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WETLAND CONSERVATION AND RESTORATION

Effects of Grazing by Native and Non-Native Terrestrial Vertebrates on the Growth of *Tecticornia arbuscula* in Australian Temperate Saltmarshes

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Abstract

The effects of grazing and browsing by terrestrial vertebrates are poorly understood for southern hemisphere saltmarshes, many of which are recovering from stock grazing. We investigated whether the native late-successional shrub, *Tecticornia arbuscula*, regenerating several years after the cessation of stock grazing, was grazed by wild herbivorous mammals to the degree of impeding recovery. We measured *T. arbuscula* growth parameters in exclosures and adjacent controls for two years and used camera trapping of animals across four consecutive austral seasons to indicate grazing pressure. Height growth was more affected by exclosure from grazing than lateral change. Notably, grazing did not prevent the recovery of the shrubs from stock grazing at either site, suggesting that the growth rate of *T. arbuscula* relative to total grazing pressure is at sustainable levels and these shrubs are in a trajectory of recovery, with the smaller plants growing the fastest. Also, we found little difference between our two sites in grazing impact, despite one site having twice the number of animals, largely native macropods, as the other site, which was dominated by introduced lagomorphs (rabbits and hares). These findings further the knowledge of native and non-native terrestrial vertebrates in austral saltmarsh ecology and conservation.

Keywords Restoration · Feral Animals · Salt Marsh · Herbivory · Shrub Growth · Vegetation Management

Introduction

Grazing and browsing by native and exotic vertebrates can strongly influence species and ecosystems (Biró et al. 2019; Bridle and Kirkpatrick 2001; Davidson et al. 2017). Vertebrate herbivores can have beneficial, benign, or deleterious effects, and affect ecosystem function through multiple and interconnected pathways, such as through herbivory and nutrient addition (Chen et al. 2022). Given the important functional role that mammalian herbivores can play in ecosystems (Lacher Jr et al. 2019), it is important to evaluate if total grazing pressure is at sustainable levels for species and ecosystems of concern (Prowse et al. 2019). This is particularly relevant, and pressing, if those species and ecosystems are on a recovery pathway from past disturbance (Qian et al. 2021).

Saltmarshes are an ecosystem of worldwide conservation concern given their important ecosystem services, ongoing depletion, and threats to their existence (Adam 2019; Gedan et al. 2009). In Australia, saltmarshes are listed as a 'threatened ecological community' under Federal legislation. The listing recognises several threats to saltmarsh (including grazing by livestock) and the need for both ecological research (including quantification of direct grazing) and on-ground conservation actions such as limiting grazing from recovering saltmarsh (Threatened Species Scientific Committee 2013). Knowledge of vertebrate grazing effects on saltmarsh plants in Australia is limited (Boon et al. 2015; Spencer et al. 2009), confined to personal observations and theory (Laegdsgaard 2006; Spencer et al. 2009). Further research is required to both quantify grazing effects and to understand the regeneration dynamics of the dominant plant species of Australian saltmarshes with the exclusion of grazing (Prahalad et al. 2020).

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Grazing and browsing are known to affect the structure and floristics of saltmarshes elsewhere in the world (Adam 2019; Gedan et al. 2009). The survival of individual herbs, grasses and shrubs, their size and reproductive success are the most affected (He and Silliman 2016). Among vertebrate grazers, the role of herbivorous birds such as geese and other waterfowl in influencing saltmarshes has been widely studied (e.g., Bazely and Jefferies 1986; Zacheis et al. 2001; Smith et al. 2012). There has also been work on mammal grazing in saltmarsh that explores the effects of domestic stock on other elements of the ecosystem (e.g., Davidson et al. 2017; Lagendijk et al. 2019; Koppenaal et al. 2022; Mondon et al. 2009). A smaller amount of work addresses the impacts of other wild grazers on shrubs. For example, in an elegant successional experiment, Dormann et al. (2000) found that inter-plant competition was more important than hare (*Lepus europaeus*) and goose (*Branta* spp.) herbivory in slowing the growth of two saltmarsh shrubs in the Netherlands, although herbivory had some effects on successional processes. Similarly, Kuijper and Bakker (2005) highlight the potential top-down control of hare and goose herbivory in saltmarsh ecosystems, particularly in preventing the establishment of late-successional plant species. Studies have also addressed the effects of vertebrate grazers on marsh geomorphology. For example, the grazing and burrowing of the introduced coypu or nutria (*Myocastor coypus*) on the Gulf Coast of the United States can starve marshes of sediment, leading to their loss (Ford and Grace 1998).

Work on the ecology and conservation of saltmarshes in Australia has largely ignored the terrestrial vertebrate fauna, notwithstanding the recognition of the role of large herbivorous mammals in the saltmarsh food web (e.g., Laegdsgaard 2006). This contrasts with the body of work on terrestrial vertebrates of the North American saltmarshes, parts of Europe (Greenberg and Maldonado 2006; Greenberg et al. 2006), a few studies from the southern hemisphere marshes (Canepuccia et al. 2015; Pascual et al. 2019), and a growing interest in vertebrates in mangroves (Rog et al. 2017). The recent global review by Canepuccia et al. (2023) of terrestrial mammals using tidal marshes further underscores this stark contrast. Despite Australia reportedly having close to a quarter of the world's marsh area, only 2.7% of the studies ($n=6$) were from this country (Canepuccia et al. 2023). These studies (4 unpublished reports and two papers) either record incidental observations of terrestrial mammals on saltmarsh (e.g., Prahalad 2014; Thalmann et al., 2015) or report mammal observations mostly outside the marsh, in the neighbouring forest areas (e.g., Bryant 2018; Driessen et al., 2011).

We know of no research on wild grazer-vegetation interactions in saltmarsh on mainland Australia (also see Boon et al. 2015; Laegdsgaard 2006; Spencer et al. 2009; Threatened Species Scientific Committee 2013). In the southern island State of Tasmania (lutruwita), the closely-cropped 'marsupial lawns' found in some brackish saltmarshes are formed by marsupial grazing (Roberts et al. 2011), but nothing is known of the effects of these herbivores on the succulent shrubs that dominate some of the more saline of the marshes (Prahalad and Kirkpatrick 2019; Prahalad et al. 2020) apart from the oft-cited observation of Kirkpatrick and Glasby (1981) that stock grazing after deliberate burning impedes the recovery of the shrub *Tecticornia arbuscula*. Tasmania, with its largely intact native terrestrial vertebrate fauna and several introduced mammal herbivores, presents an opportunity to determine the interactions between herbivorous mammals and saltmarsh shrubs. This work is also timely given the number of saltmarsh restoration projects is on the rise, and in that these projects typically exclude stock grazing.

Mammal species that commonly use saltmarsh in Tasmania include native species such as Bennett's wallaby (*Macropus rufogriseus*), Tasmanian pademelon (*Thylogale billardierii*) and common wombat (*Vombatus ursinus*) (Prahalad et al. 2020; Spencer et al. 2009; Roberts et al. 2011) and introduced animals, such as European rabbit (*Oryctolagus cuniculus*) and European hare (*Lepus europaeus*) (Wong et al. 1993). European rabbits are a recognised management concern in Tasmanian coastal saltmarshes because of their grazing, digging, and burrowing (e.g., Parks and Wildlife Service, 2013). Evaluation of the effects of total grazing pressure on saltmarsh plants, including potential trampling damage, could help determine whether these animals require active management in the restoration process (Sievers et al. 2022). Of particular concern are the habitat-forming dominant plants that aid the restoration of saltmarsh function after the cessation of stock grazing.

Tecticornia (family Chenopodiaceae) is a genus of 30 species and 13 subspecies (Shepherd and Wilson 2007), all halophytic shrubs that are mostly endemic to Australia. Of these species, *T. arbuscula* has the largest range. It is the only recorded species in the genus in Tasmania. It has a limited climate envelope (Prahalad and Kirkpatrick 2019), and is known to be vulnerable to drier climates and sea level rise (Prahalad et al. 2012; Coleman et al. 2017). The species has also been subject to other direct threats such as clearing and grazing (Kirkpatrick and Glasby 1981), and part of the national recovery of saltmarsh as a threatened ecological community requires effective regeneration of *T. arbuscula* shrublands across their range. Their important habitat function as a late-successional species is highlighted by the use of this shrub by several passerines (Prahalad et al. 2015), including the vulnerable Samphire Thornbill (*Acanthiza iredalei rosinae*) in South Australia (Coleman et al. 2017).

Information on growth rates relative to grazing pressure of this important shrub is likely to be vital in managing both its sustainable regeneration post-disturbance, and its landward establishment in response to sea level rise.

In the present paper, our primary aim was to examine the effects of grazing by both native and non-native mammal species on the growth of the late-successional succulent shrub *T. arbuscula* in two marshes with distinct landscape contexts and inferred mammal species compositions, both recovering from stock grazing. We hypothesised that differences in grazing pressure, as indicated by camera captures, would be reflected in differences in the loss of foliage to grazing terrestrial mammals. In doing so, we sought to quantify the growth rate of this conservation-dependent shrub, with and without grazing pressure in order to inform planning for its restoration. With the data from our camera traps, we expected to offer insights in the Australian context, into the nature and extent of terrestrial vertebrate herbivore use of temperate coastal saltmarshes.

Methods

Study Area

We selected two sites within the southeast bioregion of Tasmania, Australia (Fig. 1a-b), that contrasted in their landscape context and inferred mammals, to test for differences related to mammal herbivore abundance and composition. Our two saltmarshes were Orielton Lagoon near Sorell, a highly modified landscape, and Marchwiel Marsh at Marion Bay, in a relatively natural setting (Fig. 1c-d). They have similar succulent communities dominated by *T. arbuscula* and the early-successional ground-cover species, *Sarcocornia/Salicornia quinqueflora* (see Fig. 1e-g). Both saltmarshes experienced similar historical degradation from agricultural use, most notably, drainage and livestock grazing (Parks and Wildlife Service, 2013; Prahalad and Aalders 2020; Van de Geer 1972).

Orielton Lagoon saltmarsh is in the Pitt Water Nature Reserve (first proclaimed in 1995) and has been included

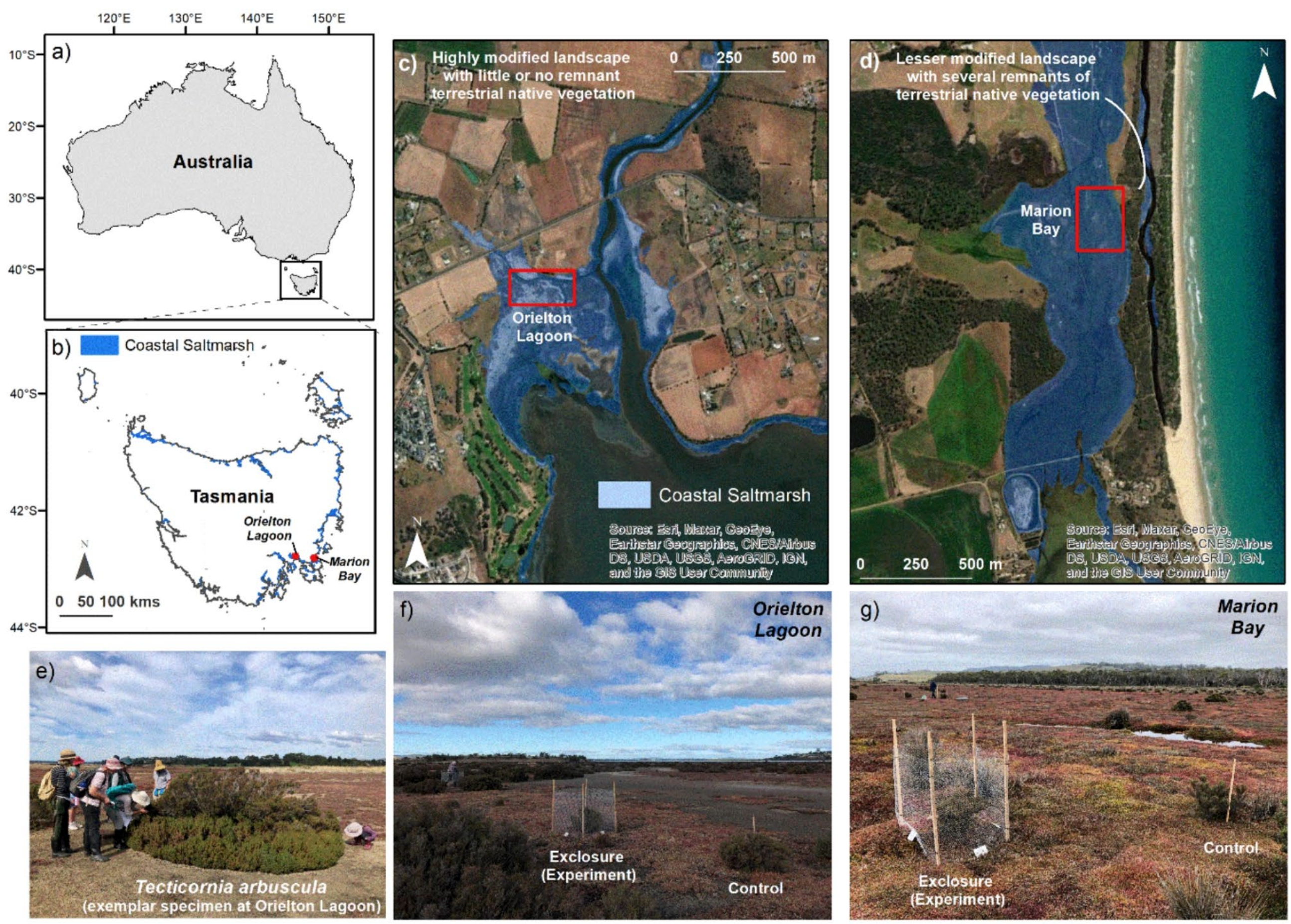

Fig. 1 Location of study area showing: **(a)** Australia; **(b)** Tasmania, with study sites identified within the south-east region; **(c)** Orielton Lagoon study site; **(d)** Marion Bay study site; **(e)** typical exemplar specimen of *Tecticornia arbuscula*; **(f)** paired plots at Orielton Lagoon; **(g)** paired plots at Marion Bay. All photos by VP. Coastal saltmarsh mapping data from Prahalad and Kirkpatrick (2019), other base data from the LIST (www.thelist.tas.gov.au, accessed 16 December 2022; © State of Tasmania)

(since 1982) as part of the Pitt Water-Orielton Lagoon Ramsar Site (Parks and Wildlife Service, 2013). The reserve is surrounded by the townships of Sorell, Orielton, Penna, and Midway Point, and agricultural and peri-urban environments, including a sewage treatment plant at Midway Point (Dunn 2012). The lagoon was cut-off from Pitt Water in 1953 by a causeway, leading to eutrophication and algal blooms (Saunders et al. 2007). Subsequently, two culverts were constructed to facilitate some tidal exchange (Dunn 2012). A study of decadal scale vegetation change in Orielton Lagoon (Prahalad et al. 2012) identified an expansion of *T. arbuscula* shrubland area associated with the removal of livestock and reinstated tidal flows. Current threats to saltmarsh regeneration include grazing by rabbits and eutrophication from agricultural runoff (Parks and Wildlife Service, 2013).

The second site, Marchwiel Marsh, is located on private land, the southern part of which falls under the Long Spit Private Nature Reserve (designated in 2005). The marsh is bordered to its south by the small coastal settlement of Marion Bay, and the rest is adjacent to tracts of native forests, pasture and a camping area associated with a festival venue (Prahalad and Aalders 2020). There is a network of agricultural ditches designed to drain surface water and facilitate access to cattle and sheep grazing (van der Geer 1972). Grazing by cattle and sheep has now been excluded except for the western area near Sedbury Creek where cattle can still access the marsh (Prahalad and Aalders 2020).

The region has a temperate maritime climate and a diurnal tidal regime with a micro-tidal range. Marion Bay has higher long term annual average rainfall of 877 mm compared to Orielton Lagoon which receives 569 mm (Bureau of Meteorology 2023), with strong inter-annal variability during the study period (2019 was dry at both sites receiving less than 70% of the long term annual average rainfall, whilst both 2020 and 2021 were wet years receiving ~ 120% of the long term annual average rainfall). At both sites, rainfall is spread evenly between months, but subject to occasional dry periods (Parks and Wildlife Service, 2013). The mean annual daily maximum temperature is similar at both sites (~ 17.5 °C) but the mean annual daily minimum temperature is lower at 8.2 °C at Orielton Lagoon, compared to 10 °C at Marion Bay (Bureau of Meteorology 2023), with low inter-annual variability during the study period (annual mean within ~ 1 °C).

Approval was received from land managers at both sites before this study was conducted. A Works Authority was granted by Tasmania Parks and Wildlife Service under the *National Parks and Reserved Land Regulations 2009* to access and undertake this study in Orielton Lagoon. An informal agreement was made with the landowner of Marchwiel Marsh for site access and the local Marion Bay Coastcare Inc., a community group, was consulted and involved with advice and data collection.

Exclosures and Vegetation Survey

At each of the two sites, a high marsh sampling area with a large number of sparsely-spaced specimens of *T. arbuscula* shrubs that were regenerating passively from seed was selected (see Fig. 1c-d). To test the hypothesis that browsing by mammals affected growth, 10 *T. arbuscula* shrubs were selected randomly for fencing at each of the two sampling areas. For each of these fenced shrubs, nearby (5–10 m away) plants of similar size and shape were selected as controls (see Fig. 1f-g). The fences consisted of 1 m high wire mesh (1–2 cm mesh size) wrapped around four 1.5 m high wooden stakes driven securely into saltmarsh substratum. The area of the exclosure varied between 1 × 1 m to 1.5 × 1.5 m depending on the size of the enclosed shrubs. The height of the exclosure was above that of the Bennett's wallaby, the largest herbivore, which attains ~ 90 cm. Steel pins were used to strongly secure the wire mesh to the saltmarsh soil to also prevent animals from digging under the exclosure to access the shrubs.

For each of the *T. arbuscula* shrubs, the following measurements were taken to the closest cm: height of shrub; longest width; width in north-south direction; and width east-west direction. Height was measured from the saltmarsh surface to the highest point of the plant above ground. Measurements were conducted over a 2-year period, with the first ('baseline') record in May-June 2019. Repeat measurements were conducted seasonally in November 2019, January 2020, May-June 2020, November 2020, March 2021 and May-June 2021. To reduce any potential observer bias and to maintain consistency, all measurements were made by the same individual (JA). During surveys any evidence of animal activity such as browsed vegetation, dieback (e.g. due to pathogens or invertebrate grazers), excessive trampling or burrowing was recorded.

Camera Trapping

The active use of saltmarshes by vertebrate animals can be determined by spotlight surveys, live trapping and camera trapping (De Bondi et al. 2010; Latham et al. 2012). Trapping methods are more reliable than spotlighting in establishing the presence of vertebrates. Comparison of live trapping and camera trapping surveys indicate that camera traps are both cost effective and reliable for the survey of small terrestrial mammals (De Bondi et al. 2010), although some species are captured more effectively in physical traps than by cameras (Driessen and Jarman 2014). Camera traps also allow for easier replication than physical traps (Burton et al. 2015) and generate fewer animal welfare concerns.

Four camera traps were set up in the vicinity of the *T. arbuscula* shrubs at both study sites. The aim was to document vertebrate graziers visiting the saltmarsh and likely to graze on the *T. arbuscula* shrubs. The cameras were fixed to temporarily installed metal stakes, separated from each other by about 150 m (Latham et al. 2012). Each camera was set up to aim at an area of saltmarsh adjacent to but not overlapping with the other cameras. The cameras were programmed to take multiple motion activated photos (three images per triggering event) during day and night over a 5-day period, amounting to 20 camera trap-days ($n=4$ camera traps). Infrared illumination was used for photos at night. The same procedure was repeated four times across the year, in austral spring (November 2019), summer (January 2020), late autumn (May 2020), spring (November 2020). University of Tasmania Animal Ethics Committee approval was received for the fauna survey (Ref: A0017893).

Data Analyses

Summary statistics of the four growth parameter measurements taken at seven different times were graphed in box plots (Fig. 2). To test the effects of grazing, site, and time, we used a General Linear Model using default options in Minitab 21 (Minitab, Inc., State College, Pennsylvania). For each growth parameter, the predictor variables were site, treatment, and time. Time and treatment were random factors, and treatment was nested in site. The residuals for

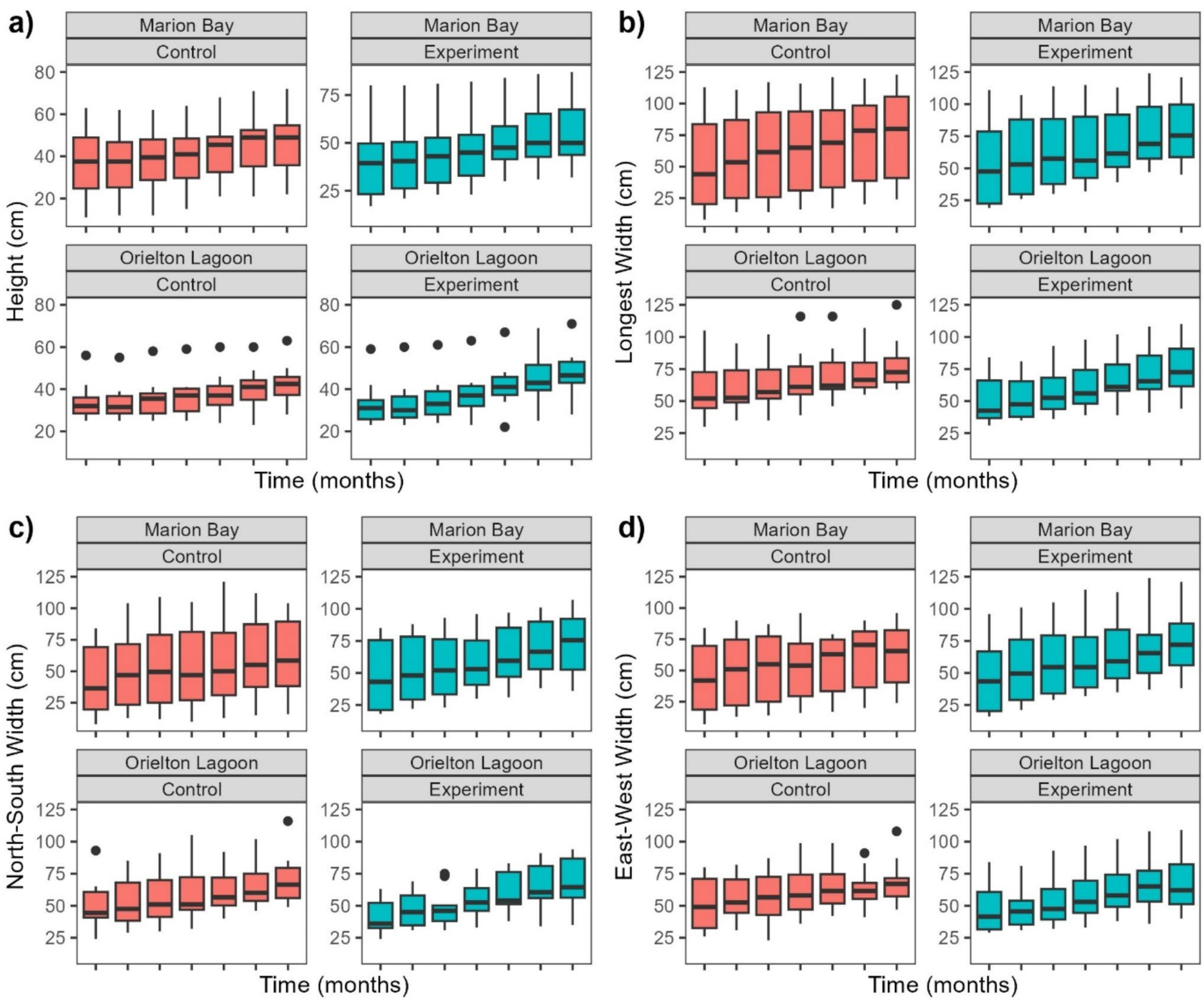

Fig. 2 Rates of change of *Tecticornia arbuscula* shrub growth parameters between site and treatment, over the sampling period: **(a)** Height; **(b)** Longest Width; **(c)** North-South Width; **(d)** East-West Width. Boxes show 50% of the values, the line the median, and dots outlying values. Sampling time periods for: Marion Bay are 0, 6, 8, 12, 18, 22 and 24 months; and Orielton Lagoon are 0, 5, 7, 12, 17, 21 and 24 months

the models were tested for normality. We then used a paired t-test to determine if the apical shoots of the unfenced controls were being grazed more than their lateral shoots (average of north-south and east-west widths). For this analysis of the grazing effect, we subtracted the control change data from the exclosure change data for each pair. The maximum width change was halved to make it equivalent to the vertical radial growth.

To understand growth characterises of the shrubs relative to size, we graphed height change and maximum width change against baseline measurement (i.e., 0 months) in scatterplots. To account for any confounding effect attributable to the activity of grazing animals, we focused this analysis on data from the exclosures, unaffected by grazers, to evaluate if growth varied with initial size. There was a clear break in distribution at 14.5 cm height change and 40 cm initial height (see Fig. 3a). A 2×2 table was constructed consisting of the number of observations in which: a) height change > 14.5 and initial height < 40.0 cm; 2) height change > 14.5 and initial height > 39.5 cm; 3) height change < 15 and initial height < 40.0 cm; 4) height change < 15.0 and initial height > 39.5 cm. Fisher's exact test was used to determine the probability of a deviation from a random distribution.

All photographs from the camera traps were screened for signs of vertebrate animals. Firstly, all photos were excluded that did not have any evidence of animals present, these having been triggered by moving vegetation and on occasions, birds, and insects (e.g., moths) in flight. Secondly, photographed animals that were difficult to identify (i.e., only part of an ear visible) were excluded from the count. Of the remaining photographs, successive photo sequences where it was clear that the same animal(s) were photographed were combined in the count. The aim was to record the species of grazing animal, the diel period (day or night), and the frequency of saltmarsh use across the trap-days to infer animal density and grazing pressure. Non-target species of vertebrate animals were also recorded. In the case of birds, those in flight were excluded from the data analyses.

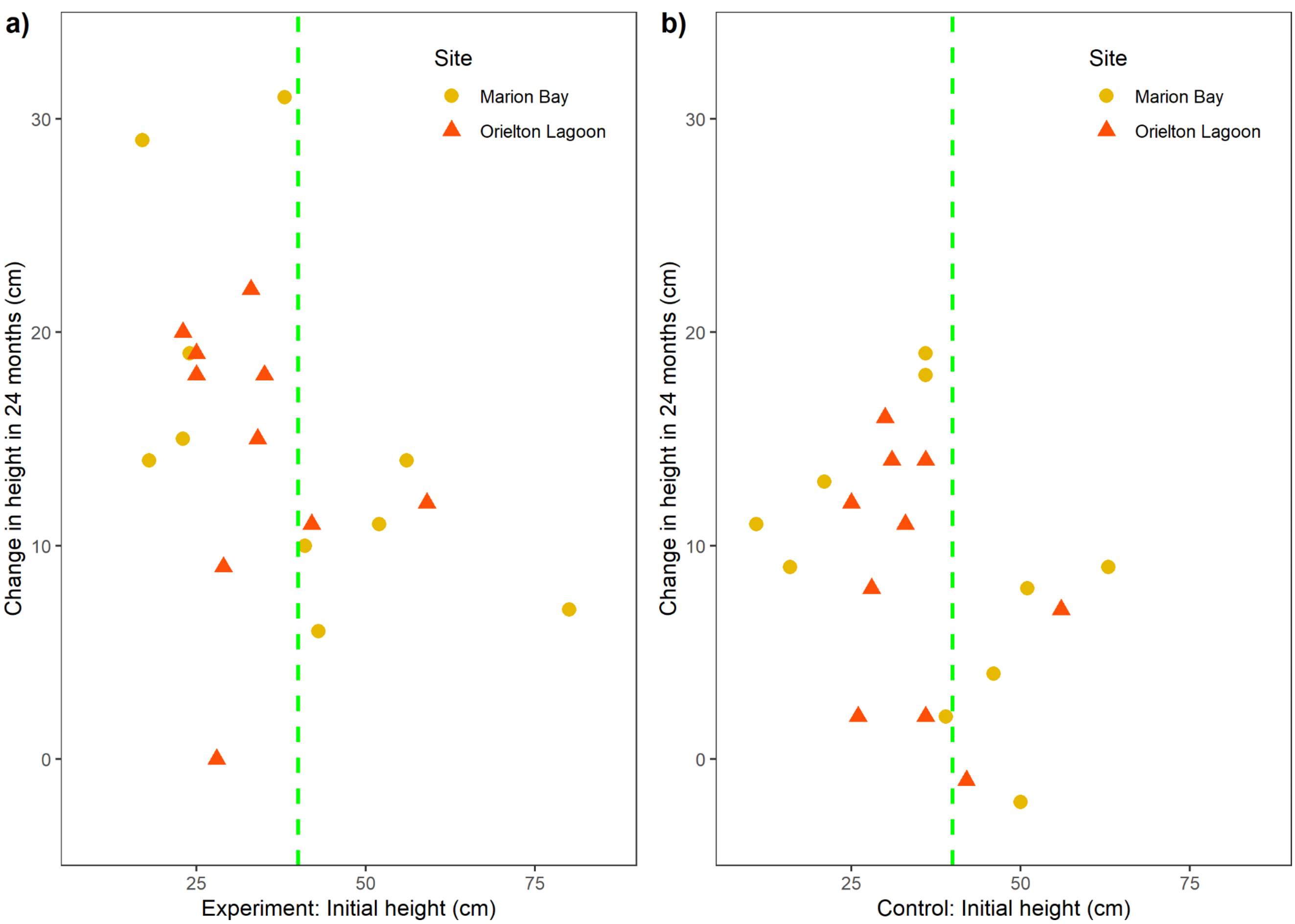

Fig. 3 Relationships between *Tecticornia arbuscula* initial shrub height (0 months) and change in height over the 24 months of the study in: **(a)** experiment (or, exclosures); **(b)** control. The discontinuous line at 40 cm height indicates the distinction between initially shorter and taller shrubs, and their relative growth over the 2-year study period

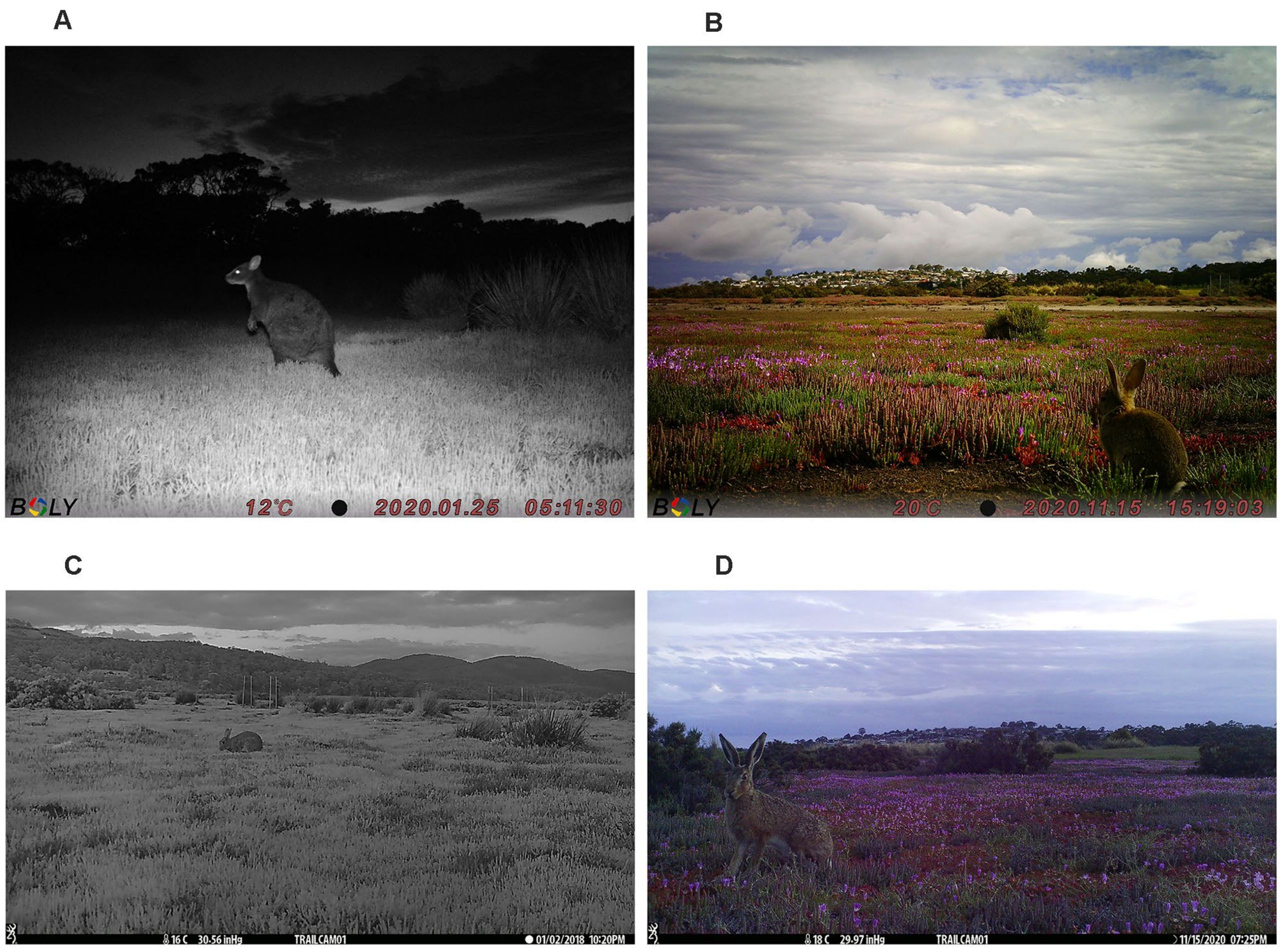

Fig. 4 Native macropod (top left: A) and introduced European rabbit (bottom left: C) at Marion Bay during the night, and introduced European rabbit (top right: B) and European hare (bottom right: D) at Orielton Lagoon during day and dusk. Photos from camera traps

Table 1 Results of general linear modelling predicting height, maximum width, north-south width and east-west width of *Tecticornia arbuscula* shrubs from site (random), treatment (random, nested in site) and time (fixed)

	Site		Treatment (site)		Time		R^2(%)
	F	P	F	P	F	P	
Height	2.96	0.227	4.25	0.015	27.84	<0.001	15.02
Maximum width	0.22	0.683	0.69	0.505	22.25	<0.001	7.96
North-south width	0.00	0.964	1.69	0.186	26.18	<0.001	9.71
East-west width	0.35	0.614	1.93	0.147	23.59	<0.001	9.29

Results

Vegetation Responses

The four growth parameter measures of *T. arbuscula* bushes all increased steadily over the 2-year period in both exclosures and controls plots at both sites (Fig. 2; also see Fig. S1-S2). Results from the GLM analysis (Table 1) indicated that there was no site effect for any of the four growth parameters, a strong time effect for all and a moderate treatment (site) effect for height only. At Orielton Lagoon, the mean height increase in the control was 8.5 cm compared to 14.4 cm in the exclosures. At Marion Bay, the height growth in the controls was 9.1 cm while in the exclosures it was 15.6 cm. The heights of the paired bushes in the exclosures were 6.2 cm taller than those in controls, while the equivalent figure for lateral growth was 3.1 cm. The paired t-test indicated that this greater effect of grazing on the vertical than lateral shoots was real ($t=2.54$, d.f. = 19, $P=0.020$). The initially taller shrubs (> 40 cm height) in the exclosures exhibited low height change, while the initially shorter shrubs (<40 cm height) put on a greater amount of height (Fig. 3a; Fishers exact probability test, $P=0.003$).

Species Detection

In all, there were a total of 20 camera trap-days, per season, per site. Some of the cameras failed to operate on some of the days, providing data for 89 trap-days at Orielton Lagoon and 86 trap-days at Marion Bay. These yielded a total of five target species of grazing mammals (three native and two introduced), one introduced non-target carnivore, and ten bird species of which one was introduced (Table 2; Fig. 4).

Of the grazing mammals, the European rabbit was the most common across both sites. European hare was regularly observed in Orielton Lagoon and absent from Marion Bay. There were no native grazing mammals present at Orielton Lagoon. The Tasmanian pademelon (*Thylogale billardierii*) was the most common species in Marion Bay. There were a few Bennett's wallabies (*Macropus rufogriseus*), with the brushtail possum (*Trichosurus vulpecula*) also present (Fig. S3). In several instances, it was difficult to differentiate the pademelons and wallabies. Hence, their counts were combined into a single group of macropods. The number of grazing animals sighted was almost twice higher at Marion Bay than at Orielton with 130 sightings of macropods, combined with the presence of rabbits (16 sightings) and possums (3 sightings). In comparison, Orielton Lagoon had 61 sightings of lagomorphs (Table 2).

All grazing mammals at Marion Bay were active only at night with no observations recorded during the day. Rabbits and hares in Orielton Lagoon were active both during the night and the day, although they were twice more active at night than during the day (21 and 9 occurrences respectively). In Orielton Lagoon, there are also several burrows in the driest part of the saltmarsh (Fig. S4), which were absent from the same situation in Marion Bay (cf. Prahalad and Aalders 2020).

Discussion

The main aim of our study was to document the effects of grazing by mammal species on the growth of late-successional succulent shrub *T. arbuscula* in two representative saltmarshes with distinct faunal compositions recovering from historic stock grazing. Within each of our sites, grazing loss of *T. arbuscula* foliage was compensated for by strong growth of the shrub across all four dimensions (Fig. 2). These findings indicate that the total grazing pressure is at sustainable levels for our focal species, *T. arbuscula*, at both sites and that these shrubs are in a trajectory of recovery to their pre-disturbance levels on a decadal timescale (cf. Prahalad et al. 2012), with the smaller plants growing the fastest. However, our findings here do not extend to loss of seed stock due to grazing, seedling establishment and other potential effects grazing might have in the early years of regeneration (Hulme 1996). Grazing may also affect other taxa more than *T. arbuscula*. For example, the structurally dominant *Gahnia filum*, a late successional sedge that either co-occurs with *T. arbuscula* or forms small colonies in high marsh areas, has been grazed down to its base at our sites (Fig. S5). Further research is therefore needed to evaluate the effects of controlling rabbits and hares (e.g., Thomsen et al. 2005) and also the effects of fencing native mammals on regeneration at early stages of seedling establishment (e.g., Bergen et al. 2000).

The grazing mammals we observed in both our study sites have strongly overlapping diets, that include browse as well as herbaceous material (Davis et al. 2008; Heaton et al. 2022; Hume 1999; Puig et al., 2017; Sprent and McArthur 2002). Yet, we found a lack of difference in grazing impact between sites, despite Marion Bay having twice the number of animals, largely native macropods, as Orielton Lagoon, which was dominated by introduced lagomorphs. The much larger number of observations of herbivores at Marion Bay seems on the surface to be inconsistent with this lack of differentiation of grazing effects. One explanation could be that all herbivores cease to eat *T. arbuscula* shoots when they attain a particular level of toughness (i.e., not as soft and palatable), moving on to other food species. Palatability may also be affected by physiolological responses of chenopods which, under stress, can increase concentrations of osmoregulatory compounds, reduce green pigments (chlorophyll) and increase purple-red pigments (betacyanin) (Marchesini et al. 2014). The browsing of apical shoots of our unfenced controls (see Fig. 3b) also points to this likely preference for softer and greener new growth (Grüner and Norton 2006).

Alternatively, the similarity in foliage consumption rates between our study sites (Fig. 5) may relate to a higher level of preference for *T. arbuscula* foliage by lagomorphs than macropods. Here, it must be noted that the European hares with a head–body length of ~55–65 cm (Bock, 2020) were able to access the shrubs used as controls in Orielton Lagoon as much as the taller Tasmanian pademelons present in Marion Bay. The possibility of lagomorphs' higher intake of *T. arbuscula* foliage at Orielton Lagoon could be tested by relating proportions within the contents of the scats (e.g., Rathbone and Barrett 2017; Puig et al., 2017). For example, Puig et al. (2017) used faecal samples of the European hares of the Andean mountains of Argentina to find that their diet included both grasses and shrubs. The proportion of lifeforms in their faeces related to available plant cover and

Table 2 Vertebrate species captured by camera traps from Orielton Lagoon and Marion Bay Saltmarsh study locations. Target species indicate herbivorous mammals that are expected to graze on saltmarsh plants. Non-target species are listed here as by-catch, including a carnivorous mammal and bird species. ^ non-native species. * are no data

Order	Common name	Scientific name	Orielton Lagoon					Marion Bay				
			Nov-19	Jan-20	May-20	Nov-20	***Total***	Nov-19	Jan-20	May-20	Nov-20	***Total***
			13 trap-days	23 trap-days	25 trap-days	25 trap-days		16 trap-days	25 trap-days	25 trap-days	23 trap-days	
Target species												
Diprotodontia	Tasmanian pademelon, Bennett's wallaby	*Thylogale billardierii, Macropus rufogriseus*	*	*	*	*	***0***	26	18	44	42	***130***
	Brushtail possum	*Trichosurus vulpecula*	*	*	*	*	***0***	*	*	1	2	***3***
Lagomorphs	European rabbit	*Oryctolagus cuniculus*^	1	7	7	9	***24***	14	1	1	3	***16***
	European hare	*Lepus europaeus*^	3	10	4	20	***37***	*	*	*	*	***0***
Non-target species												
Carnivora	Cat	*Felis catus*^	1	*	1	1	*3*	*	*	*	*	*0*
Gruiformes	Tasmanian native-hen	*Tribonyx mortierii*	*	*	3	5	*8*	*	*	*	*	*0*
Anseriformes	Australian shelduck	*Tadorna tadornoides*	*	*	*	*	*0*	*	*	6	*	*6*
	Pacific black duck	*Anas superciliosa*	*	*	*	*	*0*	*	*	2	*	*2*
Charadriiformes	Masked lapwing	*Vanellus miles*	*	*	*	8	*8*	*	*	*	*	*0*
	Kelp gull	*Larus dominicanus*	*	*	*	1	*1*	*	*	*	*	*0*
Passeriformes	Forest raven	*Corvus tasmanicus*	3	*	1	*	*4*	4	1	*	4	*7*
	White-fronted chat	*Epthianura albifrons*	*	*	*	*	*0*	*	2	*	*	*2*
	Superb fairywren	*Malurus cyaneus*	2	*	*	*	*2*	1	*	*	*	*1*
	Common starling	*Sturnus vulgaris*^	6	*	*	104	*110*	5	*	10	54	*50*
Accipitriformes	Swamp harrier	*Circus approximans*	*	*	*	1	*1*	*	*	*	*	*0*

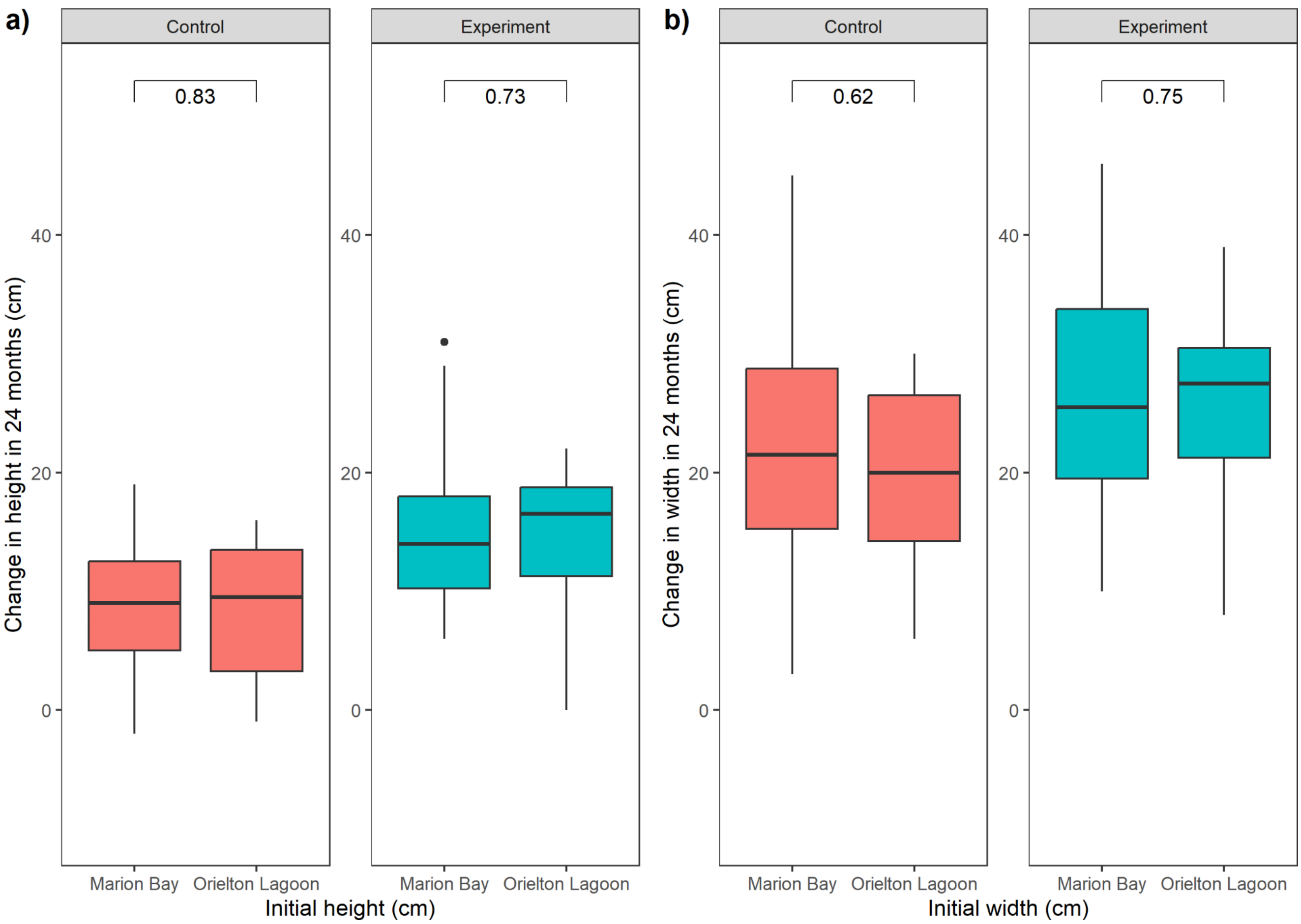

Fig.5 Comparison between the two study sites of growth in *Tecticornia arbuscula* shrub height (**a**) and longest width (**b**) between treatments. Boxes show 50% of the values, the line the median. P values (> 0.05) shown under the crossbars are derived from paired t-tests

diversity, with a seasonal effect also apparent (Puig et al. 2017).

A subsidiary aim of our study was to understand the growth rate relative to total grazing pressure on *T. arbuscula*, as a species of conservation concern and restoration focus. Given it is a dominant species in high temperate latitude Australian saltmarshes (Boon et al. 2015), and provides faunal habitat (Coleman et al. 2017), information about the biology and ecology of the species is likely to be valuable for management. Our two-year seasonal measurement of the growth characteristics of this shrub across two sites is the first such dataset for the species, showing positive rates of growth both with and without grazing (see Fig. 2 and 5). Also, our finding that *T. arbuscula* grows quickly as a seedling (see Figs. 3a-b and 6), with reduced growth rates for larger shrubs mirrors similar non-linear growth pattern characteristic of woody plants. Of more interest here is the greater widths than heights in our data set, which are consistent with other allometric measurements of *T. arbuscula* (Knight, Prahalad et al., unpublished data), indicating reduced investment in height relative to canopy width, depth, and branching. These adaptation strategies are likely to reflect environmental factors, including soil biomes, which require further investigation (e.g., Ding et al. 2021).

Tecticornia arbuscula individuals at Marion Bay are up to ~ 1.1 m high and 3 m wide (Prahalad and Aalders, unpublished data), similar in size to the few larger shrubs present at Orielton Lagoon (pers. obs. by VP and JA; see Fig. 1e). Orielton Lagoon had suffered a near complete loss of its historic stands of *T. arbuscula* with regeneration happening over the past half century (Kirkpatrick and Glasby 1981; Prahalad et al. 2012). Marion Bay has maintained some of its historic stands having been fenced off from grazing and other impacts (Prahalad and Aalders 2020). In this context, our findings suggest that grazing of these historically stock-grazed marshes by lagomorphs or macropods is insufficient to prevent passive regeneration and sustainable growth after stock exclusion. From a restoration perspective, research is needed to investigate the age of the larger shrubs, and in turn, determine expected timeframes for the passive establishment of advanced stands of *T. arbuscula* across their range with or without grazing controls.

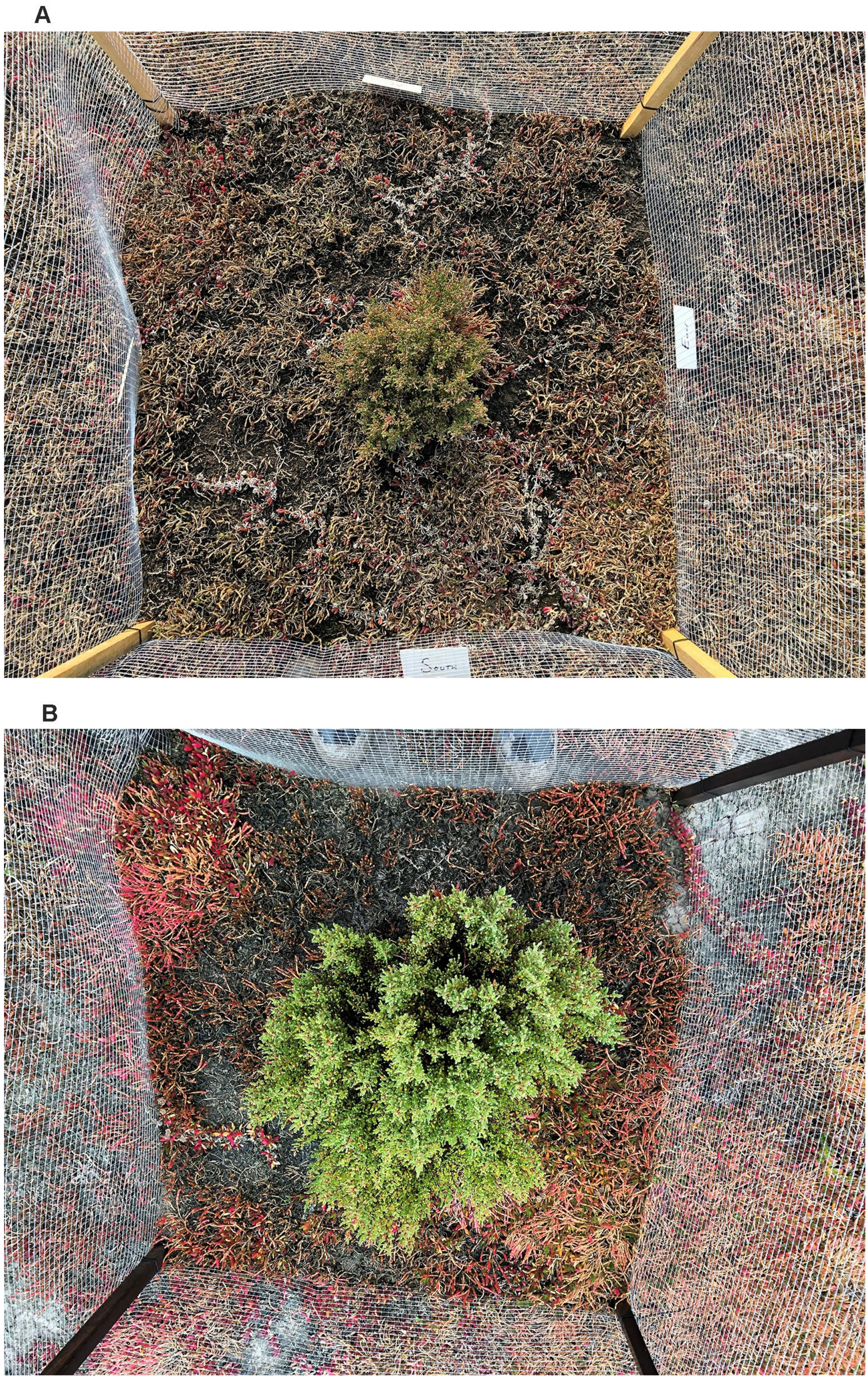

Fig. 6 An example of an exclosure specimen (OLE8) from Orielton Lagoon showing growth increments in 2 years (from June 2019 to June 2021) of 20 cm in height, 22 cm along the longest width, 25 cm in north-south and 22 cm in east-west directions. Initial measurements (**A**) were 23 cm in height, 39 cm along the longest width, 34 cm in north-south and 29 cm in east-west directions. Final measurements (**B**) were 43 cm in height, 61 cm along the longest width, 59 cm in north-south and 50 cm in east-west directions. Photos by VP

Terrestrial vertebrates, despite their role in shaping the structure and floristics of saltmarshes, have largely been overlooked in global scholarly reviews on saltmarsh (e.g., Roman and Burdick 2012; Kimball et al. 2021). The recent work of Canepuccia et al. (2023) begins to address this gap, but the Australian continent is disproportionately underrepresented. Our study addresses this gap and has shown that saltmarshes are regularly used (and grazed) by native terrestrial mammals, with high numbers of Tasmanian pademelon (Fig. S6), and occasional individuals of Bennett's wallaby and the Brushtail possum (see Table 2). This finding underscores the need for better consideration of terrestrial vertebrates in saltmarsh ecology and restoration planning (e.g., Sievers et al. 2022), especially given the attention given to the 'co-benefits' of restoring blue carbon habitats by enhancing biodiversity (Hagger et al. 2022; Soto-Navarro et al. 2020).

Notably, our study reveals a stark contrast between the mammalian assemblages of our two sites, with a complete lack of native mammals at Orielton Lagoon. The deleterious effects of land clearing and habitat fragmentation has been extensively and intensively studied for many species and habitats, including in the case of bats, in Australian saltmarshes (Gonsalves et al. 2012). The marked absence of autochthonous species in the saltmarshes at Orielton Lagoon provide evidence for the effect of habitat disturbance and fragmentation on the loss of large mammals, as previously hypothesised by Laegdsgaard (2006). Indeed, in the Atlantic coast marshes of Canepuccia et al. (2015) found that the surrounding landscape characteristics (i.e., presence or absence of 'adjacent inland habitats') influence small mammal richness and composition. These considerations indicate the potential role that landscape-scale restoration such as with the restitution of buffer zones habitats may play in structuring the mammalian fauna of coastal saltmarshes.

Conclusion

Our data force us to reject the research hypothesis that differences in numbers and types of herbivorous mammals result in differences in the growth rates of regenerating *T. arbuscula* shrubs, while not fully understanding the reasons for constancy. Whatever the reasons, grazing pressure from either the exotic lagomorphs or the native macropods has not impeded saltmarsh shrub regrowth several years after the cessation of stock grazing. However, saltmarsh restoration projects may still require consideration of grazing by native and non-native mammals, and potential exclusion or control measures especially at early stages of the regeneration of late successional species. Furthermore, we have highlighted some research needs that can address gaps in knowledge of the biology and ecology of *T. arbuscula* as a key habitat-forming species of Australia's saltmarsh. Also, by demonstrating the regular use of saltmarsh by terrestrial vertebrates, we hope to see further research in this neglected aspect of Australian saltmarsh ecology, and that these mammals be explicitly considered and integrated as part of the 'biodiversity co-benefits' of coastal restoration.

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Author Contributions VP, JA and JBK co-designed the research. VP and JA organised permits. JA and VP conducted fieldwork and collated data. JBK and VP analysed the data and developed visualisations. VP and JBK led the writing of the paper with inputs from JA.

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Data Availability Data available from the corresponding author on request.

Declarations

Conflict of interest All authors declare there are no conflicts of interest.

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