Z = -1.237, p = 0.216	Z = -1.966, p = 0.049*	Z = -2.238, p = 0.025*
Vermiform shaped	Z = -3.223, p = 0.001*	Z = -2.451, p = 0.014*	Z = -2.619, p = 0.009*
No body armour	Z = -2.524, p = 0.012*	Z = -2.493, p = 0.013*	Z = -3.117, p = 0.002*
0.5-1 mm body armour	Z = -0.832, p = 0.405	Z = -1.436, p = 0.151	Z = -3.441, p = 0.001*
Temporary attached	Z = 0.000, p = 1.000	Z = 0.000, p = 1.000	Z = -3.310, p = 0.001*
Planktotrophic	Z = -0.310, p = 0.756	Z = -0.990, p = 0.322	Z = -0.441, p = 0.659
Deposit feeder	Z = -2.069, p = 0.039*	Z = -0.219, p = 0.827	Z = -1.193, p = 0.233
Suspension feeder	Z = -2.891, p = 0.004*	Z = -0.131, p = 0.896	Z = -3.241, p = 0.001*
Predator/scavenger	Z = -1.406, p = 0.160	Z = -0.461, p = 0.645	Z = -1.698, p = 0.090
>50 mm sed. depth	Z = -0.731, p = 0.465	Z = -1.367, p = 0.172	Z = -1.468, p = 0.142
Sessile	Z = -0.577, p = 0.564	Z = -0.655, p = 0.513	Z = -2.500, p = 0.012*
Free movement	Z = -0.622, p = 0.534	Z = -0.520, p = 0.603	Z = -1.370, p = 0.171
Surface modifier	Z = -1.768, p = 0.077	Z = -0.085, p = 0.932	Z = -1.737, p = 0.082

Biodiffusers	Z = -1.346, p = 0.178	Z = -1.098, p = 0.272	Z = -1.869, p = 0.062
No habitat modification	Z = -1.258, p = 0.209	Z = -0.284, p = 0.777	Z = -0.555, p = 0.579

B.5. Simulations of species and traits composition and functional change

The addition or removal of species from the baseline scenario changed the number of individuals within the unconstrained assemblage while the total abundance of individuals in the assemblage was capped for the constrained scenarios. The species composition (in both constrained and unconstrained analyses) differed significantly between the 5 scenarios in both seasons (Fig. B.3), with scenario 5 differing significantly from the remaining 4 scenarios in every case (ANOSIM p<0.05 in each case) (Table B.6).

The trait composition, in trials with the constrained total abundance, differed significantly between the 5 scenarios for winter (ANOSIM, global R = 0.209, p = 0.002, Fig. B.3A) and summer (ANOSIM, global R = 0.254, p = 0.001, Fig. B.3B). The pairwise ANOSIM results showed that the trait composition of scenario 5 differed significantly from the trait compositions of the remaining 4 scenarios, in line with the changed species composition (Table B.7-8).

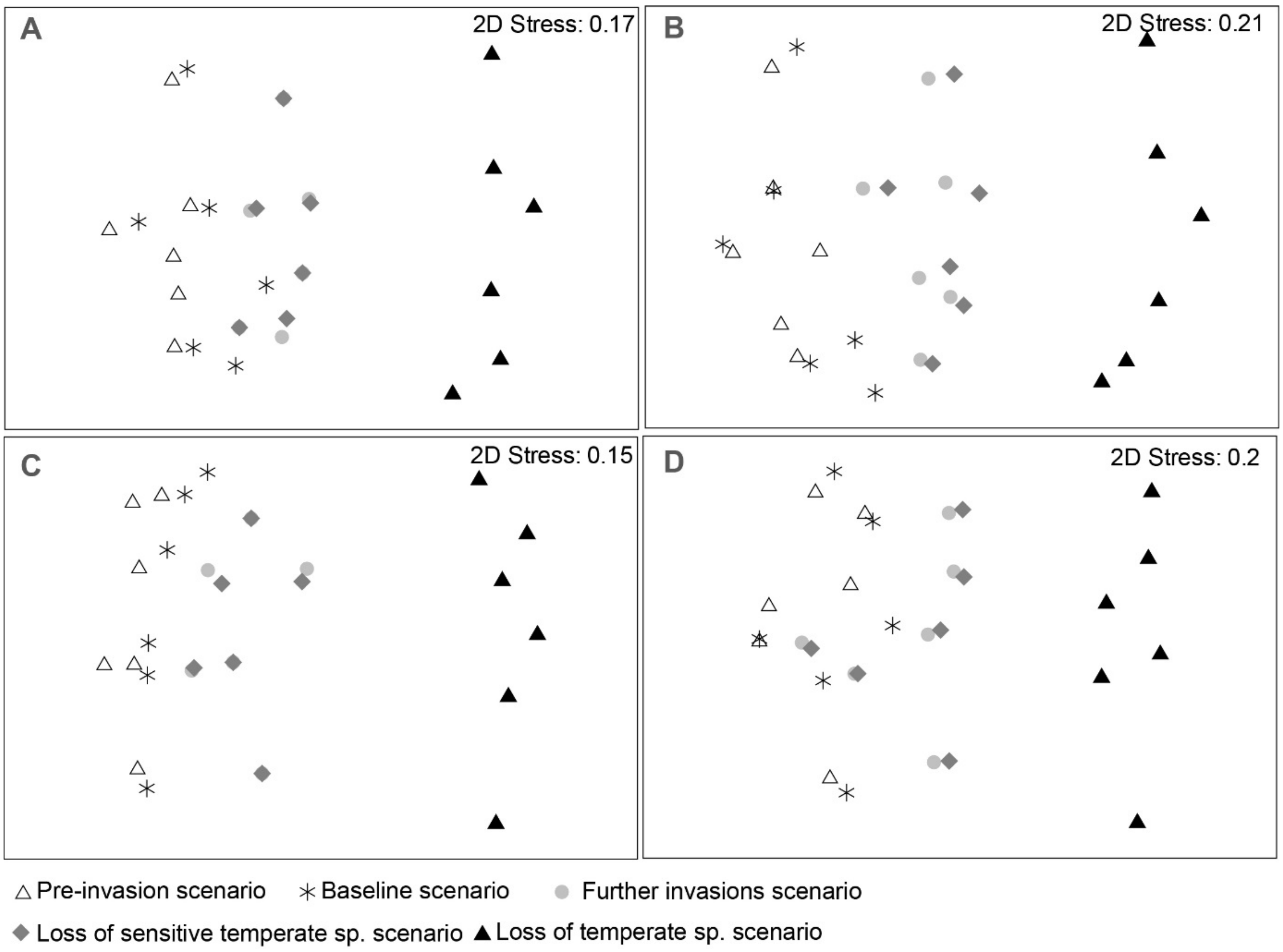


Fig. B.3. nMDS ordination of the Bray-Curtis similarity of the taxonomic composition (log (X+1) transformed) of the simulated mudflat macrofaunal assemblages observed in the six southernmost mudflats in SE Queensland. For the five scenarios based on unconstrained density (A) in winter 2016 and (B) in summer 2017; species composition (constrained density) (C) in winter 2016 and (D) in summer 2017.

Table B.6. Comparisons of the simulated macrofaunal species composition in SE Queensland mudflats (unconstrained and constrained density; pairwise ANOSIM) and SIMPER dissimilarity between the five range shift scenarios for winter 2016 and summer 2017. Species that contributed >5% to the dissimilarity between each of the scenarios is shown. Species that differed significantly between the two scenarios are indicated in ‘*’ sign. *A. australiensis* = *Aglaophamus australiensis*, *B. lepte* = *Barantolla lepte*, *H. alba* = *Hiatula alba*, *Li. anatina* = *Lingula anatine*, *Lu. impar* = *Lutraria impar*, *M. setosus* = *Macrophthalmus setosus*, *M. dakini* = *Magelona dakini*, *N. torquatus* = *Notomastus torquatus* and *P. ebeninus* = *Pyrazus ebeninus*.

Scenario comparisons	ANOSIM statistics	SIMPER dissim. (%)	Species that contributed >5% to SIMPER dissimilarity
Winter density (unconstrained)			
5 & 1	R = 0.906,p=0.002*	83.01	*A. australiensis*, *B. lepte*, *M. dakini*, *N. torquatus*
5 & 2	R = 0.983,p=0.002*	87.54	*A. australiensis*, *B. lepte*, *M. dakini*, *N. torquatus*, *H. alba*, *M. setosus*
5 & 3	R = 0.785,p=0.002*	69.44	*A. australiensis*, *B. lepte*, *M. dakini*, *N. torquatus*, *H. alba*, *M. setosus*
5 & 4	R = 0.783, p=0.002*	68.84	*A. australiensis*, *B. lepte*, *M. dakini*, *N. torquatus*, *H. alba*, *M. setosus*
Summer density (unconstrained)			
1 & 4	R = 0.250,p=0.019*	49.20	*Lu. impar*, *H. alba*
2 & 3	R = 0.250,p=0.032*	47.00	*Lu. impar*, *H. alba*
2 & 4	R = 0.309,p=0.009*	49.66	*Lu. impar*, *H. alba*
5 & 1	R = 0.870,p=0.002*	78.48	*A. australiensis*, *M. dakini*, *Lu. impar*, *N. torquatus*
5 & 2	R = 0.993,p=0.002*	81.53	*A. australiensis*, *M. dakini*, *Lu. impar*, *N. torquatus*, *B. lepte*
5 & 3	R = 0.700,p=0.002*	63.66	*A. australiensis*, *M. dakini*, *N. torquatus*, *B. lepte*
5 & 4	R = 0.650,p=0.002*	61.90	*A. australiensis*, *M. dakini*, *N. torquatus*, *B. lepte*, *M. setosus*
Winter density (constrained)			
5 & 1	R = 0.970,p=0.002*	80.92	*Lu. impar*, *A. australiensis*
5 & 2	R = 0.998,p=0.002*	83.77	*Lu. impar*, *A. australiensis*
5 & 3	R = 0.872,p=0.002*	68.37	*A. australiensis*, *M. dakini*
5 & 4	R = 0.859,p=0.002*	66.90	*A. australiensis*, *M. dakini*
Summer density (constrained)			
5 & 1	R = 0.917,p=0.002*	77.60	*A. australiensis**, *B. lepte*, *Lu. impar*, *M. dakini*, *Li. anatina*
5 & 2	R = 1.000,p=0.002*	80.78	*A. australiensis*, *B. lepte*, *Lu. impar*, *M. dakini*, *Li. anatina*
5 & 3	R = 0.783,p=0.002*	67.18	*A. australiensis*, *B. lepte*, *Lu. impar*, *M. dakini*
5 & 4	R = 0.752, p=0.002*	66.56	*A. australiensis*, *B. lepte*, *Lu. impar*, *M. dakini*

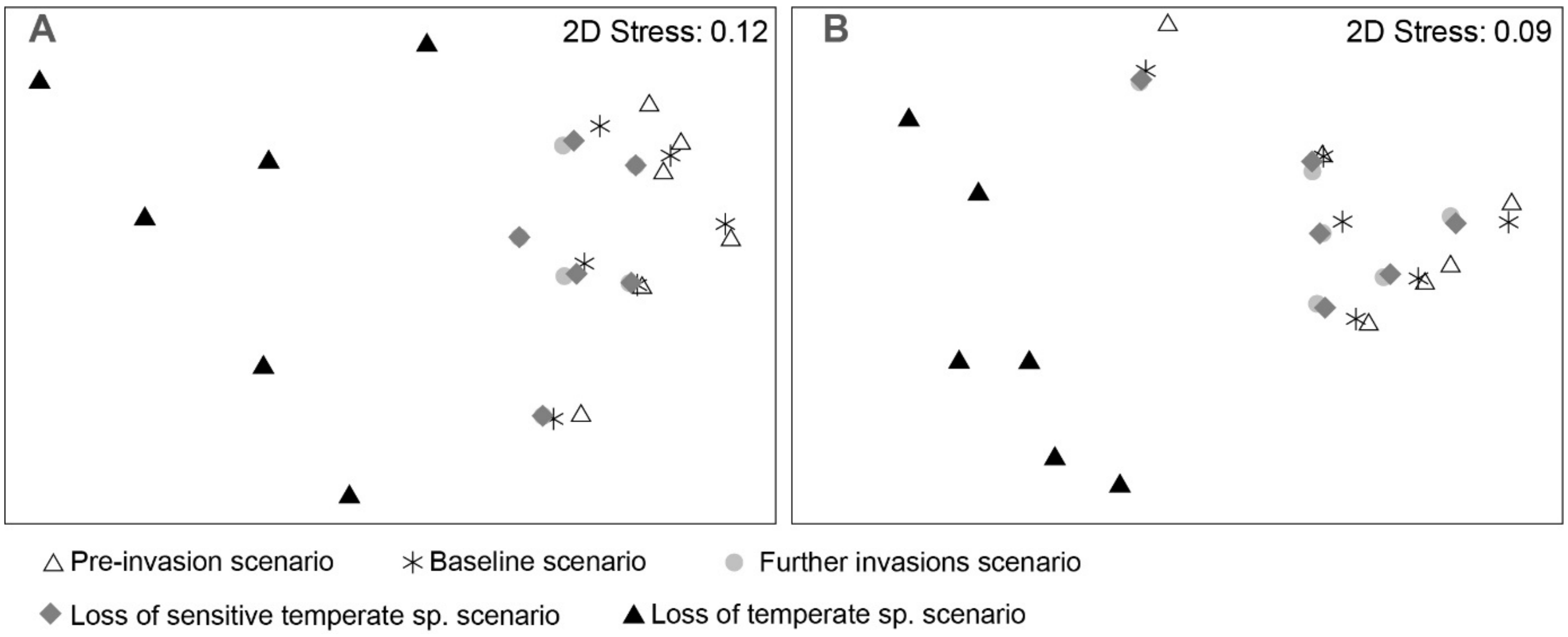
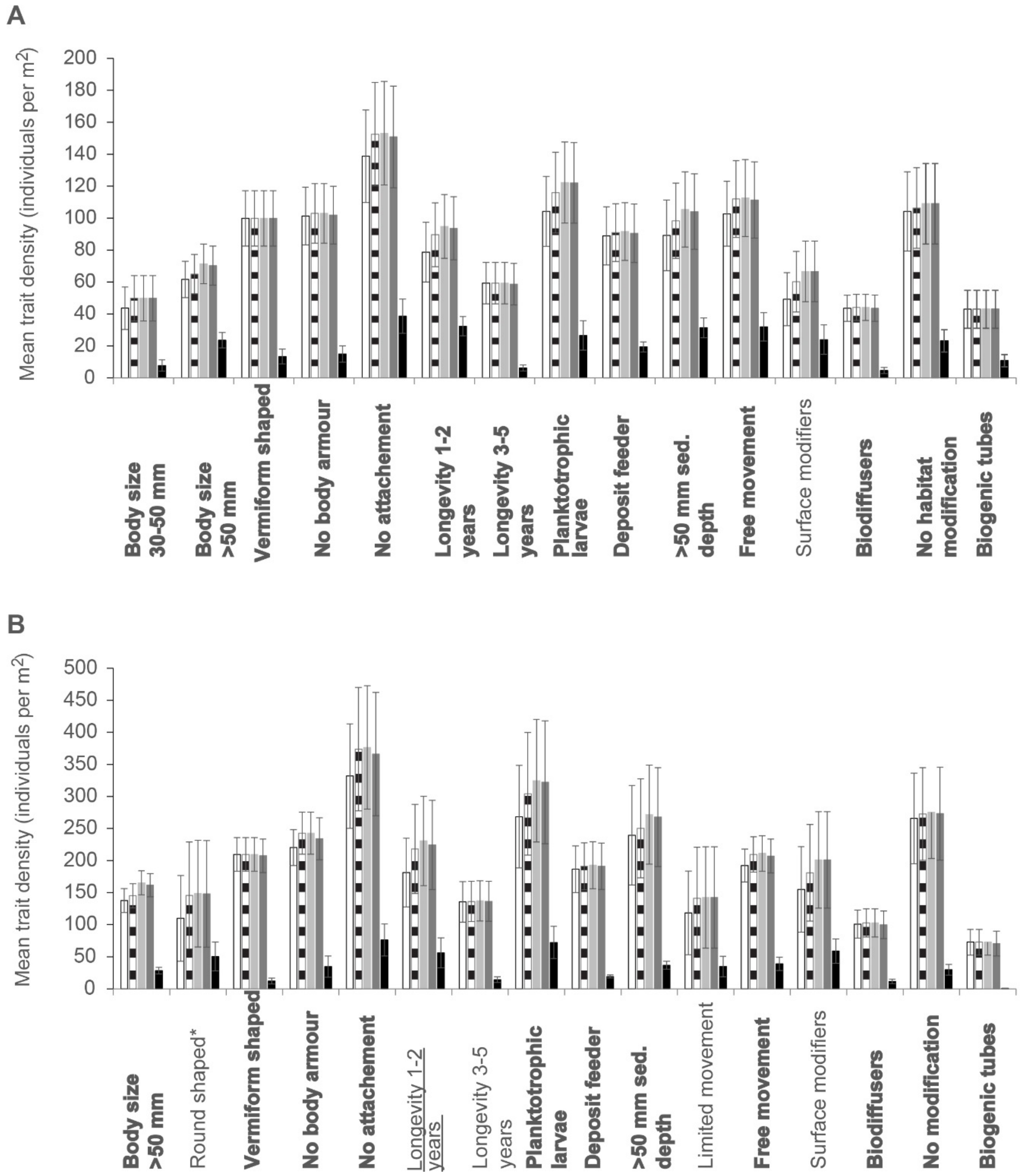


Fig. B.4. nMDS ordination of the Bray-Curtis similarity of the trait composition (density constrained) simulated mudflat macrofaunal assemblages observed in the SE Queensland southernmost 6 mudflats (A) in winter 2016 and (B) in summer 2017.

Table B.7. Comparisons of the simulated macrofaunal trait composition of SE Queensland southernmost 6 mudflats (density unconstrained and constrained; pairwise ANOSIM) and SIMPER dissimilarity between the five range shift scenarios for winter 2016 and summer 2017. Significant differences are indicated in '*' sign.

Scenario comparisons	ANOSIM results	Average SIMPER dissimilarity (%)
Winter density unconstrained		
5 & 1	R = 0.572, p = 0.009*	58.74
5 & 2	R = 0.580, p = 0.009*	57.91
5 & 3	R = 0.578, p = 0.006*	57.97
5 & 4	R = 0.569, p = 0.009*	57.75
Summer density unconstrained		
5 & 1	R = 0.726, p = 0.002*	67.27
5 & 2	R = 0.733, P = 0.002*	66.86
5 & 3	R = 0.707, p = 0.002*	66.45
5 & 4	R = 0.700, p = 0.002*	66.04
Winter density constrained		
5 & 1	R = 0.765, p =0.002*	29.92
5 & 2	R = 0.815, p =0.002*	31.74
5 & 3	R = 0.646, p =0.002*	27.66
5 & 4	R = 0.659, p =0.002*	27.92
Summer density constrained		
5 & 1	R = 0.880, p =0.002*	36.98
5 & 2	R = 0.946, p =0.002*	39.61
5 & 3	R = 0.765, p =0.002*	33.62
5 & 4	R = 0.776, p =0.002*	34.19


A
Mean trait density (individuals per m2)
0
20
40
60
80
100
120
140
160
180
200
Body size 30-50 mm
Body size >50 mm
Vermiform shaped
No body armour
No attachement
Longevity 1-2 years
Longevity 3-5 years
Planktotrophic larvae
Deposit feeder
>50 mm sed. depth
Free movement
Surface modifiers
Biodiffusers
No habitat modification
Biogenic tubes
B
Mean trait density (individuals per m2)
0
50
100
150
200
250
300
350
400
450
500
Body size >50 mm
Round shaped*
Vermiform shaped
No body armour
No attachement
Longevity 1-2 years
Longevity 3-5 years
Planktotrophic larvae
Deposit feeder
>50 mm sed. depth
Limited movement
Free movement
Surface modifiers
Biodiffusers
No modification
Biogenic tubes

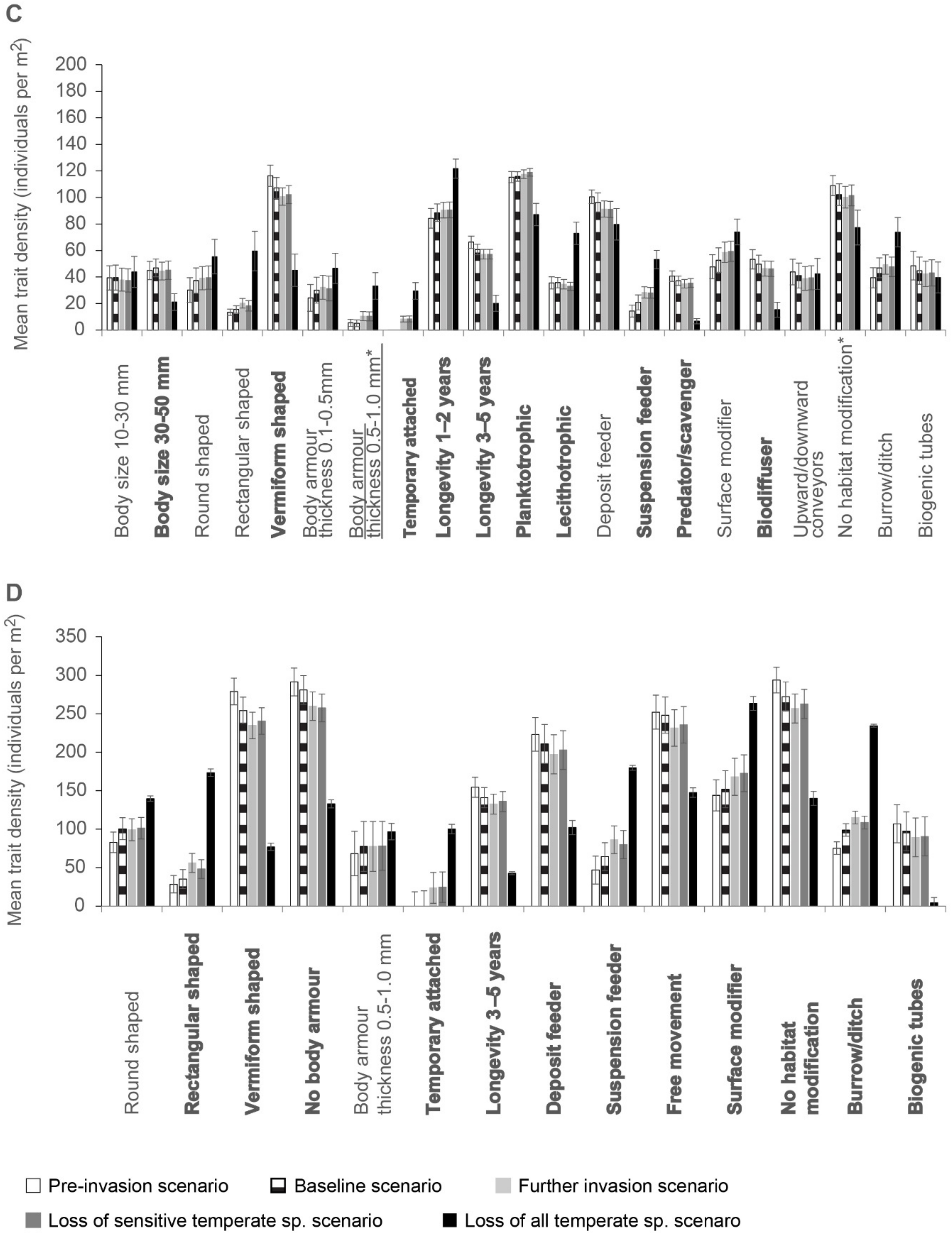


Fig B.5. The trait modalities (mean ± SE) that contributed to >70% cumulative dissimilarity (SIMPER analysis) between the pairwise unconstrained trait compositional scenario groups in SE Queensland southernmost 6 mudflats (A) winter 2016 and (B) summer 2017, and constrained trait compositional scenario groups (C) winter 2016 and (D) summer 2017. The trait modalities in **bold** indicate that the trait composition of scenario 5 differed significantly ($p < 0.05$) from the remaining 4 scenarios, and the underlined trait modalities indicate that 2 scenarios have differed significantly from scenario 5 (Table B.8-9).

Table B.8 Results of T-test to compare means abundances of trait modalities that contributed to the 70% of the dissimilarity between the five biogeographic range shift scenarios for mudflat macrofaunal assemblages in winter in SE Queensland. Results from both unconstrained and constrained macroinvertebrate density in winter 2016. Degrees of freedom=10. The biological traits that showed significant differences between the pairs are indicated in * sign

Trait modalities (for winter)	**Scenario comparisons (unconstrained density)**				**Scenario comparisons (constrained density)**			
	1 & 5	2 & 5	3 & 5	4 & 5	1 & 5	2 & 5	3 & 5	4 & 5
Body size 30–50 mm	t = 2.889 p = 0.016*		t = 2.889 p = 0.016*	t = 2.889 p = 0.016*	t = 2.800, p = 0.019*		t = 2.533 p = 0.030*	t = 2.580 p = 0.027*
Body size >50 mm	t = 3.116 p = 0.011*	t = 3.059, p = 0.012*	t = 3.116, p = 0.011*	t = 3.548, p = 0.005*				
Rectangular shaped					t = -2.893 p = 0.016*	t = -3.049 p = 0.012*	t = -2.558 p = 0.028*	t = -2.669 p = 0.024*
Round shaped					t = -1.117 p = 0.290	t = -1.567 p = 0.148	t = -1.030 p = 0.327	t = -1.004 p = 0.339
Vermiform shaped	t = 4.819, p = 0.001*	t = 4.819, p = 0.001*	t = 4.819, p = 0.001*	t = 4.819, p = 0.001*	t = 4.294, p = 0.002*	t = 4.895, p = 0.001*	t = 4.021, p = 0.002*	t = 4.099 p = 0.002*
No body armour	t = 4.545, p = 0.001*	t = 4.602, p = 0.001*	t = 4.545, p = 0.001*	t = 4.618, p = 0.001*				
0.1-0.5 mm body armour thickness					t = -1.095 p = 0.299	t = -1.095 p = 0.299	t = -0.979 p = 0.350	t = -1.036 p = 0.325
0.5-1.0 mm body armour thickness					t = -2.707 p = 0.022*	t = -2.707 p = 0.022*	t = 2.147 p = 0.057	t = -2.151 p = 0.057
No attachment	t = 3.345, p = 0.007*	t = 3.246, p = 0.009*	t = 3.364, p = 0.007*	t = 3.341, p = 0.007*				
Temporary attached					t = -4.721 p = 0.001*	t = -4.729 p = 0.001*	t = -3.200 p = 0.009*	t = 3.178, p = 0.010*
Longevity 1-2 years	t = 2.743, p = 0.021*	t = 2.364, p = 0.040*	t = 2.992, p = 0.014*	t = 2.965, p = 0.014*	t = -3.382 p = 0.007*	t = -3.382 p = 0.007*	t = -3.335 p = 0.008*	t = -3.303 p = 0.008*
Longevity 3-5 years	t = 4.033, p = 0.002*	t = 4.033, p = 0.002*	t = 4.033, p = 0.002*	t = 3.975, p = 0.003*	t = 5.664, p<0.0001*	t = 5.664, p<0.0001*	t = 5.271, p<0.0001*	t = 5.281 p<0.0001*
Planktotrophic larvae	t = 3.316, p = 0.008*	t = 3.363, p = 0.009*	t = 3.553, p = 0.005*	t = 3.555, p = 0.005*	t = 3.160, p = 0.010*	t = 3.160, p = 0.010*	t = 3.391, p = 0.007*	t = 3.609 p = 0.005*
Lecithotrophic larvae					t = -4.009 p = 0.002*	t = -4.009 p = 0.002*	t = -4.211 p = 0.002*	t = -4.479 p = 0.001*
Deposit feeder	t = 3.896 p=0.003*	t = 3.769 p=0.004*	t = 3.932 p =0.003*	t = 3.840 p =0.003*	t = 1.192, p = 0.261	t = 1.192, p = 0.261	t = 0.864 p = 0.408	t = 0.846 p = 0.417
Suspension feeder					t = -3.603 p = 0.005*	t = -3.603 p = 0.005*	t = -3.057 p = 0.012*	t = -3.128 p = 0.011*
Predator/scavenger					t = 7.685, p<0.0001*	t = 7.685 p<0.0001*	t = 7.584 p<0.0001*	t = 7.571, p<0.0001*
>50 mm sed. Depth	t = 2.748 p =0.021*	t = 2.519 p =0.030*	t = 3.038 p =0.013*	t = 2.978 p =0.014*				
Free movement	t = 3.123 p =0.011*	t = 3.195 p = 0.010*	t = 3.149 p = 0.010*	t = 3.115 p = 0.011*				
Surface modifiers	t = 1.724, p = 0.115	t = 1.332, p = 0.212	t = 2.029, p = 0.070	t = 2.029, p = 0.070	t = -1.597 p = 0.141	t = -1.597 p = 0.141	t = -1.254 p = 0.238	t = -1.187 p = 0.263
Biodiffusers	t = 4.675 p = 0.001*	t = 4.629 p = 0.001*	t = 4.675 p = 0.001*	t = 4.582 p = 0.001*	t = 3.840 p = 0.003	t = 3.840, p = 0.003	t = 3.840, p = 0.003	t = 3.834 p = 0.003
Upward/downward conveyors					t = -0.079 p = 0.939	t = -0.079 p = 0.939	t = 0.234 p = 0.820	t = -0.197 p = 0.848
No habitat modification	t = 3.177 p = 0.010*	t = 3.157, p = 0.010*	t = 3.278, p = 0.008*	t = 3.278, p = 0.008*	t = 1.599, p = 0.141	t = 1.599 p = 0.141	t = 1.478, p = 0.170	t = 1.576 p = 0.146
Burrow/ditch					t = -2.004 p = 0.070	t = -2.004 p = 0.070	t = -1.835 p = 0.095	t = -1.953 p = 0.079
Biogenic tubes		t = 2.586, p = 0.027*			t = 0.335, p = 0.745	t = 0.335, p = 0.745	t = 0.177, p = 0.863	t = 0.227 p = 0.825

Table B.9. Results of T-tests to compare mean abundance of trait modalities that contributed to 70% of the dissimilarity between the five biogeographic range shift scenarios for mudflat macrofaunal assemblages in summer in SE Queensland. Results from both unconstrained and constrained macroinvertebrate density in summer 2017. Degrees of freedom=10. The biological traits that showed significant differences between the pairs are indicated in * sign

Trait modalities (for summer)	**Scenario comparisons (unconstrained density)**				**Scenario comparisons (constrained density)**			
	1 & 5	2 &5	3 & 5	4 & 5	1 & 5	2 & 5	3 & 5	4 & 5
Body size >50 mm	t = 5.981 p<0.0001*	t = 3.059, p = 0.012*	t = 7.018, p<0.0001*	t = 7.048, p<0.0001*				
Rectangular shaped					t = -4.517 p = 0.001*	t = -4.840 p = 0.001*	t = -3.735 p = 0.004*	t = -4.034 p = 0.002*
Round shaped	t = 1.106, p = 0.296			t = 1.134, p = 0.283	t = -0.675 p = 0.515	t = -0.998 p = 0.346	t = -0.707 p = 0.495	t = -0.670 p = 0.518
Vermiform shaped	t = 7.370, p<0.0001*	t = 4.819, p = 0.001*	t = 7.370, p < 0.001*	t = 7.409, p < 0.001*	t = 4.197, p = 0.002*	t = 4.607, p = 0.001*	t = 4.069 p = 0.002*	t = 4.116, p = 0.002*
No body armour	t = 5.663 p<0.0001*	t = 5.706, p = 0.001*	t = 5.663, p<0.0001*	t = 5.434, p<0.0001*	t = 3.916, p = 0.003*	t = 3.608, p = 0.005*	t = 3.680 p = 0.004*	t = 3.644 p = 0.005*
0.1-0.5 mm body armour thickness					t = -0.451 p = 0.661			
0.5-1.0 mm body armour thickness						t = -0.601 p = 0.561	t = -0.464 p = 0.652	t = -0.448 p = 0.664
No attachment	t = 2.993, p = 0.013*	t = 3.002, p = 0.013*	t = 3.020, p = 0.013*	t = 2.919, p = 0.015*				
Temporary attached					t = -5.151 p<0.0001*	t = -5.151 p<0.0001*	t = -3.826 p = 0.003*	t = -3.765 p = 0.004*
Longevity 1-2 years	t = 2.206, p = 0.051	t = 2.364, p = 0.040*	t = 2.376, p = 0.039*	t = 2.291, p = 0.045*	t = -0.230 p = 0.823	t = -0.533 p = 0.606	t = -0.200 p = 0.846	t = -0.214 p = 0.835
Longevity 3-5 years	t = 3.847, p = 0.003*	t = 4.033, p = 0.002*	t = 2.376, p = 0.039*	t = 3.886, p = 0.003*	t = 5.954 p<0.0001*	t = 6.314, p<0.0001*	t = 5.773, p<0.0001*	t = 5.985, p<0.0001*
Planktotrophic larvae	t = 2.343, p = 0.040*	t = 3.363, p = 0.009*	t = 2.548, p = 0.029*	t = 2.520, p = 0.030*				
Deposit feeder	t = 4.675, p = 0.001*	t = 3.769, p = 0.004*	t = 4.717, p = 0.001*	t = 4.743, p = 0.001*	t = 4.124, p = 0.002*	t = 5.384 p<0.0001*	t = 3.882, p = 0.003*	t = 3.952 p = 0.003*
Suspension feeder					t = -4.052 p = 0.002*	t = -5.109 p<0.0001*	t = -3.677 p = 0.004*	t = -3.731 p = 0.004*
>50 mm sed. Depth	t = 2.755, p = 0.020*	t = 2.519, p = 0.030*	t = 3.030, p = 0.013*	t = 2.988, p = 0.014*				
Free movement	t = 5.773 p<0.0001*	t = 3.195, p = 0.010*	t = 5.826, p<0.0001*	t = 5.909, p<0.0001*	t = 2.907, p = 0.016*	t = 3.032, p = 0.013*	t = 2.659, p = 0.024*	t = 2.709 p = 0.022*
Limited movement	t = 1.318, p = 0.217		t = 1.132, p = 0.213	t = 1.132, p = 0.213				
Surface modifiers	t = 1.572, p = 0.147	t = 1.332, p = 0.212	t = 1.833, p = 0.097	t = 1.833, p = 0.097	t = -2.752 p = 0.020*	t = -2.826 p = 0.018*	t = -2.574 p = 0.028*	t = -2.464 p = 0.033*
Biodiffusers		t = 4.629, p = 0.001*	t = 4.112, p = 0.002*	t = 4.041, p = 0.002*				
No habitat modification	t = 3.343, p = 0.007*	t = 3.157, p = 0.010*	t = 3.380, p = 0.007*	t = 3.343, p = 0.007*	t = 5.088, p<0.0001*	t = 5.998, p<0.0001*	t = 4.438, p = 0.001*	t = 4.632, p = 0.001*
Burrow/ditch					t = -5.652 p<0.0001*	t = -6.520 p<0.0001*	t = -4.936 p = 0.001*	t = -5.181 p<0.0001*
Biogenic tubes		t = 2.586, p = 0.027*			t = 3.126, p = 0.011*	t = 3.122, p = 0.011*	t = 3.198, p = 0.010*	t = 3.160, p = 0.010*

B.5.1 Mudflat ecological functioning past, present and future

For model A (constrained density), nutrient cycling (ANOVA, winter: F = 0.294, p = 0.879; summer: F = 0.061, p = 0.993, Fig B.6A) and c-cycling (ANOVA, winter: F = 0.039, p = 0.997; summer: F = 0.156, p = 0.958, Fig. B.6B) functions did not differ significantly between the scenarios in either season. However, the biogenic habitat provision function differed significantly between the 5 scenarios (ANOVA, F = 8.659, p < 0.0001, Fig. B.5C) with scenario 1 to 4 differing significantly from scenario 5 (p < 0.05, Table B.10).

The unconstrained estimates of nutrient cycling significantly differed between scenarios for model B (ANOVA, winter: F = 3.197, p = 0.030, summer: F = 3.117, p = 0.033; Table B.10, Fig. B.7A). Nutrient cycling in scenario 3 and 4 were 5 fold higher in summer and 3 fold higher in winter compared to scenario 5. There were no significant differences observed for constrained density in both seasons.

Unconstrained estimates for c-cycling differed significantly between the 5 scenarios in model B for both seasons (ANOVA, winter: F = 3.172, p = 0.031; summer: F = 3.128, p = 0.032; Table B.10, Fig. B.6B) but did not show a significant difference between the scenarios for constrained density (ANOVA, winter: F = 0.559, p = 0.694; summer: F = 1.782, p = 0.164; Table B.10, Fig.B.7D). The mean c-cycling was significantly higher in scenario 3 than in scenario 5 in for both seasons in model B (p<0.05).

Biogenic habitat provision (unconstrained and constrained estimates) significantly differed between scenarios, with scenarios 3 and 4 differing from scenario 5 in summer for model B unconstrained, and scenario 1 differing from scenario 5 for constrained model B (ANOVA, unconstrained: F = 3.079, p = 0.034, Fig B.7E; constrained: F = 3.495, p = 0.021, Table B.10, Fig. B.7F).

Table B.10. Results of ANOVA and post-hoc tests (Tukey test or Mann-Whitney U[1]) to compare delivery of estimates for three ecological functions (e.g. nutrient cycling, c-cycling and biogenic habitat provision) in SE Queensland's southernmost 6 mudflats for the 5 scenarios. Models are based on trait modalities with affinities for each function (Model A) and application of differential weighting (Model B) (Table A.2). Hyphen indicates no post-hoc test because of non-significant ANOVA. The pairs that differed significantly (p<0.05) are indicated in '*' sign.

Ecosystem function		Winter	Summer
Unconstrained density			
Nutrient cycling	Model A[1]	F = 2.868, p = 0.044*	F = 2.362, p = 0.080
	Scenario 1 & 5	Z = -2.402, p = 0.016*	-
	Scenario 2 & 5	Z = -2.401, p = 0.017*	-
	Scenario 3 & 5	Z = -2.565, p = 0.010*	-
	Scenario 4 & 5	Z = -2.564, p = 0.011*	-
	Model B	F = 3.197, p = 0.030*	F = 3.117, p = 0.033*
	Scenario 3 & 5	p = 0.043*	p = 0.045*
	Scenario 4 & 5	p = 0.05*	p = 0.05*
C-cycling	Model A[1]	F = 2.956, p = 0.040*	F = 2.301, p = 0.087
	Scenario 1 & 5	Z = -2.242, p = 0.025*	-
	Scenario 2 & 5	Z = -2.244, p = 0.026*	-
	Scenario 3 & 5	Z = -2.562, p = 0.010*	-
	Scenario 4 & 5	Z = -2.563, p = 0.011*	-

	Model B	F = 3.172, p = 0.031*	F = 3.128, p = 0.032*
	Scenario 3 & 5	p = 0.045*	p = 0.044*
Biogenic habitat provision	Model A	F = 2.266, p = 0.091	F = 4.240, p = 0.009*
	Scenario 3 & 5	-	p = 0.046*
	Scenario 4 & 5	-	p = 0.046*
	Model B	F = 1.753, p = 0.170	F = 3.079, p = 0.034*
	Scenario 3 & 5	-	p = 0.049*
	Scenario 4 & 5	-	p = 0.049*
Constrained density			
Nutrient cycling	Model A	F = 0.294, p = 0.879	F = 0.061, p = 0.993
	Model B	F = 0.650, p = 0.054	F = 1.148, p = 0.357
C-cycling	Model A	F = 0.039, p = 0.997	F = 0.156, p = 0.958
	Model B	F = 0.961, p = 0.446	F = 0.131, p = 0.969
Biogenic habitat provision	Model A	F = 1.442, p = 0.250	F = 8.659, p < 0.0001*
	Scenario 1 & 5	-	p < 0.0001*
	Scenario 2 & 5	-	p < 0.0001*
	Scenario 3 & 5	-	p = 0.009*
	Scenario 4 & 5	-	p = 0.012*
	Model B	F = 0.146, p = 0.963	F = 3.495, p = 0.021*
	Scenario 1 & 5	-	p < 0.030*

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[1] Post-hoc tests (Tukey, Student-Newman-Keuls) failed to identify pairwise differences between the scenarios, therefore Mann-Whitney U tests were performed (with Bonferroni correction) to identify which scenarios differed.

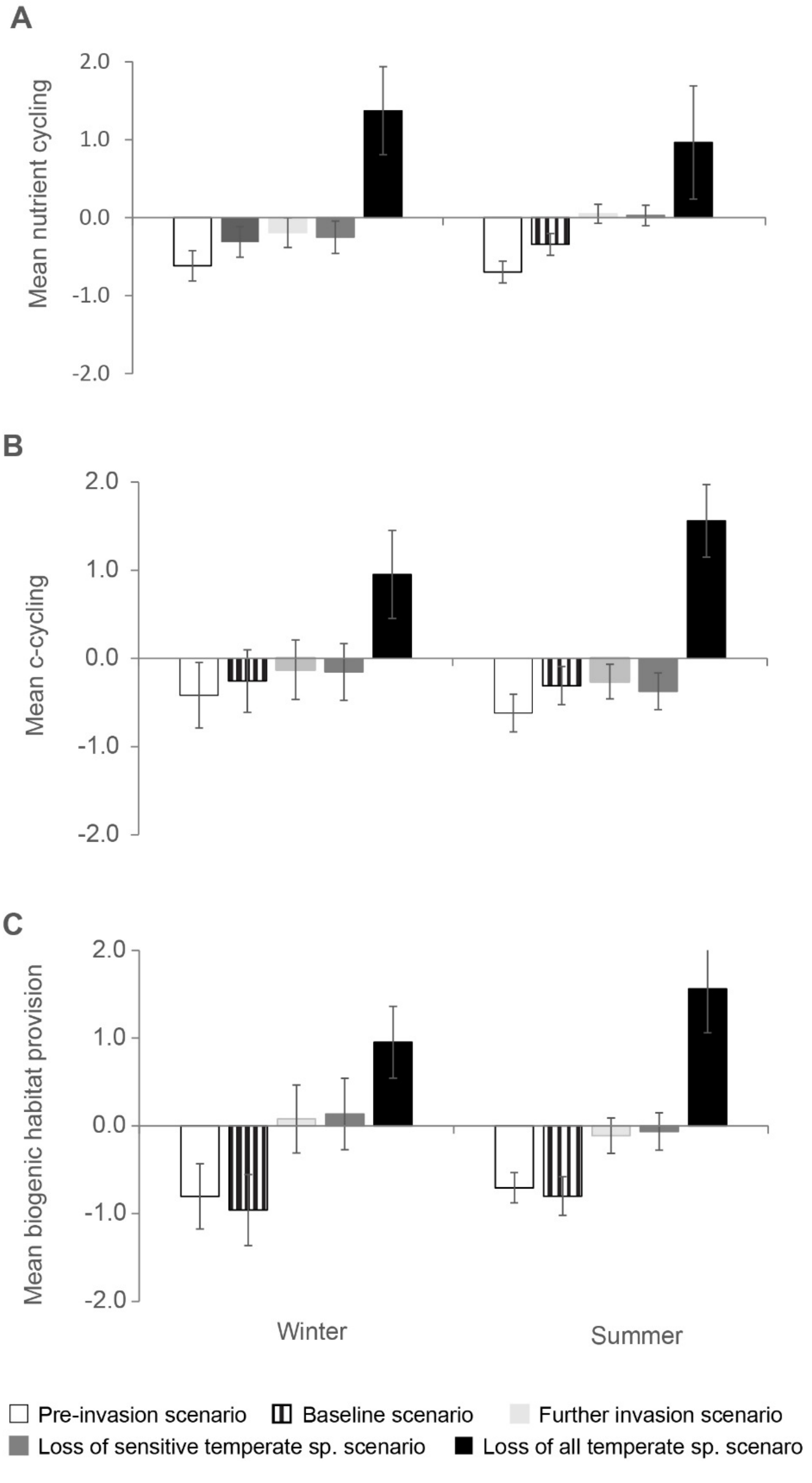

Fig B.6. Delivery of three ecological functions (mean ± SE of 6 sites) of the SE Queensland mudflats, standardised to zero mean and unit variance under five scenarios of species compositional change (A) nutrient cycling, (B) c-cycling and (C) biogenic habitat provision in **model A** (weighted by density **constrained**) in both winter and summer. For unconstrained estimates see Fig. 7

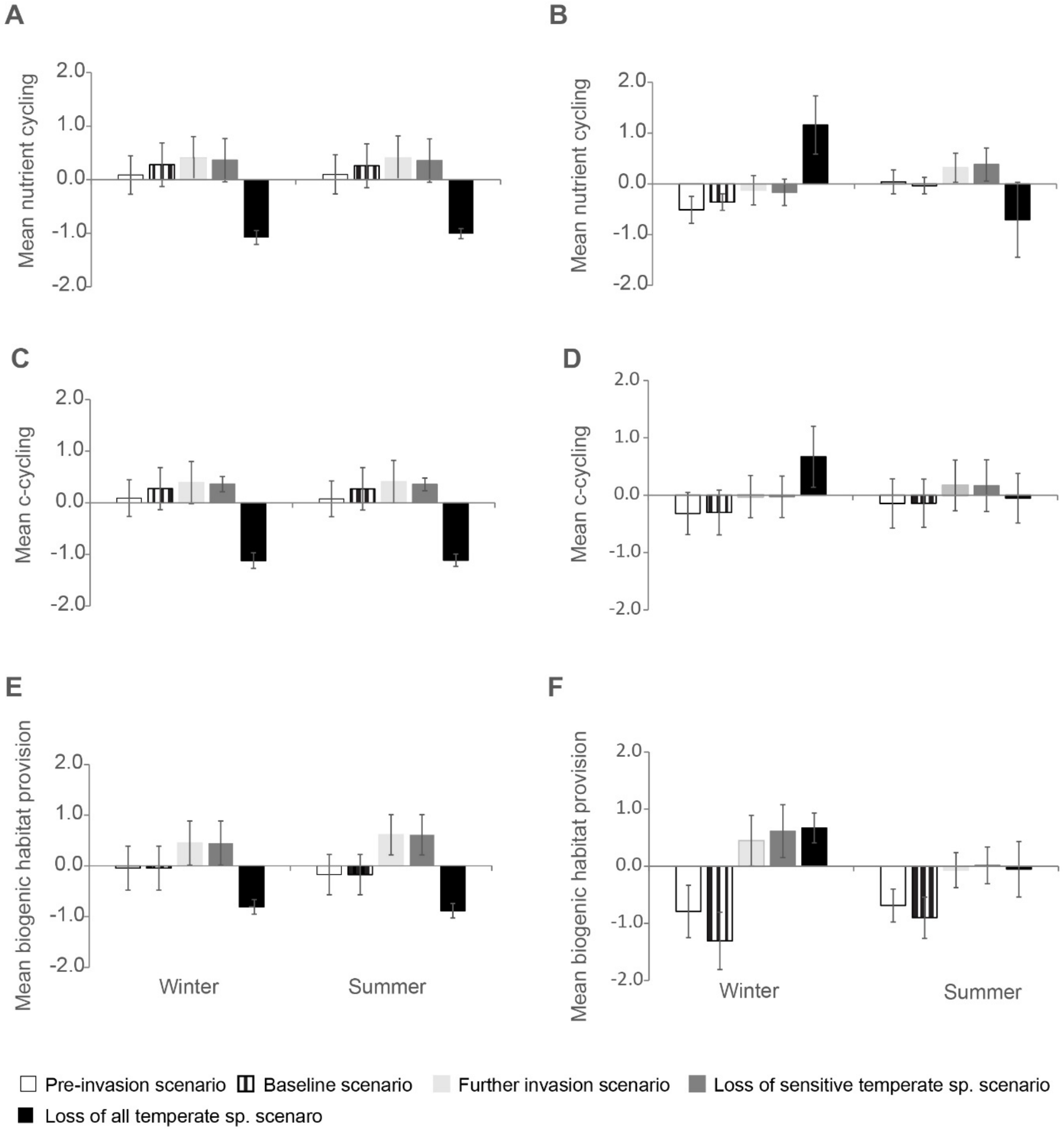

Fig. B.7. Delivery of three of ecological functions (mean ± SE) of the SE Queensland mudflats, standardised to zero mean and unit variance under five scenarios of species compositional change (A) nutrient cycling density unconstrained, (B) nutrient cycling density constrained, (C) c-cycling density unconstrained, (D) and c-cycling density constrained (E) biogenic habitat provision density unconstrained and (F) biogenic habitat provision density constrained between the five scenarios in **model B** in both winter and summer.

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