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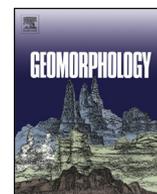
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## Q2 Patterns of early-colonising species on eroding to prograding coasts; implications for 2 foredune plant communities on retreating coastlines

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### ABSTRACT

Shoreline erosion is predicted to increase as the result of climate change, yet the effects on foredune-building species and associated dune processes remain poorly understood. To predict the response of foredune plant communities to increased erosion we examined the abundance of six early colonising dune-building species across 71 beach-foredune sites in south-east Australia. The assumption being that those species better adapted to shoreline retreat will be more frequent and have increased abundance on erosional coasts than species lacking the capacity to withstand or re-establish following periods of storm-induced erosion. All species were frequently recorded regardless of the rate of shoreline progradation or erosion, which ranged 3.8 to  $-2.2$  m year<sup>-1</sup>. Species presence was not related to erosion rates; however, there was a significant association between the rate of shoreline change and abundance for some of the studied species. Variation in traits related to tolerance to salinity and burial and the ability to establish following erosion appear to correspond to the observed patterns of species abundance. While this study examined only six species, it appears that species that are restricted to zones closer to the spring-tide level, that have a persistent rather than opportunistic growth-history or that are limited in their ability to recolonise following erosion, are more likely to be negatively impacted by increased rates of coastal erosion. Given the association between vegetation and foredune morphology these findings have important implications for the management of sandy coasts.

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### 43 1. Introduction

Coastal dunes are important environments on sandy shores. The conditions that enable dune development, namely a supply of sand-sized sediment, wind energy above a minimum transport threshold, and vegetation, occur at all latitudes from the tropics to circumpolar regions (Martínez et al., 2004). Coastal dunes provide a range of environmental and socio-economic functions, including recreation, reservoirs for drinking water, and habitat for a diverse and disproportionately endangered complement of species (Everard et al., 2010; Barbier et al., 2011). Foredues, the seaward-most dunes formed on top of the backshore by aeolian sand deposition within vegetation (Hesp, 2002), are further valued due to their role in mitigating coastline erosion and flooding, and in many regions have been encouraged to form or been created as defences against coastal hazards (Everard et al., 2010).

Projected climate change threatens the potential for dunes to provide these environmental and ecological services, due in part to anticipated increases in the frequency and magnitude of coastal erosion (Defeo et al., 2009). Consequently, there is considerable interest in

identifying the effects of coastal erosion on foredunes over both short-term (hours to days; storm events) and longer timescales (years). Physical changes in dune shape and function in response to increased erosion are generally expected, based on the historic response of foredunes to past events and the predicted changes to the processes involved in sand transport, deposition and foredune development (Davidson-Arnott, 2003; Carter, 2004; Psuty and Silveira, 2010). Recent studies have also recognised the potential for increasingly frequent or severe erosion to affect foredune vegetation (Feagin et al., 2005; Gornish and Miller, 2010; Gallego-Fernandez and Martínez, 2011; Ciccarelli et al., 2012; Bitton and Hesp, 2013). Shifts in foredune system morphodynamics related to changes in vegetation cover when exposed to increasingly erosive conditions have also been identified (Durán and Moore, 2015). Yet, geomorphologists and engineers have largely ignored the relationships between dune plants and coastline erosion (Bitton and Hesp, 2013; Feagin et al., 2015). This is despite a general acceptance of the central role played by vegetation in foredune development and system function (e.g. Arens, 1996; Hesp, 2002; Durán and Moore, 2013).

Conceptual models of foredune morphodynamics as a function of the presence/absence and abundance (cover) of dune-building species provide a useful starting point for evaluating the effects of increasing

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erosion. Foredunes are the direct result of the interaction between vegetation and aeolian processes, whereby the growth of dune-building plants causes local reduction of wind velocities and the deposition of sand (Arens, 1996; Hesp, 2002). Burial stimulates the growth of dune-building plants (Maun, 1998), facilitating further sand deposition in a sequence of events that can culminate in foredune development (Duran and Moore, 2013; Keijsers et al., 2015; van Puijenbroek et al., 2017). Fore dune development principally depends on plant density, distribution, height and cover, as well as wind and sand transport (Hesp, 2002). Shifts in geomorphic processes (e.g. wind flow, sediment transport, sediment deposition, landform development) follow changes in species dominance in coastal dunes because of these coupled biogeomorphic interactions (e.g. Stallins and Parker, 2003; Hilton et al., 2006; Zarnetske et al., 2012; Konlechner et al., 2016).

Foredune recovery following erosion is similarly related to vegetation growth and its ability to colonise the upper beach and can be expected to also vary between species (Feagin et al., 2015). Species-specific differences in the ability to mitigate coastal erosion have also been identified (Kobayashi et al., 2013; Charbonneau et al., 2017). Importantly, such changes to coastal processes have been identified even when the original vegetation is replaced by a functionally similar species. For example, comparison of two congeneric (of the same genus) dune-building species along the Pacific Coast of North America demonstrated a significant change in dune height and volume following shifts in species dominance (Hacker et al., 2012; Zarnetske et al., 2012, 2015). These changes in dune morphology were due to slight differences in congener morphology (e.g., extent of lateral spreading growth habit) and their respective responses to burial. Differences in lateral growth rates have also been linked to variation in alongshore dune shape (Goldstein et al., 2017). Such studies suggest that even relatively subtle species-specific differences can have significant implications for coastal landscapes.

Traditionally, studies on vegetation dynamics in coastal dunes have focused on progradational (seaward-building) coasts; with less consideration of plant community patterns on eroding coasts. Bitton and Hesp (2013), in one of the few analyses of vegetation community patterns on erosional foredunes, identified a decrease in the onshore width of the pioneer plant zone and the abundance of pioneer species as erosion increased on the Gulf coast of Florida. Plant communities were increasingly dominated by mid-to-late successional species as the incipient foredunes were removed and the foredunes merged with older landward dunes (Bitton and Hesp, 2013). Similar changes in species in response to erosion have been observed in other coastal regions (e.g. Ciccarelli et al., 2012), or predicted by models (e.g. Feagin et al., 2005; Gornish and Miller, 2010). These studies suggest that the response of any assemblage of dune species to increased erosion will be determined by both the life history attributes (traits) of the species that comprise that community (particularly those that enhance survival or regrowth following erosion), and the rate of coastal change. However, to date, comparisons have typically been made between pioneer and later successional dune species. There remains a paucity of data on the effect of shoreline erosion on early colonising dune species, despite a general recognition that changes in species composition can have profound implications for foredune morphology and function (Hesp 2002; Hilton et al., 2006; Wolner et al. 2013; Brantley et al., 2014; Zarnetske et al., 2015).

This study explores the potential for increased erosion to alter the abundance of different species of early colonising dune-building plants. We were primarily interested in those species that play a role in the early stages of dune building, since the distribution of such species has implications for dune formation and future resilience following changes to sediment supply and erosion regimes predicted to occur with climate change. Specifically, we examined the presence and abundance of six species across beaches and foredunes undergoing varying levels of erosion (landward retreat of the shoreline) or progradation (seaward building) in south-east Australia. The aim was to assess the patterns of

species abundance in relation to variability in recent shoreline change rates to determine if there is a relationship between species patterns and shoreline erosion/progradation. These results are discussed in relation to species-specific plant traits and the implications for foredunes under conditions of increased coastal erosion are explored.

## 2. Methods

### 2.1. Study area

The focus of this study was the beach and foredune environment of the open-coast of Victoria, south east Australia (Fig. 1). The Victorian coastline extends 1230 km from the Glenelg River in the west to Cape Howe in the east. Approximately 66% of the coastline is sandy, with beaches ranging in size from 176 km long to only a few metres in length separated by rocky headlands and cliffs (Short, 2006). Wave energy is highest in the west and decreases in an easterly direction with a mean significant wave height of 2.4 m (Hughes and Heap, 2010). Tidal range is micro-tidal, with a mean tidal range of <2 m (Australian Bureau of Meteorology (BoM), 2012). The coastline of Victoria is broadly south-facing and extends over a narrow latitudinal range from approximately 37.5–39.1°S. This means that strong latitudinal temperature gradients that limit species geographic ranges are absent, and it can be assumed that the present distribution of species reflect local variations in climate, disturbance or other local variables rather than broad-scale regional climate patterns. The open coast of Victoria is also relatively remote from urban centres and undisturbed, and so provides an ideal area to conduct studies that explore the influence of abiotic coastal processes on vegetation patterns.

Overall, coastal Victoria experiences a maritime temperate climate (Köppen–Geiger classification: Cfb), characterised by warm dry summers and cool wet winters (BoM, 2017). Average monthly temperatures range from a maximum of 17–20 °C in summer (January–February) to a minimum of 10–12 °C in late winter (August) with little variation along the coast (BoM, 2017). Precipitation typically exceeds 500 mm per year, and is largely deposited during the winter in the west and is more uniformly distributed in the east (BoM, 2017). All shorelines, even coasts displaying overall progradational shifts in shoreline position, are periodically affected by episodic erosion events. These are usually associated with high winds and storm surge generated by eastward moving cold fronts through western and central Victoria, and extratropical cyclones through eastern Victoria (Bird, 1993).

### 2.2. Study species

Beach and foredune plant communities in coastal Victoria are dominated by six species; the native species *Spinifex sericeus* (Poaceae), and the introduced *Ammophila arenaria* (Poaceae), *Euphorbia paralias* (Euphorbiaceae), *Thinopyrum junceiforme* (Poaceae), and the *Cakile* species — *Cakile maritima* and *C. edentula* (Brassicaceae) (Heyligers, 1985). These species are the focus of the present study as they play a disproportionate role in early dune development in Victoria. The native shrub, *Atriplex cinerea* (Chenopodiaceae), is of local importance but plays a secondary role as a dune-building species in comparison to the species identified above. All the non-native species were present in Victoria by the mid-1970s and have since naturalised. It can be assumed, therefore, that the current geographic-scale distribution of these 200 species is somewhat in equilibrium with the broader Victorian coastal environment.

#### 2.2.1. *Ammophila arenaria*

*A. arenaria* is perennial rhizomatous grass associated with the foredune and mobile dune environments (Huiskes, 1979; Appendix 1a). It has a distribution, both natural and human-induced, between 32° and 60° latitude in both hemispheres (Wiedemann and Pickart, 2004). Native to Europe, *A. arenaria* was deliberately introduced to

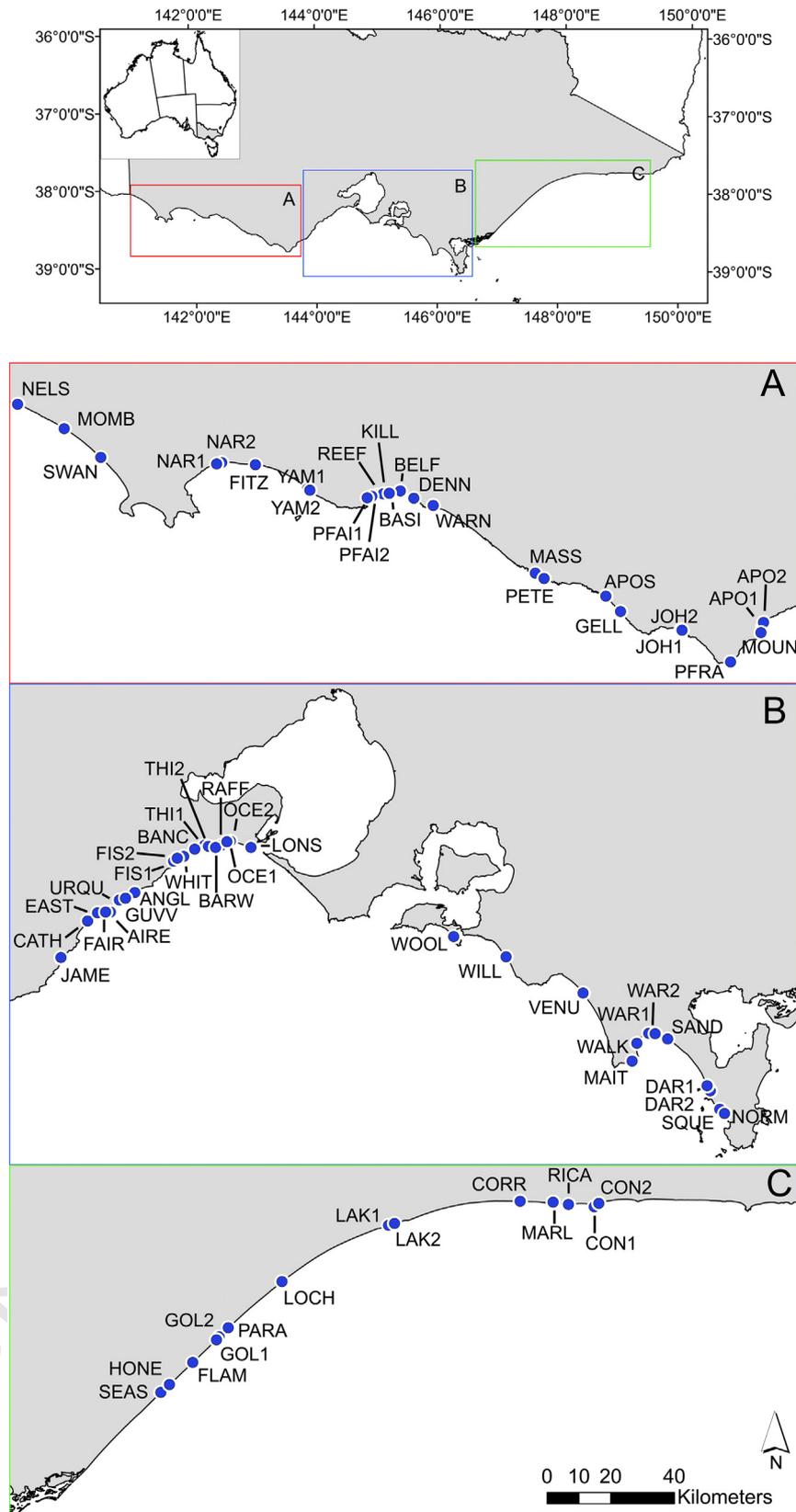


Fig. 1. Location of study sites, coastal Victoria, Australia (full site names, latitude and longitude of sites are listed in Appendix 2).

209 several countries including North America (Wiedemann and Pickart,  
 210 2004), South Africa (Lubke et al., 1995; Hertling and Lubke, 1999),  
 211 Australia (Wiedemann and Pickart, 2004) and New Zealand (Hilton

et al., 2006) during the mid-1800s to early-1900s for dune reclamation  
 and stabilisation. *A. arenaria* has also been planted extensively within its  
 natural range (Wiedemann and Pickart, 2004) and is now a defining

species of temperate coasts worldwide. *A. arenaria* was introduced to Victoria in the 1880s (Heyligers, 1985), and was widely planted until the 1980s. It is now distributed throughout coastal Victoria.

*A. arenaria* has a moderate tolerance to high soil salinities in comparison to other common early colonising foredune species (Sykes and Wilson, 1989), and is most commonly associated with developed foredunes inland of the initial incipient dune area (Huiskes, 1979; Doing, 1985). *A. arenaria* is, however, capable of establishing on the beach, and particularly in those regions outside its native range, is associated with primary colonisation and growth of new foredunes following dune erosion (e.g. Heyligers, 1985; Hilton and Konlechner, 2011). Primary colonisation by *A. arenaria* occurs through the lateral growth of rhizomes from inland populations, or from fragments of rhizome eroded during storms and stranded above the usual reach of spring-high tides (Hilton and Konlechner, 2011). Establishment from seed occurs infrequently (Huiskes, 1979). Range expansion occurs through the transport of plants by people or by the marine-dispersal of the buoyant and salt-resistant rhizomes (Buell et al., 1995; Konlechner and Hilton, 2009). Once present in a region, *A. arenaria* spreads rapidly with reported rates of population expansion of 12 to 130% year<sup>-1</sup> (Buell et al., 1995; Hilton et al., 2005).

The rhizome system of *A. arenaria* consists of vertically extending rhizomes with a minor proportion of horizontal rhizomes, meaning net growth is primarily vertical in direction (Konlechner et al., 2016). The expansion of individual colonies of *A. arenaria* occurs largely through the extension and branching of the vertical rhizomes in response to burial by sand (Gemmell et al., 1953). Aerial shoots form stout, erect tussocks comprised of multiple tillers, up to 120 cm high. Growth is seasonal with the main period of shoot production in its native range during spring and summer (Huiskes, 1979). Tiller numbers decline, but growth does not stop completely during autumn and winter.

### 2.2.2. *Thinopyrum junceiforme*

*T. junceiforme* is also a perennial rhizomatous European dune grass with a wide native latitudinal range (from 62° N to 36°N latitude) (Hilton et al., 2006; Appendix 1b). It has naturalised in Oregon and California on the west coast of the United States of America, and the temperate coast of Australia (Hanlon and Mesgaran, 2014). *T. junceiforme* is also found in New Zealand but has not naturalised (Hilton et al., 2006).

*T. junceiforme* was introduced to Victoria by at least the 1930s (Heyligers, 1985). The exact mode of introduction is not known, but may have been the result of accidental transport of seed or rhizome with ballast (Heyligers, 1985). In contrast to *A. arenaria*, there has been little deliberate planting of *T. junceiforme* in coastal Victoria and it is restricted largely to central Victoria with only isolated occurrences west of Anglesea and east of Wilsons Promontory.

*T. junceiforme* is exceptionally tolerant of salinity and occasional tidal inundation (Sykes and Wilson, 1989), and can grow closer to the sea than most dune species, including *A. arenaria* (Bond, 1952; Hilton et al., 2006). In its native range, *T. junceiforme* occupies the seaward-most foredune zone (Doing, 1985). It similarly forms incipient foredunes seaward of the native dune vegetation in Southern Australia (Hilton, et al., 2006). Tiller density and vigour typically decrease with distance inland, but *T. junceiforme* can still survive in inland dune environments (Hilton et al., 2006). The establishment of *T. junceiforme* on the back-beach occurs through the lateral growth of rhizomes from inland populations, from stranded fragments of rhizome, or from seed (Harris and Davy, 1986). There is little research on the dispersal mechanisms of *T. junceiforme*, but it is likely to occur through the transport of rhizomes in the sea (Hilton, et al., 2006; Hanlon and Mesgaran, 2014).

In contrast to *A. arenaria*, the rhizome system of *T. junceiforme* consists mostly of horizontally spreading rhizomes (personal obs., first author). The rates of colony expansion have not been documented; however, under glasshouse conditions the rhizomes of *T. junceiforme*

can extend by >30 m over one season, suggesting that the lateral spread of this species is rapid (Hanlon and Mesgaran, 2014). As with *A. arenaria*, the growth of *T. junceiforme* in its native range is at a maximum during spring and summer and decreases but does not cease during autumn and winter months (Harris and Davy, 1986).

### 2.2.3. *Euphorbia paralias*

*E. paralias* is a multi-stemmed perennial herb, 30–55 cm high (Heyligers, 2002; Appendix 1c). It is native to the beach and foredune environments of southern and western Europe and northern Africa. In Australia, it is naturalised across much of the southern coast of the mainland and Tasmania (Heyligers, 2002). *E. paralias* was recorded in Victoria by the mid-1970s following the marine drift of seed from South Australia (Heyligers, 2007). It is now widely established in dune-systems throughout western and central Victoria with localised occurrences through the east.

Relatively little is known regarding the autecology of *E. paralias*. It can withstand moderate burial by sand by producing side-branches along the stems (Heyligers, 2002). Reproduction occurs by the production of abundant seed (may be over 20,000 seeds per plant) (Heyligers, 2002). Seeds can float and remain viable for at least 6 years in seawater (Heyligers, 2007).

### 2.2.4. *Cakile edentula* and *Cakile maritima*

*C. edentula* and *C. maritima* are two species of closely related annual herbs (Appendix 1d). *C. edentula* ranges from North Carolina to Labrador on the Atlantic coast of North America and is naturalised over a similar latitudinal range on the Pacific coast (Davy et al., 2006). *C. maritima* is native to Europe and North Africa (Davy et al., 2006; Cousens et al., 2013). *C. edentula* was recorded in Victoria by 1863 and *C. maritima* by 1922 (Heyligers, 1985). It can be difficult to distinguish *C. maritima* and *C. edentula*. Most observations are likely to be *C. maritima*, as *C. edentula* is now probably absent from the Victorian coast (Cousens et al., 2013), and so *Cakile* was treated as a single taxon in this study. *Cakile* is now widely distributed throughout the Victorian coast.

The *Cakile* spp. are characteristic of strandline communities globally (Doing, 1985). Annual colonisation occurs through dispersal of by tides and wind with seeds viable for periods of up to six months in seawater (Heyligers, 2007). Most populations are ephemeral being removed by equinoctial tides and winter storms (Davy et al., 2006), although can also represent the earliest stages of dune succession (Davy and Figueroa, 1993). The growing season is determined by different constraints in different parts of its range (Davy et al., 2006). On the meso- and macro-tidal British strandlines, the 6-month window in summer between equinoctial spring tides is important (Ignaciuk and Lee, 1980). Elsewhere summer temperatures and drought terminate the winter growing season (Watkinson and Davy, 1985).

### 2.2.5. *Spinifex sericeus*

*S. sericeus* is a stoloniferous perennial grass associated foredunes through southeast Australia and northern New Zealand (Maze and Whalley, 1992). It is the primary native foredune building species in Victoria and is widely distributed across the state (Appendix 1e). Expansion occurs by the extension of horizontal stolons or wind dispersed seed. There is little information on marine dispersal capacity of *S. sericeus*. As with *A. arenaria* and *T. junceiforme*, the vigour of *S. sericeus* is greatest where it receives some burial by sand (Maze and Whalley, 1992).

## 2.3. Field data collection

The abundance of the six species was measured at 71 locations in 2012 (Fig. 1). Sampling sites were selected to maximise coverage of the coastline along the open coast. The south Gippsland coast and east of Cape Conran were not sampled due to limited accessibility and time constraints. The distance between sampling sites ranged from 0.5–340

24.0 km and covered 990 km of coastline. Each site was surveyed once within a three-month period at the end of the summer warm-dry season and before the onset of winter storms between March and May to obtain a comparative dataset of species abundance across the Victorian Coast.

Percentage cover (henceforth 'abundance') for each of the species was estimated at each site using a modified ACFOR scale (Crisp and Southward, 1958). The ACFOR scale is based on approximately logarithmic categories of relative cover (Table 1), and facilitates rapid assessments of the abundance of species across large geographic areas (Mieszkowska et al., 2013). Estimates of species abundance at each site were made by three people over a 30-minute period along a 200 m section of coast.

The seaward extent of the survey area was defined by the high-tide line. The landward extent of the survey area was defined by the boundary between the foredune zone and the secondary or non-dune landscape, and was identified as the seaward edge of coastal cliffs, relic dunes, transgressive or parabolic dune fields, or human structures such as roads or lawns.

#### 2.4. Measurement of recent rates of shoreline movement

Rates of shoreline movement were determined from two digitised aerial or satellite images per site in ArcGIS 10.4.1. Suitable images with an appropriate acquisition time, of sufficient resolution, and with low cloud cover were available for 44 sites (Appendix 3). Images covered time spans between 5.8 and 10.8 years, similar to that used by Ciccarelli et al. (2012) and Bitton and Hesp (2013), and were selected to give the widest date range possible from the available imagery. We selected images so that the acquisition time of the most recent imagery was within  $\pm 1.5$  years of the field vegetation surveys, and that of the older image between 6 and 10 years before field sampling. Images were georeferenced prior to analysis in ArcGIS using control points extracted from the most recent image.

Shoreline positions for each site were defined by the seaward edge of the foredune vegetation and were digitised manually by a single operator. Annual rates of shoreline change were estimated using the Digital Shoreline Analysis System (DSAS) (Thieler et al., 2017). Transects were cast at 5 m intervals along a baseline created parallel to the most recent shoreline. The End Point Rate (EPR), calculated by dividing the distance of shoreline movement by the time between the oldest and most recent shoreline measures, quantified erosional and progradational change in shoreline position. The total uncertainty in the rate of shoreline change between the two image dates for each site was calculated as the quadratic sum of the shoreline error for each image divided by the number of years between images (Del Río and Gracia, 2013). This annualised total error in shoreline change ranged between 0.2 and 0.7 m year<sup>-1</sup> (Appendix 3).

The calculated EPR of shoreline movement was not considered to be significant when it was equal to or less than the annualised total uncertainty in shoreline position (Del Río and Gracia, 2013). Fourteen sites displayed no significant change in shoreline position. There was little change in shoreline position at ten of these sites ( $< \pm 0.25$  m year<sup>-1</sup>) and so they were classified as stable (no net shoreline retreat or

advancement). The calculated EPR for the remaining four sites exceeded  $\pm 0.25$  m year<sup>-1</sup> so these sites were not included in analysis.

#### 2.5. Data analysis

Data for each species was tabulated to obtain measures of overall abundance and frequency of occurrence (total number of sites where each species was recorded as present). Zonational patterns in species distribution were examined by recording the presence of each species in one of four zones for each site; 1) the backshore between the high-tide line and the toe of the foredune, 2) the lower foredune stoss face, 3) the upper foredune stoss, and 4) inland of the foredune crest. These four categories do not encompass the complete range of zones in all beach-foredune systems but were sufficient to distinguish zonal patterns on the foredunes on the Victorian Coast.

Associations between species abundance and rates of shoreline change were examined for both each individual species (henceforth, species level) and collectively (henceforth, community level); although we recognise that the species examined represent an incomplete, albeit dominant component of the total foredune plant community). Assessment at the community level allows the presence, relative abundance and zonal patterns of the dominant dune-building species assemblages to be characterised in relation to shoreline change. Assessment of the relationship between shoreline change and abundance at the species level allows relative tolerances to shoreline erosion to be compared between species. Collectively they provide a means for exploring potential shifts in foredune plant communities as a shoreline shifts from progradational to an erosional state.

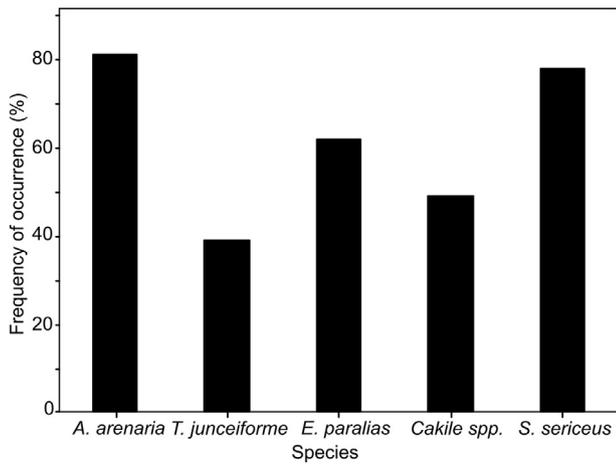
Community-level associations with shoreline change were explored using multivariate analysis, like the approach employed by Ciccarelli et al. (2012). A two-way PERMANOVA (Anderson, 2001) based on Bray-Curtis dissimilarities was carried out on the abundance data with shoreline change (positive, erosion, stable) and coastal region (Cape Nelson, Portland, Warrnambool, Port Campbell-Otway, Hobsons Bay, Ninety-mile, Tylers-Snowy) as random factors. Shoreline change was included as a factor to test for significant differences in community composition between each shoreline change category. Coastal region was included to control for the restricted distribution of some species of interest unrelated to shoreline change rates (e.g. *T. junceiforme*, Appendix 1). We used the framework of Australian secondary sediment compartments to define the coastal regions (Thom et al., 2018). The significance of each factor on plant species composition was tested using a reduced model based on 999 permutations.

Principal coordinate analysis (PCO; Anderson and Willis, 2003) and agglomerative hierarchical cluster analysis (McCune and Grace, 2002) were then performed on the matrix of species abundance to investigate the effect of coastline change rate on plant communities. Data were square-root transformed and the dissimilarity matrix was calculated using the Bray-Curtis index for both analyses (Ciccarelli et al., 2012). Pearson's correlation was used to investigate if PCO axes were related to the rate of shoreline change and to investigate the relationship between the PCO axis and the abundance of each species.

To explore species-level associations with shoreline change, shoreline change rates were compared between sites where species were absent versus those where present (irrespective of abundance) using *t*-tests. The Spearman correlation coefficient between abundance and shoreline change rates was calculated using only sites where the species was present (i.e. excluding those sites where a species was not recorded). To test whether high species abundances were related to shoreline change rates comparisons were also made between sites with high abundances versus lower abundances for each species using *t*-tests. It was necessary to define 'high' and 'low' abundance category sites differently between species to obtain sufficient observations for the *t*-test. Comparisons were made between sites with abundances in Category 5 and Categories 2–4 for *A. arenaria*, *S. sericeus* and *T. junceiforme*, between Category 4 and Category 2–3 sites for

**Table 1**  
Modified ACFOR scale used to record abundances of the target species.

Abundance category	Definition
1. Absent	No individuals seen.
2. Rare to occasional	A few scattered individuals or small patches.
3. Frequent	Many scattered individuals or small-medium patches.
4. Common	Many large patches but discontinuous alongshore.
5. Abundant	Peak abundance. Species forming large patches that are extensive alongshore with close to 100% cover within patches.



**Fig. 2.** Frequency of occurrence for four non-native species (*A. arenaria*, *T. junceiforme*, *E. paralias*, *Cakile spp.*) and one native (*S. sericeus*) at 71 sites along the Victorian coast, Australia.

**Table 2**  
Percentage of sites where each co-occurring pair of species was recorded.

	<i>S. sericeus</i>	<i>T. junceiforme</i>	<i>E. paralias</i>	<i>Cakile spp.</i>
<i>A. arenaria</i>	66.2	23.9	43.7	39.4
<i>S. sericeus</i>		28.2	47.9	39.4
<i>T. junceiforme</i>				15.5
<i>E. paralias</i>				29.6

Species abundances varied between sites for all species, and except for *Cakile spp.* all abundance categories were observed for all species (Fig. 3).

Species co-occurrence was high with at least two species present at all but one site. The most frequently observed species were also the most commonly co-occurring pairs but no species were mutually exclusive (Table 2). Species were recorded in across multiple beach/foredune zones but were preferentially associated with at least one specific zone (Fig. 4). *S. sericeus* and *T. junceiforme* were frequently observed in the backshore and stoss zones, but seldom recorded inland of the foredune crest. The occurrence of *A. arenaria* and *E. paralias* increased with distance from the sea and were associated principally with environments inland of the foredune crest. The distribution of *Cakile spp.* was restricted almost entirely to the backshore and was not observed inland of the foredune crest.

### 3.2. Shoreline change

There was no significant correlation between the rate of shoreline change and the time between the image date and date of vegetation sampling (Pearson's  $r = 0.14$ ;  $P = 0.36$ ) suggesting that the variation in image dates between sites has little effect on the calculated patterns of shoreline change. The calculated rates of shoreline change can therefore be considered a robust measure of the recent changes in shoreline position.

Sites displayed both erosional and progradational shifts in shoreline position over the 5.9–10.2 years before the field surveys in 2012 (Fig. 5). There was almost double the number of erosional sites than progradational and stable location; however, some spatial autocorrelation is likely given the close proximity of several of the sample sites and this data should not be considered as indicative of overall rates of shoreline change across the Victorian Coast. Eleven sites displayed progradational shifts in shoreline position, 19 sites displayed erosional shifts, and 10 sites displayed no significant shift in shoreline position. Rates of progradation ranged from 0.3 to 3.9 m year<sup>-1</sup>. Erosion rates were similar in magnitude, ranging from 0.3 m year<sup>-1</sup> to 2.2 m year<sup>-1</sup>.

*E. paralias*, and between Category 3–4 sites and Category 2 sites for the *Cakile* species.

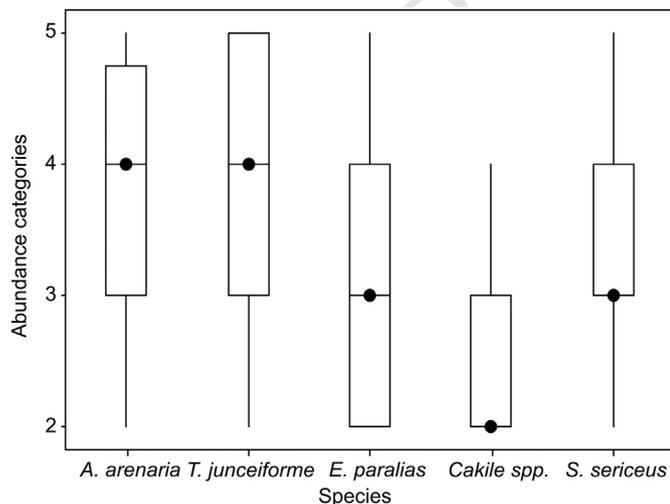
Finally, significant differences in species richness (number of species), average abundance and similarity in vegetation composition in each shoreline change category (erosion, stable, progradation) were tested using one-way ANOVA followed by Tukey's HSD test. Average abundance was calculated using only those species present at each site. Similarity was calculated using the Sørensen Index, which compares the presence or absence of species at each site in each shoreline category against every other site in the same category (Bitton and Hesp, 2013).

Datasets were tested for normality and homogeneity of variance prior to analysis. The PERMANOVA and PCO analysis were conducted in PRIMER 7.0.13. All other analyses were conducted in MINITAB 17.1.0.

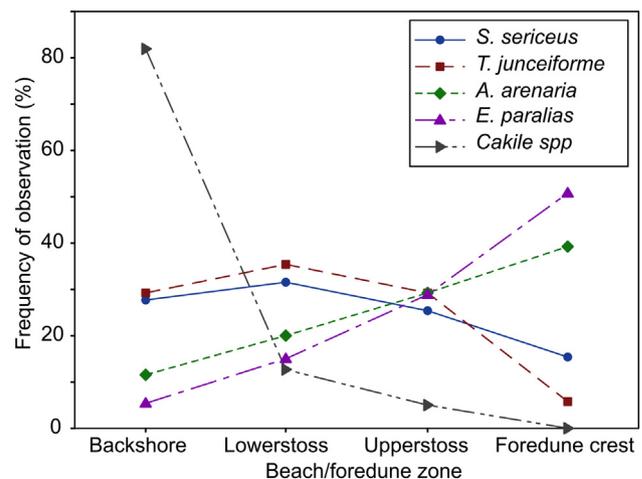
## 3. Results

### 3.1. Species abundance, co-occurrence and zonal patterns

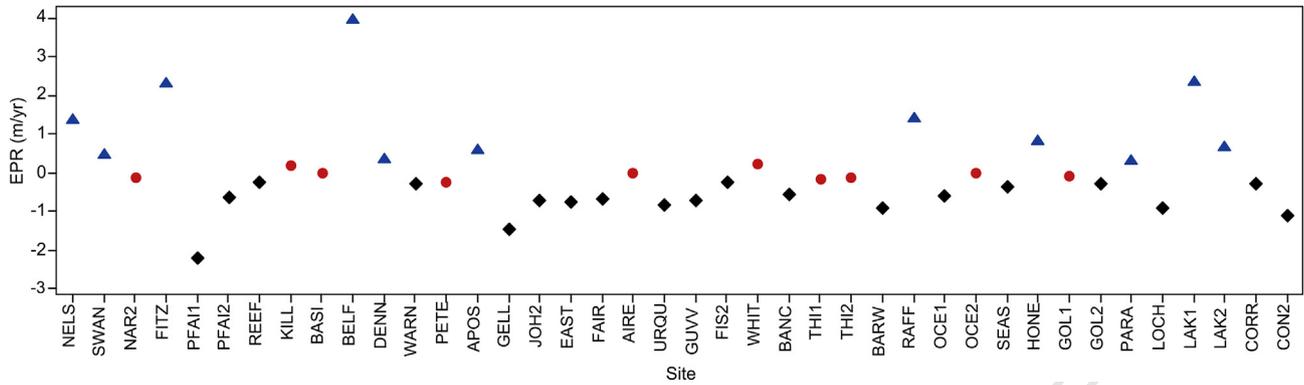
*A. arenaria* and *S. sericeus* were the most commonly recorded of the five species of interest—present at 81% and 78% of the surveyed sites, respectively (Fig. 2). All species, however, were recorded at multiple sites.



**Fig. 3.** Relative proportion of observations in each abundance category for each target species. Sites where species were not present were excluded from the analysis. Each box extends from the 25th percentile to the 75th percentile. The whiskers show the highest and lowest values for each species.



**Fig. 4.** Zonal patterns of the target species expressed as a percentage of total observations.



**Fig. 5.** Rates of medium term (5.9–10.2 years) shifts in shoreline position for 40 sites on the Victorian Coast. Negative values indicate erosion (black diamonds), positive numbers indicate progradation (blue triangles), and red circles indicate a stability in shoreline position over the study period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

510 The average rate of change for all progradational sites was  $1.3 \pm$   
 511  $1.1 \text{ m year}^{-1}$  and  $-0.8 \pm 0.5 \text{ m year}^{-1}$  for all erosional sites. Average  
 512 shoreline change rates did not differ significantly between sediment  
 513 compartments (Welsh's ANOVA;  $P = 0.43$ ); although few progradational  
 514 sites were recorded within central Victoria (Fig. 5).

515 **3.3. Community-level associations with shoreline change**

516 The PERMANOVA analysis found that both shoreline change cate-  
 517 gory ( $P < 0.05$ ) and coastal compartment ( $P < 0.1$ ) explained a

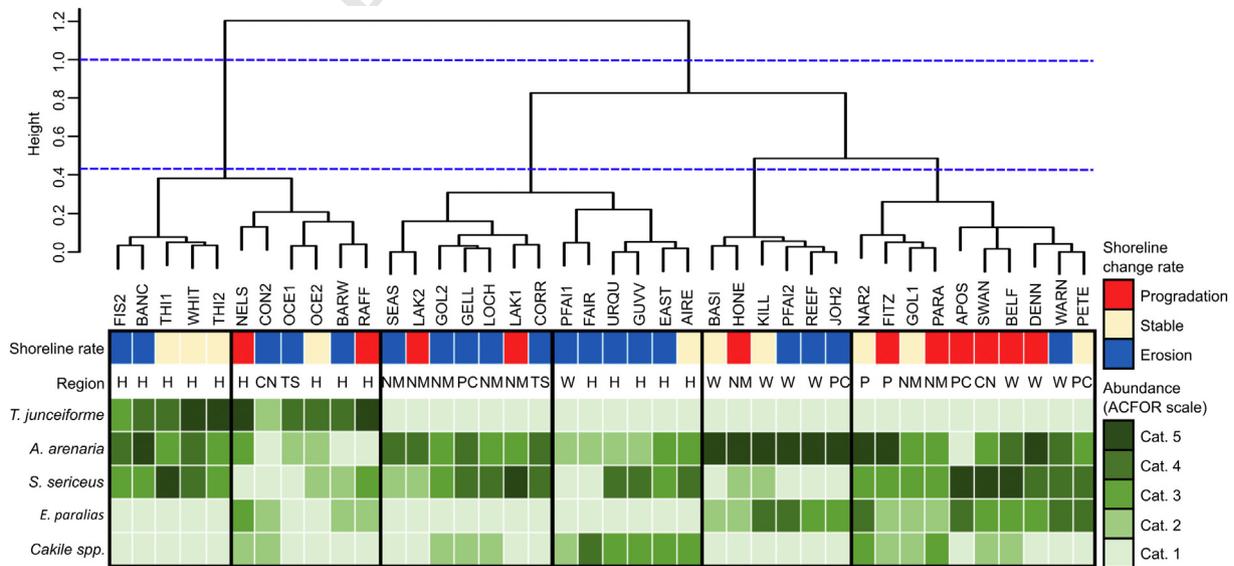
significant proportion of variance in community composition between 518  
 the surveyed sites when species abundance was included as the re- 519  
 sponse variable (Table 3). The interaction term between shoreline 520  
 change and sediment compartment was not significant. Collectively, 521  
 shoreline change and sediment compartment explained 50.2% of total 522  
 variation in species abundance. 523

The cluster analysis, performed on the site to site species abundance 524  
 dissimilarity matrix, identified two major associations of site (Fig. 6). 525  
 The first association distinguished two groups of site at 1.0 distance 526  
 and separates sites based on the presence or absence of *T. junceiforme*, 527  
 reflecting the restricted distribution of this species. The second associa- 528  
 tion distinguished six groups of site at 0.45 distance. Sites in this second 529  
 association were primarily separated by differences in the relative 530  
 abundances of several species, instead of any one single species 531  
 (Figs. 6, 7). For example, Group 1 and 2 were distinguished from Groups 532  
 3–6 by the presence of *T. junceiforme* at the first association and distin- 533  
 guished from each other at the second association by differences in the 534  
 abundances of both of *S. sericeus* and *A. arenaria*. Likewise, Group 5 was 535  
 distinguished from the other groups of site by a moderate to high abun- 536  
 dance of both *A. arenaria* and *E. paralias* with low or absent abundances 537  
 of the other three species. This is not unexpected given the restricted 538  
 distribution of *T. junceiforme* and the high co-occurrence of species 539  
 within the study sites. All six groups of site contained sites from 540

13.1 **Table 3**  
 13.2 Permutational analysis of variance (PERMANOVA) results testing the effect of shoreline  
 13.3 change (change) and sediment compartments (compar.) on species relative abundances.

Source	df	SS	MS	Pseudo-F	P
Change	2	5881.6	2940.8	3.66	0.042*
Compar.	6	14,507	2417.9	3.00	0.074**
Change × compar.	7	5353.1	764.73	0.69	0.798
Residuals	24	26,628	1109.5		
Total	39	52,112			

13.10 \* Significant at  $P < 0.05$ .  
 13.11 \*\* Significant at  $P < 0.1$ .



**Fig. 6.** Dendrogram showing the results of the cluster analysis (Ward's method with squared Euclidean distance) regarding the relative abundance of *S. sericeus*, *A. arenaria*, *E. paralias*, *T. junceiforme*, and *Cakile* spp. and shoreline change rates. Dashed blue line demarks the distance along which groupings were defined. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

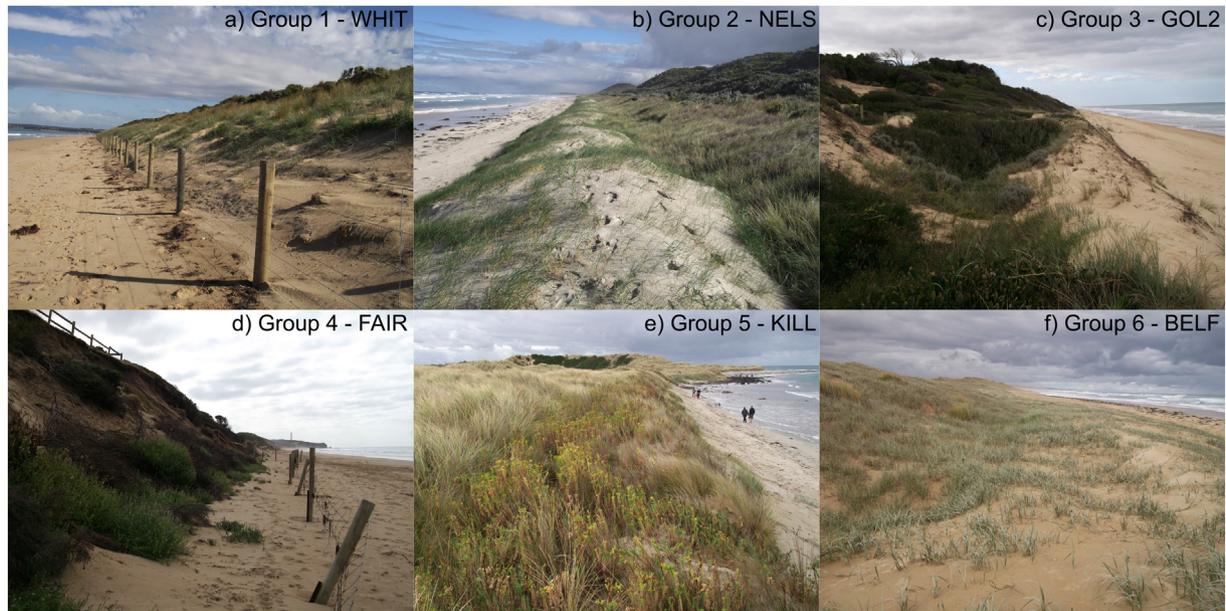


Fig. 7. Representative sites for each foredune grouping identified by cluster analysis.

more than one shoreline change rate category suggesting that shoreline change rates were not the primary determinant of community composition on the Victorian Coast. There was no significant difference in the average rate of shoreline change between groups (ANOVA;  $F(5) = 1.77, P = 0.18$ ).

The PCO analysis provides further evidence that the rate of shoreline change was not the primary determinant of community composition but does show a secondary separation of sites related to shoreline change rates. The first three PCO axes (PCO1, PCO2 and PCO3) collectively explained 70.3% of the total floristic variation. PCO1 and PCO2 were not significantly correlated with shoreline change rates. There was, however, a positive correlation between PCO3, which explained 18.3% of the total floristic variation, and the rate of shoreline change (Pearson's  $r = 0.35, P = 0.03$ ). Generally, sites experiencing high rates of erosion were located at the lower end of PCO3 and progradational sites located at the higher end of PCO3 (Fig. 8). Two broad groupings of sites are apparent. Most sites were located at the higher PCO3 values (Fig. 8) with no clear separation of community composition within this group (Fig. 6). Three sites (PFAI1, CON2 and FAIR) were located at the lower PCO3 values (Fig. 8). These sites were characterised by a moderate abundance of *Cakile* spp. and absent or low abundances of all other species (Figs. 6, 7d).

Two species showed a high correlation with PCO3 axes. *Cakile* abundance was negatively correlated to PCO3 (Pearson's  $r = -0.56, P = 0.00$ ), indicating a positive association between this species and the rates of coastal erosion. The opposite pattern was shown with *S. sericeus* ( $r = 0.68, P = 0.00$ ), indicating that this species is more likely to be abundant on progradational coasts. *T. junceiforme* and *A. arenaria* were more weakly but also significantly correlated with PCO3 ( $P < 0.1$ ), with both species showing a positive relationship between abundance and positive shoreline change rates (*T. junceiforme*:  $r = 0.29, P = 0.07$ ; *A. arenaria*:  $r = 0.27, P = 0.09$ ).

### 3.4. Species-level associations with shoreline change

There was a significant difference in shoreline change rates between sites with and without *E. paralias* (two sample  $t$ -test;  $t(38) = -2.18, P = 0.04$ ; Fig. 9a). This suggests that *E. paralias* is more likely to be found on progradational coasts than erosional coasts. There was, however, no significant correlation between abundance and the rates of shoreline change when sites without *E. paralias* were excluded from

the analysis (Spearman's rho ( $r_s$ ) =  $-0.15, P = 0.51$ ), nor was there any significant difference in the rate of shoreline change when sites with the highest abundance categories were compared with sites with low abundances of *E. paralias* ( $t(18) = 1.12, P = 0.28$ ).

In contrast, there was no significant difference in shoreline change rates between sites with *T. junceiforme* ( $t(34) = 0.46, P = 0.65$ ) or *S. sericeus* ( $t(38) = -1.76, P = 0.09$ ) compared to sites without these species. The correlation between the abundance of *T. junceiforme* and rates of shoreline change was not tested because of the few measurements in the lower abundance categories, and there was no significant correlation between *S. sericeus* abundance and the rates of shoreline change when sites where species were absent were excluded ( $r_s = -0.10, P = 0.59$ ). However, sites had significantly greater rates of shoreline progradation when sites with high abundances (category 5) were

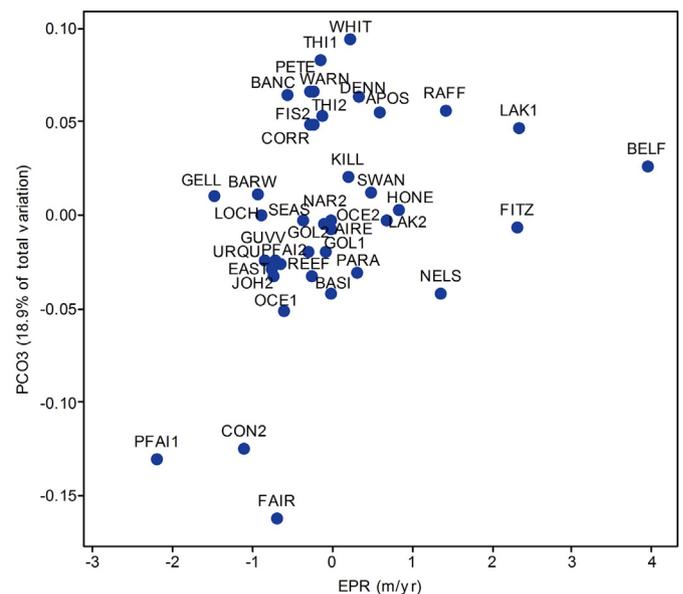
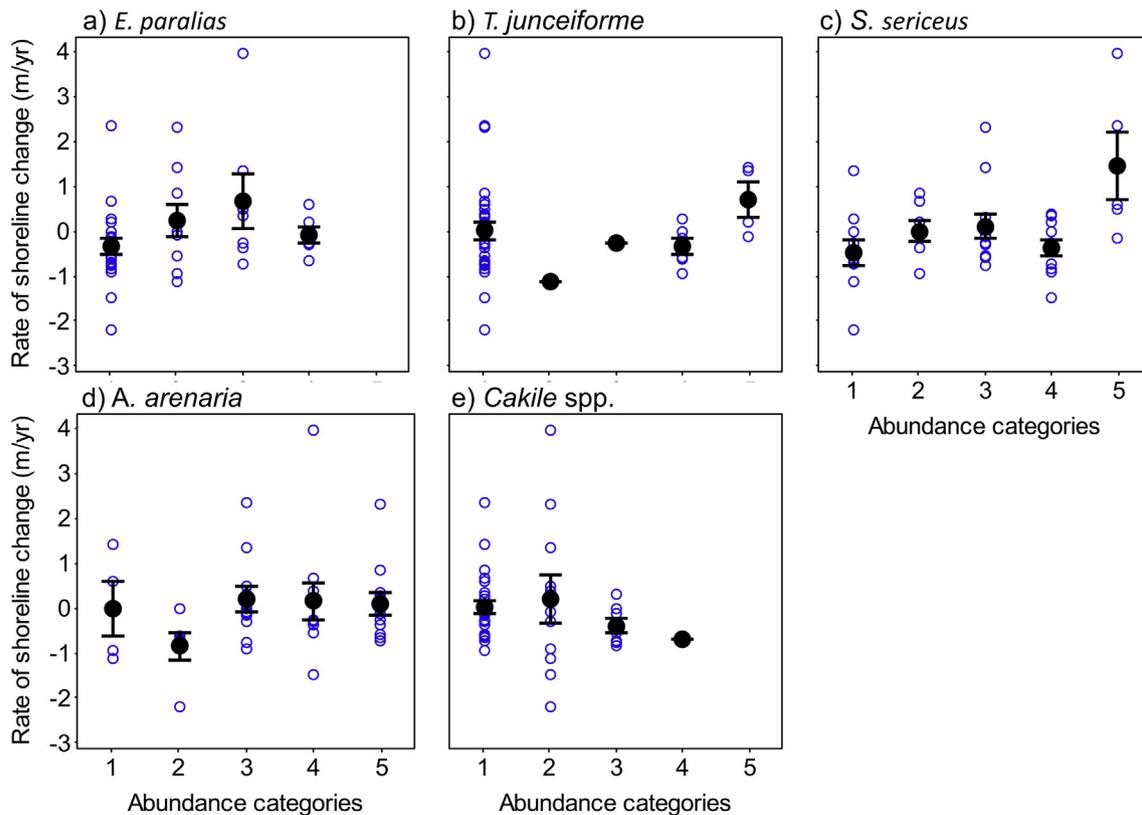


Fig. 8. EPR vs PCO3. Site codes: 1 WHIT, 2 TH11, 3 PETE, 4 WARN, 5 BANC, 6 DENN, 7 APOS, 8 RAFF, 9 LAK1, 10 BELF, 11 TH12, 12 CORR, 13 FIS2, 14 GELB, 15 BARW, 16 KILL, 17 SWAN, 18 LOCH, 19 HONE, 20 FITZ, 21 SEAS, 22 NAR2, 23 OCE2, 24 AIRE, 25 LAK2, 26 GOL2, 27 GOL1, 28 PFAI2, 29 URQU, 30 GUVV, 31 EAST, 32 JOH2, 33 REEF, 34 PARA, 35 NELS, 36 BASI, 37 OCE1, 38 PFAI2, 39 CON2, 40 FAIR.



**Fig. 9.** Average shoreline change rates per abundance category for a) *E. paralias*, b) *T. junceiforme*, c) *S. sericeus*, d) *A. arenaria*, and e) *Cakile* spp. Interval bars indicate 1 standard error from the mean. Hollow circles show individual data points.

594 compared to sites with low abundances (categories 2–4) ( $t(9) = 3.50$ ,  
595  $P = 0.01$ ) and ( $t(29) = -3.26$ ,  $P = 0.00$ ) for *T. junceiforme* and  
596 *S. sericeus*, respectively. This suggests that the rate of shoreline change  
597 did not determine the presence (or absence) of *T. junceiforme* and  
598 *S. sericeus* at a site, but that these species are more likely to form exten-  
599 sive and dense populations (Category 5; Table 1) on progradational  
600 rather than erosional shorelines (Fig. 9b, c).

601 There was no evidence that rates of shoreline change significantly  
602 influenced the presence or the abundance of *A. arenaria* or *Cakile* spp.  
603 (Fig. 9d, e). There was no significant difference in rates of shoreline  
604 change when sites with these species were compared to sites where  
605 these species were absent ( $t(38) = -0.02$ ,  $P = 0.98$  and  $t(38) = 0.27$ ,  
606  $P = 0.78$  for *A. arenaria* or *Cakile*, respectively); no significant correla-  
607 tion between abundance and rates of shoreline change ( $r_s = 0.26$ ,  $P =$   
608 **Q10**  $0.12$  and  $r_s = -0.06$ ,  $P = 0.83$ ); and no significant difference in rates  
609 of shoreline change between sites with high species abundance and  
610 low abundances ( $t(34) = -0.42$ ,  $P = 0.67$  and  $t(15) = -0.84$ ,  $P = 0.41$ ).

### 611 3.5. Overall species richness, similarity and abundance

612 Species richness and similarity were significantly lower at erosional  
613 sites, compared with prograding or stable sites (Table 4). Average abun-  
614 dance did not differ between shoreline change classes.

14.1 **Table 4**

14.2 Average species richness, species abundance for present species, and Sørensen Index  
14.3 values (similarity) for erosional, stable and progradational sites. Standard deviations are  
14.4 presented in brackets. Different letters indicate significant differences between shoreline  
14.5 categories at  $P < 0.05$  calculated using a one-way ANOVA followed by Tukey's HSD test.

14.6	Erosional	Stable	Progradational	<i>P</i> -values	
14.7	Species richness	2.5 (0.5) <sup>A</sup>	3.2 (0.9) <sup>AB</sup>	3.1 (0.6) <sup>B</sup>	0.01*
14.8	Average abundance	3.2 (0.7)	3.5 (0.6)	3.4 (0.5)	0.44
14.9	Similarity	0.6 (0.2) <sup>A</sup>	0.7 (0.2) <sup>B</sup>	0.7 (0.2) <sup>B</sup>	0.00*

## 615 4. Discussion

### 616 4.1. Associations with shoreline change rates

617 Increased coastal erosion due to climate change has the potential to  
618 alter foredune communities by selecting for species better adapted to  
619 withstand and/or re-establish after storm-induced disturbance  
620 (Cheplick, 2016). We found little evidence that shoreline change rates  
621 limit the presence of a foredune species. All species were recorded on  
622 both prograding and erosional shores. Even *E. paralias*, which is more  
623 likely to occur on prograding coasts (Fig. 9a), occurred on shores with  
624 varying shoreline change rates, from erosion of up to 1 m year<sup>-1</sup> to  
625 progradation of 4 m year<sup>-1</sup>.

626 The rates of shoreline change calculated in the present study were  
627 relatively moderate (compared with those reported by Bitton and  
628 Hesp, 2013, for example), and dune species are known to persist, but  
629 not thrive, in moderately stressful environments (Henriques and Hay,  
630 1998). More extreme rates of shoreline change could be expected to  
631 exert a stronger selection pressure on the studied species by restricting  
632 the growth of less erosion-resilient species (Feagin et al., 2005; Gornish  
633 and Miller, 2010). Nevertheless, our results indicate the potential of all  
634 the studied species to grow under a range of at least moderate rates of  
635 progradation and erosion. Such a result is not totally unexpected as  
636 coastal foredunes are an extremely selective habitat, and the capacity  
637 to persist when exposed to repeated erosion is a recognised characteris-  
638 tic of floral species associated with this environment (Hesp, 1991;  
639 Garcia-Mora et al., 1999; Ciccarelli et al., 2012).

640 Species abundances are positively correlated with environmental  
641 suitability (Weber et al., 2017). Moreover, dominant species exert a dis-  
642 proportionate influence over community dynamics and ecosystem  
643 function (Grime, 1998). This study identified significant associations be-  
644 tween the rate of shoreline change and species abundance at both the  
645 species and at the community level. At the species level, rates of

646 progradation rather than erosion explained the observed associations  
647 with shoreline change. For example, *S. sericeus* and *T. junceiforme* were  
648 more abundant at progradational than erosional sites. In contrast,  
649 *A. arenaria*, *E. paralias* and *Cakile* formed equally abundant populations  
650 on both progradational and erosional coasts. These findings imply  
651 that as erosion rates increase the abundance of *S. sericeus* and  
652 *T. junceiforme* will decrease, while those species capable of forming  
653 large populations on eroding coasts, such as *A. arenaria*, may increase  
654 in relative dominance. This result has important implications for coastal  
655 management and species conservation, because it indicates the poten-  
656 tial for shifts in the relative importance of foredune species in response  
657 to climate change.

658 At the community level most sites contained more than one poten-  
659 tial dune-building species. Sites were able to be grouped based on either  
660 the presence or absence of species and differences in the relative abun-  
661 dance of species shared by multiple groups of sites. Overall, the groups  
662 were not strongly defined by differences in shoreline change rates.  
663 However, it is important to note that this study examined only a subset  
664 of the total foredune plant community and focused only on the early  
665 colonising dune-building species that are highly adapted to coastal dy-  
666 namics (Hesp, 1991). Consideration of the total plant community  
667 would potentially have yielded a stronger result though the inclusion  
668 of less adapted species.

669 Site-specific environmental conditions superimposed on the history  
670 of species introduction and anthropogenic disturbance have been  
671 shown to influence foredune plant community composition  
672 (Henriques and Hay, 1998; da Silva et al., 2008; Barrett-Mold and  
673 Burningham, 2010; Santoro et al., 2012). It is likely that similar factors  
674 also play a role in determining the composition of the communities  
675 identified along the Victorian Coast. A range of different communities  
676 comprised of several species in differing abundances could be antici-  
677 pated irrespective of overlying erosional or progradational shoreline  
678 change rates when considering spatial and temporal patterns among  
679 coastal sites.

680 That said, the PCO analysis did identify one group of sites that was  
681 positively associated with increased erosion rates that warrants further  
682 discussion. The three sites comprising this group contained moderate  
683 amounts of *Cakile* spp. and very low abundances of the other species.  
684 The foredune at these sites was poorly formed or absent and vegetation  
685 communities on the seaward dunes were mainly comprised of second-  
686 ary or mid-successional species commonly associated with stable inland  
687 dune surfaces (Fig. 7d). A similar decline in early-colonising species as  
688 erosion rates increase has been observed elsewhere (Feagin et al.,  
689 2005; Ciccarelli et al., 2012; Bitton and Hesp, 2013). These results are  
690 suggestive of the potential for a shift from early colonising dune-  
691 building species to a flora comprised of remnant inland dune communi-  
692 ties exposed by shoreline retreat following erosion.

#### 693 4.2. Species traits

694 Species traits provide a partial explanation for the patterns of species  
695 abundance observed in the present study (Garcia-Mora et al., 1999;  
696 Feagin et al., 2005; Gornish and Miller, 2010). Of particular importance  
697 to the persistence and survival of plants on a retreating shoreline are  
698 traits that facilitate seedling recruitment and/or vegetative regrowth  
699 despite episodes of major salt spray; substrate erosion; sand accumula-  
700 tion; and traits that determine proximity to shoreline (Cheplick, 2016).  
701 For example, although wind-blown or bird-dispersed seed allows occa-  
702 sional establishment further inland, *Cakile* spp. compete poorly with the  
703 perennial dune grasses associated with most temperate incipient  
704 foredunes (Davy et al., 2006). Consequently, the occurrence of *Cakile*  
705 spp. is restricted to between the upper limit of the spring-high tides  
706 and the toe of the foredune (Doing, 1985; Davy et al., 2006), as was ob-  
707 served in this study. This zone can be wide on prograding coasts but is  
708 more usually narrow and experiences high salinity and frequent erosion  
709 by waves. *Cakile* spp. are tolerant of salt spray and transient seawater

inundation (Barbour and DeJong, 1977). In addition, rapid growth, 710  
high fecundity, a persistent seed-bank, and buoyant and salt tolerant 711  
seeds aid population persistence and recolonisation following distur- 712  
bance (Davy et al., 2006). The wide distribution of small populations 713  
of *Cakile* spp. on both erosional and progradational coasts in Victoria 714  
suggests it is an opportunistic species that can persist on erosional 715  
coasts by establishing between disturbance events, but one that rarely 716  
forms extensive populations due to its annual life cycle and its confine- 717  
ment to a narrow, frequently disturbed, environment. 718

In comparison, the perennial life cycle of *A. arenaria*, *S. sericeus*, 719  
*T. junceiforme* and *E. paralias* allow these species to form large popula- 720  
tions in the absence of disturbance. These species share other traits 721  
that enhance survival in the beach dune environment; namely a toler- 722  
ance to substrate mobility and salinity, vertical growth and increased 723  
vigour following burial, and an ability to recolonise following beach 724  
and dune erosion (Hesp, 1991; Garcia-Mora et al., 1999; Gallego- 725  
Fernandez and Martínez, 2011). Despite these similarities, onshore zoni- 726  
ation of *A. arenaria*, *S. sericeus*, *T. junceiforme* and *E. paralias* was appar- 727  
ent at many sites in the present study. For example, *T. junceiforme* was 728  
usually restricted to the seaward margins of the foredune when grow- 729  
ing in association with *A. arenaria*. This is consistent with observations 730  
in South Australia (Hilton et al., 2006) and patterns of foredune zoni- 731  
ation in its native range where *T. junceiforme* strongly associated with 732  
the seaward-most dunes (Doing, 1985). Similar zonation was observed 733  
at sites with co-occurring *S. sericeus* and *A. arenaria*. Interestingly, zoni- 734  
ation in the present study was most apparent when species were co- 735  
occurring. *S. sericeus*, *A. arenaria* and *T. junceiforme*, in particular, 736  
would occupy all coastal zones in the absence of other species. 737

The observed zonal patterns likely reflect subtle distinctions in 738  
species' adaptations to the beach and foredune. For example, several 739  
studies have identified a correlation between the distance of a plant 740  
species inland of the high tide line and differences in relative species tol- 741  
erances to salinity (salt-spray, seawater inundation and soil salinity) 742  
and burial (e.g. Barbour and DeJong, 1977; Maun and Perumal, 1999; 743  
Sykes and Wilson 1988). Indeed, the zonal patterns observed in 744  
this study broadly reflect the tolerance of the study species to salinity. 745  
For example, *T. junceiforme* is more tolerant of higher soil salinities com- 746  
pared to *A. arenaria* allowing it to persist closer to the high-tide line 747  
(Sykes and Wilson, 1989). Similarly, the *Cakile* spp. are very tolerant 748  
of high salinity allowing this species to thrive in the backshore environ- 749  
ment (Barbour and DeJong, 1977). Differences in species traits also pro- 750  
vide a possible explanation for the positive association between 751  
*T. junceiforme* and *S. sericeus* abundance on prograding coasts in this 752  
study (Fig. 9). Both these species have the capacity for rapid lateral 753  
growth by the production of horizontal rhizomes or stolons. On 754  
progradational coasts, *T. junceiforme* and *S. sericeus* can form large popu- 755  
lations by the seawards expansion from existing populations on the 756  
seaward margin of the current foredune. Limited available habitat suit- 757  
able for colonisation and frequent disturbance by waves limits such 758  
population growth on eroding coasts, resulting in a decrease in relative 759  
abundance of these species. 760

Pioneer plant communities on any given erosional foredune can 761  
comprise a range of different species depending on the antecedent 762  
dune vegetation or the ability of new species to disperse and establish 763  
from other populations. In the study area, plant communities show 764  
greater heterogeneity at eroding sites as also observed at the Gulf 765  
coast of Florida and central Italy (Ciccarelli et al., 2012; Bitton and 766  
Hesp, 2013). These authors suggest that plant communities on 767  
retreating shores will be dominated by mid- to late successional species 768  
that had originally established inland of the pioneer foredune zone and 769  
are subsequently exposed by coastal erosion. As relatively amicable con- 770  
ditions for plant growth inland of the foredune allow a broad range of 771  
species to establish depending on the local availability of species and ar- 772  
rival histories, these later successional plant communities show consid- 773  
erable diversity in species composition. An important finding of the 774  
present study is that similar inter-site heterogeneity on eroding coasts 775

776 can also occur within pioneer plant communities. Moreover, in contrast  
777 to [Bitton and Hesp \(2013\)](#), we found that species richness declined on  
778 eroding coasts, while total abundance remained constant. Collectively,  
779 these results suggest that foredunes on some eroding coasts, at least  
780 those within the erosional range of the present study, will be dominated  
781 by fewer species; but that compensatory growth maintains a dense veg-  
782 etation cover.

#### 783 4.3. Implications for foredunes under conditions of increased coastal 784 erosion

785 These results in combination with existing studies allow for the de-  
786 velopment of a preliminary model of the response of dune-building  
787 foredune plant species to increasing erosion. Under conditions of  
788 sustained progradation coasts can develop a wide to very wide pioneer  
789 plant zone ([Bitton and Hesp, 2013](#)). Species distributions exhibit strong  
790 zonation reflecting onshore gradients in environmental factors when  
791 multiple species are present ([Doing, 1985](#); this study). A typical se-  
792 quence on the Victorian Coast comprised *T. junceiforme* or *Cakile* spp.  
793 on the beach and lower stoss face of the foredune, *S. sericeus* and then  
794 *A. arenaria*, with *E. paralis* inland of the foredune crest. A low magnitude  
795 single erosion event, such as might occur during spring tides, may only  
796 remove the beach or embryo dune communities. Larger events will pro-  
797 gressively affect increasingly inland communities proportional to the  
798 magnitude of the event and, in extreme cases, may remove the pioneer  
799 plant zone entirely. On coastlines in dynamic equilibrium, or where high  
800 magnitude erosion occurs infrequently, vegetation is more likely to  
801 recolonise the back-beach and foredunes at least to partially reform  
802 ([Durán and Moore, 2015](#)). The post-erosion plant community may differ  
803 from the antecedent community depending on local propagule pres-  
804 sure and the relative ability of the available species to colonise the  
805 shoreline (e.g. [Hilton, et al. 2005](#)). Species already occupying a site or  
806 with the capacity to disperse from nearby populations could be ex-  
807 pected to be more likely to recolonise following an erosive event.

808 Increasing sea-level or storm frequency will increase the frequency  
809 of erosion events with a corresponding decline in the time available  
810 for vegetation and dune recovery between events ([Feagin et al., 2005](#);  
811 [Q12 Duran and Moore, 2015](#)). A moderate increase in erosion frequency  
812 may have little impact on annual species that complete their life cycle  
813 between events, such as *Cakile* spp., but could result in significant de-  
814 clines in the abundance of slower growing more persistent species. Ini-  
815 tial increases in erosion frequency because of increasing sea levels will  
816 influence mostly the beach and incipient foredune environments but  
817 with an increasingly greater effect on inland communities as shorelines  
818 progressively retreat. Erosion will still occur episodically with the po-  
819 tential for some post-storm vegetation recovery between events, thus  
820 short-term foredune development can occur on coasts with an other-  
821 wise overall trend of retreat (e.g. [Morton et al., 1994](#); [Suanez et al.,](#)  
822 [2012](#)). Each subsequent erosion and recovery period can be viewed as  
823 a selective event for those species more capable of establishing and  
824 thriving in the post-erosion environment. Over time this may lead to a  
825 progressive decline in the number of foredune species at any given  
826 beach and increasing dissimilarity between beaches as plant communi-  
827 ties develop along divergent pathways.

828 Foredunes build vertically and relocate inland under some condi-  
829 tions on eroding coasts. This study suggests that on some coasts a cor-  
830 responding decrease in the width of pioneer plant zone, a loss of strong  
831 zonation, and increased selection for those species more tolerant of  
832 burial (i.e. *A. arenaria*) will also occur, particularly under moderate  
833 rates of erosion. However, persistent long-term erosion and coastal re-  
834 treat are expected to result in the eventual loss of all foredune habitat  
835 ([Feagin et al., 2005](#)). In this case pioneer plant communities will then  
836 be restricted to the back-beach as small populations that establish be-  
837 tween erosive events.

838 This shift from early colonising dune-building species to a flora com-  
839 prised of remnant inland dune communities exposed by shoreline

840 retreat indicates a complete breakdown of the colonisation and succes-  
841 sional processes necessary for foredune recovery following erosion (as  
842 described by [Feagin et al., 2005](#)). Once this threshold for dune recovery  
843 is passed, foredune resilience is effectively non-existent. Active manage-  
844 ment, such as the reintroduction of dune-building plants, maintenance  
845 of nearby propagule dispersal sites or dune reshaping, will then be re-  
846 quired to maintain any potential for foredune development ([Feagin](#)  
847 [et al., 2015](#)).

848 Consideration of the geomorphic implications that may follow such  
849 shifts in species cover on foredunes is beyond the scope of this paper.  
850 Nevertheless, all five non-native species have the potential to alter  
851 foredune development. For example, the geomorphic changes that fol-  
852 low the establishment of *A. arenaria* have been the subject of several  
853 studies on temperate coasts of the U.S, New Zealand, and south-east  
854 Australia (e.g. [Heyligers, 1985](#); [Wiedemann and Pickart 2004](#); [Hilton](#)  
855 [et al. 2005, 2006](#); [Hacker et al. 2012](#); [Hayes and Kirkpatrick 2012](#);  
856 [Konlechner et al., 2016](#)). In general, *A. arenaria* is associated with  
857 changes increased dune height; dune stabilisation; the displacement  
858 of the native biota; and may adversely affect the long-term develop-  
859 ment of coastal barriers by inhibiting transgressive dune development.  
860 Relatively little is known regarding the impact of *T. junceiforme* on  
861 foredunes outside its native range; however, observations within  
862 south-east Australia suggest that *T. junceiforme* initiates foredune devel-  
863 opment; forms foredunes seaward of those associated with *S. sericeus* or  
864 *A. arenaria*; facilitates localised progradation; and potentially inhibits  
865 the development of transgressive dunes ([Heyligers, 1985](#); [Hilton et al.,](#)  
866 [2006](#)). *Cakile* spp., in contrast, typically form low hummocky dunes  
867 within a narrow zone between the high-tide and toe of the dunes. The  
868 annual life-cycle of *Cakile* ssp. and the frequent disturbance of the  
869 upper beach by waves mean that these dunes are usually ephemeral  
870 landforms ([Davy et al., 2006](#)). Any shift from, for example, an  
871 *A. arenaria* dominated foredune community to a *Cakile* dominated com-  
872 munity that could be expected under conditions of prolonged erosion  
873 could also therefore be associated with a reduction in foredune building  
874 capacity or changes in dune form.

## 875 5. Conclusions

876 Increased frequency and magnitude of coastal erosion has the poten-  
877 tial to alter foredune plant communities. Changes in landform develop-  
878 ment and function can occur following any shifts in the species  
879 abundance and/or distribution given the association between vegeta-  
880 tion and foredune morphology, with potential implications for the  
881 maintenance of resilient foredunes. Foredune-building species possess  
882 traits that enable survival in frequently disturbed shoreline environ-  
883 ments; however, this study suggests that slight variations between spe-  
884 cies may also allow some species to establish stronger populations than  
885 others following coastal erosion. Importantly, this study has shown that  
886 even moderate increases in erosion frequency and magnitude have the  
887 potential to result in changes to foredune species and abundance. While  
888 this study examined only six species, it appears that species that are re-  
889 stricted to zones closer to the spring-tide level, that have a persistent  
890 rather than opportunistic growth-history or that are limited in their  
891 ability to recolonise following erosion, are more likely to be negatively  
892 impacted by increased rates of coastal erosion. Finally, despite signifi-  
893 cant associations in species abundances with erosional rates, all species  
894 in this study were recorded forming large populations under a range  
895 progradation and erosional shoreline change rates suggesting that  
896 past rates of shoreline change alone are not a sufficient predictor of  
897 foredune plant community composition. Further work on the vegeta-  
898 tion dynamics and post-erosion dune recovery processes is required be-  
899 fore predictions regarding the effect of increasing coastal erosion  
900 foredune plant communities can be made with high confidence.

901 Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geomorph.2018.11.013>.

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