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Disturbance affects the contribution of coastal dune vegetation to carbon storage and carbon sequestration rate

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Abstract

Coastal dune vegetation has been proved to contribute to several crucial ecosystem services, as coastal protection, water purification, recreation; conversely, its capacity to regulate the concentration of greenhouse gases received less attention. To fill this gap, the present work focalized on the assessment of the contribution of coastal dune herbaceous vegetation to carbon storage and carbon sequestration rate, also in relation to possible effects of disturbance. To this aim, we measured the dry biomass and carbon sequestration rate in three different vegetation types (foredune, dry grasslands, humid grasslands), and habitat patch attributes as proxies of the disturbance regime. Relationships between disturbance, and carbon storage and sequestration rate have been analysed by GLMMs. The target vegetation types did not equally contribute to the medium-long term sequestration of carbon with a gradient that increased from the seashore inlands and related to both the growth form and the strategy of resource acquisition of dominant species, and plant community attributes. Disturbance in the form of trampling negatively affected carbon sequestration rate. Results suggest that, when different plant communities are spatially interconnected, the landscape scale results in a better understanding of ecosystem dynamics, functioning and resistance to perturbations and allows to plan coherent management strategies.

Keywords

biomass, climate regulation service, ES quantitative estimate, landscape spatial pattern, trampling

Introduction

Aquatic Coastal sand dune systems provide human society with several valuable ecosystem services (ES), ranging from coastal defence to water purification, carbon sequestration, and recreational benefits (Rova et al. 2015, Drius et al. 2019).

Vegetation plays a vital role in dune formation, stabilization and maintenance over time and is widely recognized as a pivotal element for the functioning of coastal dune systems, since it enhances the resistance of coastal ecosystems to storms and reduce erosion by mitigating the energy of waves action (de Battisti and Griffin 2020, Hanley et al. 2020). Plants build the dunes by trapping sand, fixing sediments, and increasing soil elevation (Borsje et al. 2011, de Battisti and Griffin 2020). The development and evolution of coastal dunes are thus led by the balance between the wind regime, sediment budget, and vegetation coverage. The role of plant communities in enhancing the functionality and the resistance and resilience of sand dune systems is so important that the plantation of sand-binding species is the most common approach to restoration (Hanley et al. 2014, Bessette et al. 2018, Della Bella et al. 2021). Dune plant communities are also recognized to support biodiversity, harbouring species with specific ecological requirements and showing high habitat specialization (Fantinato et al. 2018, Del Vecchio et al. 2019).

However, while the role of dune plant communities in providing these important services has been well documented, a quantitative assessment of their contribution to the "climate regulation" ES is still lacking. This ES refers to the capacity of ecosystems to regulate the concentration of greenhouse gases in the atmosphere (TEEB 2010, Burkhard and Maes 2017). This occurs through two main processes: carbon storage and carbon sequestration (Sil et al.

2017, Quijas et al. 2019). Carbon storage refers to the stock of carbon trapped in ecosystems, particularly in their biomass and soil, while carbon sequestration represents the net removal of CO2 from the atmosphere, mainly driven by the primary production of plant communities (Egoh et al. 2012, Estrada et al. 2015, Burkhard and Maes 2017, Sil et al. 2017, Quijas et al. 2019). By removing and trapping CO2 from the atmosphere, these processes play a role in the attenuation of climate change (Pörtner et al 2021), and thus become extremely important considering the widespread adverse impacts that climate change has produced (and is projected to produce) on people and nature (IPCC 2022). Plant communities of other coastal habitats have been already shown to play a large and crucial role in the regulation of greenhouse gas emissions: significant contribution of the vegetation to biogeochemical cycles and to primary production has been highlighted for mangroves ecosystems (Sahu and Kathiresan 2019), while marine vegetation (e.g., seagrasses beds and saltmarshes) was recognized as excellent carbon sink (Duarte et al. 2013). In coastal sand dune systems, quantitative estimates of carbon accumulation and sequestration rate have been mainly done for soil (Jones et al. 2008, Rohani et al. 2014, Drius et al. 2016), while the role of vegetation in regulating greenhouse gas emissions received less attention.

Ecosystem services have been so far mostly assessed on an ecosystem or habitat level, thereby neglecting their being influenced by the landscape spatial pattern (Grêt-Regamey et al. 2014). Coastal dune landscapes are characterized by a complex coast-to-inland environmental gradient, due to differences in the intensity of factors such as wind, salt spray and salinity, and sand burial (Hesp and Martínez 2007) which decreases with increasing distance from the sea. The steep environmental gradient gives rise to the typical coastal vegetation zonation (Doing 1985, Torca et al. 2019), i.e., a precise sequence of vegetation belts arranged parallel to the coastline. Such turnover of plant communities is a remarkable attribute of coastal systems worldwide, and is considered as a useful indicator of the conservation status of these environments (Buffa et al. 2005, Carboni et al. 2009, Gigante et al. 2016, Fenu et al. 2017, Del Vecchio et al. 2019, Pinna et al. 2019). In particular, when the vegetation zonation is well defined, and the turnover of plant communities is complete (i.e., it ranges from the pioneer herbaceous plant communities that occur on the drift line, to the woody scrubs and forests that occur inland), the dune system is considered in a good conservation status (Ciccarelli 2014, Acosta and Ercole 2015, Del Vecchio et al. 2019).

We can thus expect that any process causing habitat loss and fragmentation will affect ecosystem functioning and reduce the provision of ecosystems services. Human disturbance is one of the main threats to habitat and landscape integrity of sand dune ecosystems. Urban expansion, agriculture, trampling and levelling of dunes lead to habitat fragmentation and loss, thereby affecting not only the species composition and the structure of vegetation, but also the landscape pattern (Drius et al. 2013, Malavasi et al. 2018), in terms of composition (e.g., the type of habitats) and configuration (e.g., shape, degree of habitat isolation or fragmentation). Nowadays, coastal landscapes are increasingly trapped between erosion on the seaside and human settlements inlands (i.e., "coastal squeeze"; Schlacher et al. 2007, McLachlan and Defeo 2017), with a dramatic reduction of the space available for the natural zonation development.

In this regard, the analysis of landscape elements and their spatial attributes can be used to explore how changes in the landscape spatial pattern driven by disturbance influenced biodiversity and ecosystem functionality (Tzatzanis et al. 2003, Fischer and Lindenmayer 2007, Carranza et al. 2010, 2018, Walz 2011). Most authors agree that changes in the patch attributes (e.g., size, shape, connectivity) determine species loss and gain, or species turnover, thereby shaping the richness and composition of local habitat species assemblages (Sgrò et al. 2011, Fletcher et al. 2018, Lindenmayer 2019, Miller-Rushing et al. 2019, Wintle et al. 2019, Synes et al. 2020). Landscape spatial pattern has also an effect on ES, as non-natural landscape elements can affect water quality (Duarte et al. 2018), while an increase in natural areas and landscape aggregation improved pollination (Duarte et al. 2018, Fantinato et al. 2018), or net primary production (Hao et al. 2017).

Given the alarming conservation status of coastal dunes (Janssen et al. 2016, Prisco et al. 2020, Guimarais et al. 2021), and the important role of plant communities in such systems, the aims of our research were a) to quantify the contribution to climate regulation service (i.e., carbon storage and carbon sequestration rate) provided by coastal dune herbaceous vegetation, and b) to analyse the effect of landscape pattern on the service provision. To this aim, we measured plant biomass and carbon sequestration rate of different vegetation types and we tested whether landscape spatial pattern influences these community attributes. We hypothesise that vegetation types occurring in well conserved, non-disturbed systems (e.g., low trampled, and with large and integer patches of vegetation) provide the service more efficiently, i.e., have a higher plant biomass and carbon sequestration rate, than those occurring in disturbed environments.

Methods

Study area

The study area corresponds to the coast of Veneto Region (north-eastern Italy; Fig. 1). Dune systems consist of narrow, recent dunes (Holocenic), and are in contact with ancient dunes (Pleistocene), alluvial or lacustrine deposits, or run bordering the Venice Lagoon (Buffa et al. 2005, Gamper et al. 2008). Sediments are sandy carbonate deposits that come from rivers that flow into the Adriatic Sea. The mean annual temperature is 14.0 °C, while annual precipitation is 830 mm. Precipitation is mainly concen-

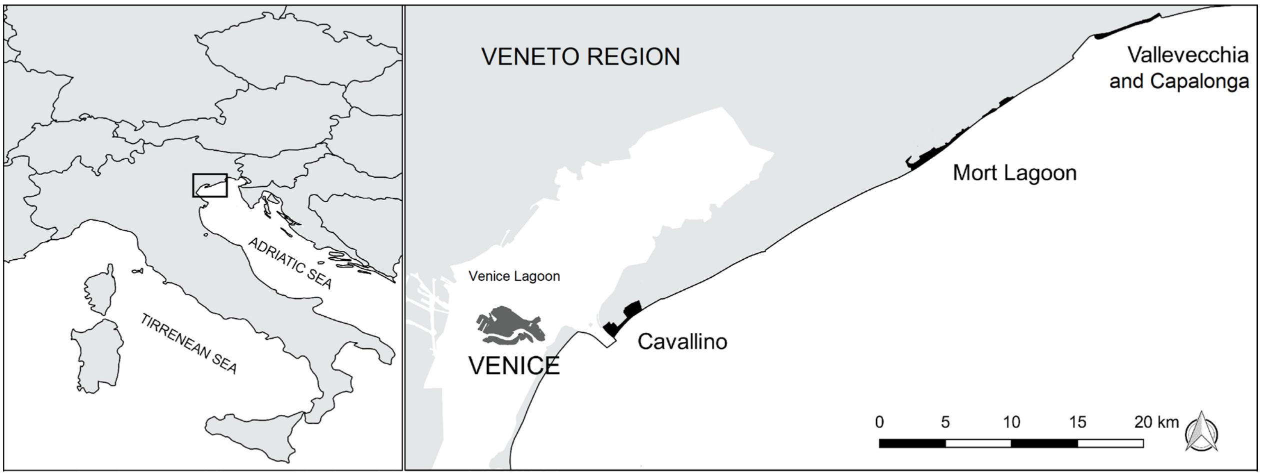

Figure 1. Study area, showing the sampling sites (in black).

trated in autumn (seasonal distribution of precipitation, mean ± sd: March-May, 66.0± 8.3 mm; June-August, 63.4 ± 8.2 mm; September-November: 92.4 ± 18.5 mm; December-February, 54.9 ± 6.4 mm; Del Vecchio et al. 2021). From the 1950s onward, large stretches of coastal dunes have been fragmented by housing and resort development, road construction, and agriculture. Based on a categorical map of the area (1:10.000; CLC categories level 1), covering 1.500 m wide stretch from the coastline inward, "Artificial surfaces" (CLC class 1), mainly represented by towns and villages, roads and tourist facilities, cover about 30% of the study area, while "Agricultural areas" (CLC class 2) are around 22%. Natural and semi-natural surfaces (CLC classes 3, 4 and 5) amount to about 47%, of which 4% is represented by natural coastal land cover types (i.e., beaches, dunes, and sand plains). Beaches and dunes include many habitats, most of which are characterized by endemic communities (Sburlino et al. 2008; 2013).

In natural condition, vegetation zonation follows the sea-inland ecological gradient. The most seaward-located plant communities, which occupy the drift line zone, are dominated by nitrophilous annual species (*Cakile maritima* Scop. ssp. *maritima* plant community). This plant community has an open structure, as a consequence of the exposure to limiting abiotic factors such as wave inundation, salt spray and intense wind. The following landward plant community occupies the shifting dune and is dominated by dune-forming plants such as *Elymus farctus* (Viv.) Runemark ex Melderis and *Calamagrostis arenaria* (L.) Roth ssp. *arundinacea* (Husn.) Banfi, Galasso & Bartolucci. Specifically, *C. arenaria* subsp. *arundinacea*, which is the dominant species, crucially contributes to foredune building and stabilization by capturing and binding the sand with its tough, fibrous rhizome system (Maun 2009). Landward, beyond the foredune crest, increased protection from physical disturbance allows the vegetation to evolve towards denser and more complex communities. The semi-fixed dune sector is occupied by perennial dry grasslands dominated by dwarf shrubs (e.g., *Fumana procumbens* (Dunal) Gren. & Godr, *Thymus pulegioides* L.), lichens (e.g., *Cladonia* sp.pl.) and mosses (e.g., *Syntrichia ruraliformis* (Besch.) Cardot). Further inland, and often intermingled with dry grasslands, interdunal depressions are colonized by a community of *Tripidium ravennae* (L.) H. Scholz ssp. *ravennae* and *Schoenus nigricans* L.. The sequence ends with woody scrubs (*Erica carnea* L. ssp. *carnea* and *Osyris alba* L. community) and forests of fixed dunes with *Quercus ilex* L. ssp. *ilex*, *Pinus pinea* L. and *P. pinaster* Aiton ssp. *pinaster* (Gamper et al. 2008, Sburlino et al. 2008, 2013). Species nomenclature follows Bartolucci et al. (2018).

Data sampling

The pool of species to be used for the quantification of biomass and carbon sequestration rate was selected from a dataset of 108 vegetation plots (size: 1 m^2) x 74 species, randomly sampled between 2017 and 2019 in coastal dunes of Veneto region (Fig. 1). Selected plots included only herbaceous vegetation belonging to the foredune, dry grasslands of semi-fixed dunes, and to the humid grasslands of interdunal depressions (Tab. 1). The foredune included both the vegetation of drift lines and the vegetation of the shifting dunes, because in the study area they often occur in mosaic and cannot be clearly distinguished from one another.

From this dataset, we selected a subset of 31 species (Suppl. Material, Tab. S1) which represented the most common and abundant species within each target habitat; namely, species were selected so that their percentage cover, i.e., standing live biomass, represented approximately 70% of the total species cover (Suppl. Material, Tab. S1), thereby ensuring an adequate description of overall habitat properties. For each target species, we recorded the percentage cover and collected the above-ground biomass through a preferential sampling design, during a pioneer inventory of plant biomass. Specifically, plant biomass was

Table 1. Sampled vegetation types and corresponding EUNIS classification at III level (Davies et al. 2004).

Vegetation type	Number of plots	Description	EUNIS Habitat classification
Foredune	54	Sparse vegetation, dominated by annual species, occupying accumulations of drift material and gravel rich in nitrogenous organic matter. Dominant species: *Cakile maritima* ssp. *maritima*, *Salsola tragus*, *Euphorbia peplis*.	B1.1 "Sand beach driftlines"
		Vegetation occupying the embryonic and mobile dunes, often with an open structure, representing the first stages of dune construction, dominated by perennial species (especially tussocks and erect leafy species). Dominant species: *Calamagrostis arenaria* ssp. *arundinacea*, *Elymus farctus*, *Eryngium maritimum*, *Echinophora spinosa*.	B1.3 "Shifting coastal dunes"
Dry grasslands	48	Well-drained or dry lands dominated by grasses or dwarf shrubs, with low productivity, growing between the foredune and the scrub of the fixed dune. Dominant species: *Fumana procumbens*, *Thymus pulegioides*, *Teucrium capitatum* ssp. *capitatum*, *Scabiosa triandra*, *Poterium sanguisorba*. Annual species as *Silene conica* and *Festuca fasciculata* can be found in grassland clearings.	B1.4 "Coastal stable dune grassland (grey dunes)"
Humid grasslands	6	Mediterranean tall, humid herb grasslands growing on non-saline or slightly saline soils with accessible groundwater, inundated or saturated for at least part of the growing season; dominant species: *Schoenus nigricans* and the large tufts of *Tripidium ravennae* ssp. *ravennae*	E3.1 "Mediterranean tall humid grassland"
Total	108		

harvested in plots of 25 cm x 25 cm size selected in the field where individuals had a fully developed vegetative biomass. The sample size for each species was on average of 8; overall, we collected species biomass in 118 25 x 25 cm plots. The biomass dry weight was determined for each species after drying the samples at 70°C for 48 hours. To limit as much as possible the damage to vegetation, the below-ground biomass was estimated, based on the above-ground one, by considering a root:shoot ratio of 0.2 g/g. This ratio was based on Stanisci et al. (2010), who analysed some common native species occurring in sand dunes along the Adriatic coast in Italy. The study included herbaceous species that colonize different habitats along the zonation, with different life- and growth forms, and showed that irrespective of species life history traits and position along the zonation, all the species showed a root:shoot biomass ratio between 0.1 and 0.3 g/g. The above- and below-ground components were then summed up to obtain the total biomass. A carbon content of 0.47 g C/g biomass d.w. has been considered for all species (IPCC 2006). For each species, the biomass dry weight was divided by the respective percentage cover. Based on this data, we estimated for each species the biomass per unit of surface that would correspond to a 100% monospecific cover (g d.w. m^{-2}). Such standardization was made to avoid biases in the values of plant biomass due to factors as species density in the sampling plot.

Data analyses

The carbon sequestration rate at the species level was estimated as the below-ground net primary production. We considered only perennial species because we focused on the contribution of dunes' vegetation to the medium-long term sequestration of carbon. Accordingly, we excluded annual species, due to their short life cycle. The net primary production was estimated from the biomass based on the relative growth rate, which was retrieved for each species according to literature data (Suppl. Material, Tab. S1), and then expressed per year assuming a vegetative growth period of three months.

To calculate plant biomass and carbon sequestration rate at plant community level, we calculated the Community Weighted Mean (CWM) for each plot, as the average of either biomass or carbon sequestration rate values of the species occurring in each plot, weighted by their relative abundance (Garnier et al. 2004).

To account for the effect of landscape patterns, we calculated some landscape variables, based on the habitat map of the Veneto region (scale 1:10.000; deliverable of the European LIFE project LIFE16 IT/NAT/000589 REDUNE; http://www.liferedune.it/; consulted 29.11.2021). For each habitat patch, in QGIS environment, we calculated: (i) the patch surface, in m^2 (hereafter "Surface"); (ii) the "Shape index", which provides information on the degree of habitat compactness according to the formula of Bosch (1978) and ranges from 0 (elongated and irregular shape) to 1 (circular and regular shape); (iii) the length of the patch perimeter in contact with paths, in m, to estimate the impact of human trampling (hereafter "Paths"); (iv) the patch proximity, as the minimum distance between edges of patches belonging to the same vegetation type, to estimate the degree of fragmentation and isolation (i.e., high distance between patch edges of the same vegetation type indicates fragmentation and isolation; hereafter “Patch proximity”). Afterwards, we associated to each plot the attributes of the patch in which it was included.

We compared biomass, carbon sequestration rate, and the relative position of the target vegetation types along the sea-inland gradient through Kruskal-Wallis ANOVA, followed by Multiple Comparison of mean ranks (Siegel and Castellan 1988). We used either biomass, carbon sequestration rate or the distance of each plot from the coastline as dependent variables and the vegetation type as independent variable (factor with three levels).

We explored the relationship between biomass, carbon sequestration rate and the patch attributes by performing GLMMs (R package lme4; Bates et al. 2014), using either biomass or carbon sequestration as dependent variables (square root-transformed to achieve normality), and the patch attributes as independent variables. The vegetation type was set as random factor. Before performing the model, we checked the correlation among independent variables. The “Shape index” and the “Patch proximity” were excluded from the model because they were highly correlated to the other patch attributes (Pearson correlation; $r > 0.80$). Therefore, “Surface” and “Paths” were the patch attributes included in the model. We found a moderate negative relation between these two variables (i.e., the patch surface decreased at increasing trampling; $r = -0.49$) but we considered this compatible with their inclusion in the model.

Furthermore, we calculated the percentage decrease in biomass and carbon sequestration rate of high-trampled patches with respect to low-trampled patches. We defined as high-trampled patches those where the length of the patch perimeter in contact with paths was higher than 450 m, and as low-trampled patches as those where the length of the patch perimeter in contact with paths was lower than 110 m. The threshold of 450 m and 110 m were selected according to a natural break in the distribution of the variable “Paths”.

Results

The spatial arrangement of vegetation types followed the sea-inland environmental gradient, and each vegetation type occupied a specific position across the zonation, being located at different distance from the sea (Kruskal-Wallis test; H(2, N=108)= 39.3190; $p < 0.0001$). In accordance with the natural community sequence, the foredune was the closest to the coastline (mean, in m, ± standard deviation: 53.44 ± 21.41), while humid grasslands were the farthest (276.83 ± 121.10), with dry grasslands in intermediate position (105.83 ± 78.71). The values of distance from the coastline of each vegetation type significantly differed to Multiple Comparison of mean ranks.

The target vegetation types had also significantly different biomass (Kruskal-Wallis test; H(2, N=108)= 17.60797; $p = 0.0002$) and carbon sequestration rate (Kruskal-Wallis test; H(2, N=108)= 6.4924; $p = 0.0389$). Humid grasslands had the highest biomass (median = 296.1 g C m^{-2}), followed by the foredune communities (median = 207.0 g C m^{-2}), and dry grasslands (median = 163.2 g C m^{-2}). As for the contribution of the three vegetation types to the medium-long term sequestration of carbon, the analysis evidenced a gradient in the sequestration rate increasing from the foredune to humid grasslands (Fig. 2; foredune, median = 139.8 g C m^{-2} yr^{-1}; dry grasslands: 212.8 g C m^{-2} yr^{-1}; humid grasslands: 279.9 g C m^{-2} yr^{-1}).

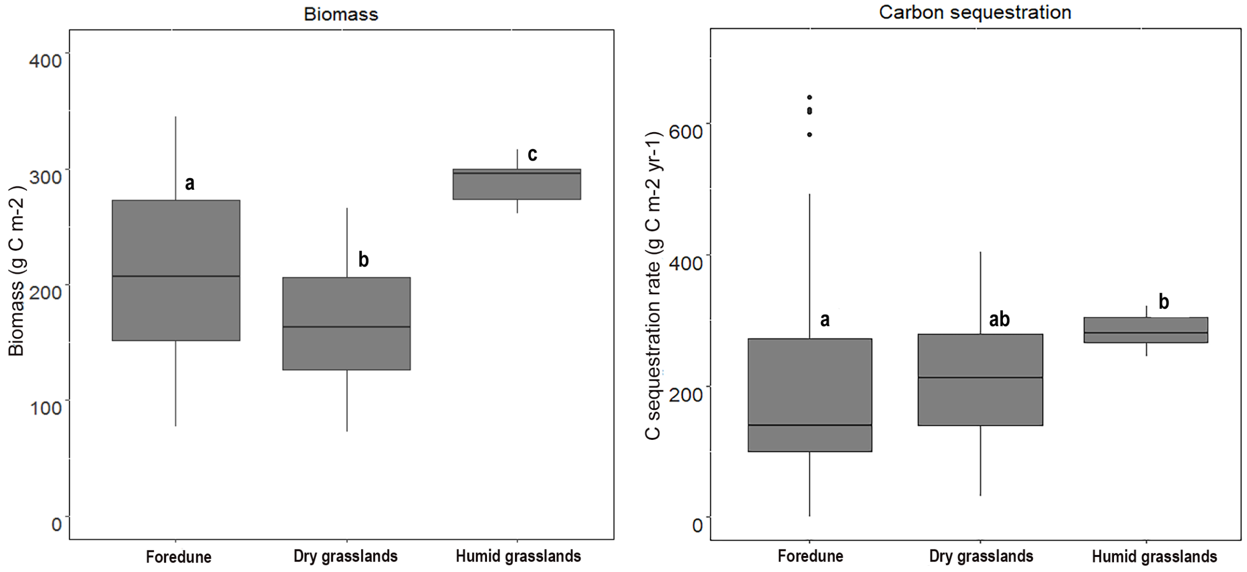

Figure 2. Box plot of biomass and carbon sequestration rate of the target vegetation types. Different letters indicate significant differences to Multiple Comparison of mean ranks.

Both biomass and carbon sequestration rate of each vegetation type decreased in highly trampled areas, as indicated by the negative trend with the variable “Paths”; i.e., biomass and carbon sequestration rate decreased with increasing length of the patch perimeter in contact with paths (Fig. 3). Specifically, in highly trampled patches the biomass and the carbon sequestration rate respectively declined on average of 31.7 %, and 60.1%, with respect to low trampled areas.

Biomass and carbon sequestration rate increased in large patches, as indicated by the positive trend with the variable “Surface”, although the trend was non-significant for both response variables (Tab. 2).

Discussion

We estimated the contribution to the climate regulation service of three coastal dune vegetation types, by measuring the vegetation’s biomass and carbon sequestration rate.

The quantification of carbon storage in vegetation’s biomass measured in our research adds to previous studies of carbon storage in these habitats. Focusing on the same geographical region, Drius et al. (2016) reported a soil carbon storage ranging between 306 and 412 g C/m^2 for dune habitats of the Adriatic coast of Italy. Our results showed a comparable order of magnitude for vegetation since we found a median value of carbon storage of 207 g C/m^2. This suggests that the overall carbon storage of dune habitats (soil + biomass) is higher than previously estimated, and that the contribution of vegetation amounts to about 40%. If we consider the alarming rate at which dune habitats are lost due to the expansion of artificial land cover (Carranza et al. 2018), this implies that the associated loss of carbon storage is higher than previously thought. This result is even more important if we consider that in natural ecosystems, soil function is influenced by plants that affect the magnitude of processes such as C and nutrient flows (Barrios 2007).

The target vegetation types did not equally contribute to the medium-long term sequestration of carbon, with a gradient which reflects biological features of most abundant species (e.g., growth form), structural attributes of the three vegetation types (e.g., standing biomass, spatial occupancy patterns) as well as the spatial arrangement of vegetation types at landscape scale.

Although we investigated a lower number of humid grassland plots compared to the other vegetation types, our results are consistent with previous studies that demonstrated that tall humid grasslands could exceed more than double the values found in other grassland types (Fan et al. 2008). The gradient we evidenced seems to be primarily related to the dominant species growth form and strategy for resource acquisition, that account for primary productivity and the accumulation of above and

Table 2. Summary table of the GLMMs, to test the effect of the patch perimeter in contact with paths and the patch surface on biomass and carbon sequestration rate of the target vegetation types.

Biomass	Scaled residuals:					
		Min	1Q	Median	3Q	Max
		-1.9906	-0.6543	0.1258	0.6277	2.172
	Random effects:					
	Groups Name	Variance	Std.Dev.			
	Habitat (Intercept)	1.443	1.201			
	Residual	5.178	2.276			
	Number of obs: 108, groups: Habitat, 3					
	Fixed effects:	Estimate	Std. Error	df	t value	Pr(>|t|)
	(Intercept)	1.49E+01	9.98E-01	4.16E+00	14.909	9.13E-05 ***
	Paths (m)	-9.26E-04	3.06E-04	9.73E+01	-3.027	0.00316 **
	Surface (m^2)	8.32E-05	7.36E-05	1.04E+02	1.131	0.26079
Carbon sequestration rate	Scaled residuals:					
		Min	1Q	Median	3Q	Max
		-3.0739	-0.5132	0.1162	0.6934	2.0911
	Random effects:					
	Groups Name	Variance	Std.Dev.			
	Habitat (Intercept)	1.184	1.088			
	Residual	11.886	3.448			
	Number of obs: 108, groups: Habitat, 3					
	Fixed effects:	Estimate	Std. Error	df	t value	Pr(>|t|)
	(Intercept)	17.34723	1.251618	13.3809	13.86	2.55E-09 ***
	Paths (m)	-0.00356	0.000452	91.07271	-7.877	6.86E-12 ***
	Surface (m^2)	0.000196	0.00011	97.10372	1.782	0.0779 .
	Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1					

below-ground biomass (Marín-Muñiz et al. 2014, Pearse et al. 2018). Coastal humid grasslands are dominated by tall grasses and sedges and have a rich and complex below-ground structure, with fine roots and below-ground organs, such as rhizomes, which have been proven to play a crucial role in carbon storage and sequestration (Fidelis et al. 2013). Moreover, they are subjected to periodic flooding with fresh or brackish water or have a high-water table for at least part of the year, adequate to influence plant community structure, and increase productivity and growth compared to the other target habitats.

The importance of growth form of most abundant species is however counterbalanced by the pattern of spatial occupancy, i.e., the cover at community level. Foredune dominant species such as *Calamagrostis arenaria* ssp. *arundinacea* or *Elymus farctus* are typical clonal plants, capable to spread laterally through below-ground organs that enable them to rapidly occupy gaps in the neighbourhood, and produce high biomass, concurrently playing a role in carbon storage and sequestration. However, due to high degrees of natural disturbance in the form of wind erosion and sand burial, blowouts, and sea storms, as well as urbanization and human trampling (Torca et al. 2019), foredune communities are often characterised by an open structure, with low average total cover as compared to that typical of inner, protected sectors covered by humid grasslands. Although variable, the relatively low total vegetation cover could thus explain the fluctuating values obtained for the foredune and the comparatively lower rate of carbon sequestration.

The interplay between plant growth form and the pattern of spatial occupancy is confirmed by results obtained for dry grasslands. In the study area, perennial dry grasslands are located inland from the shore and benefit from

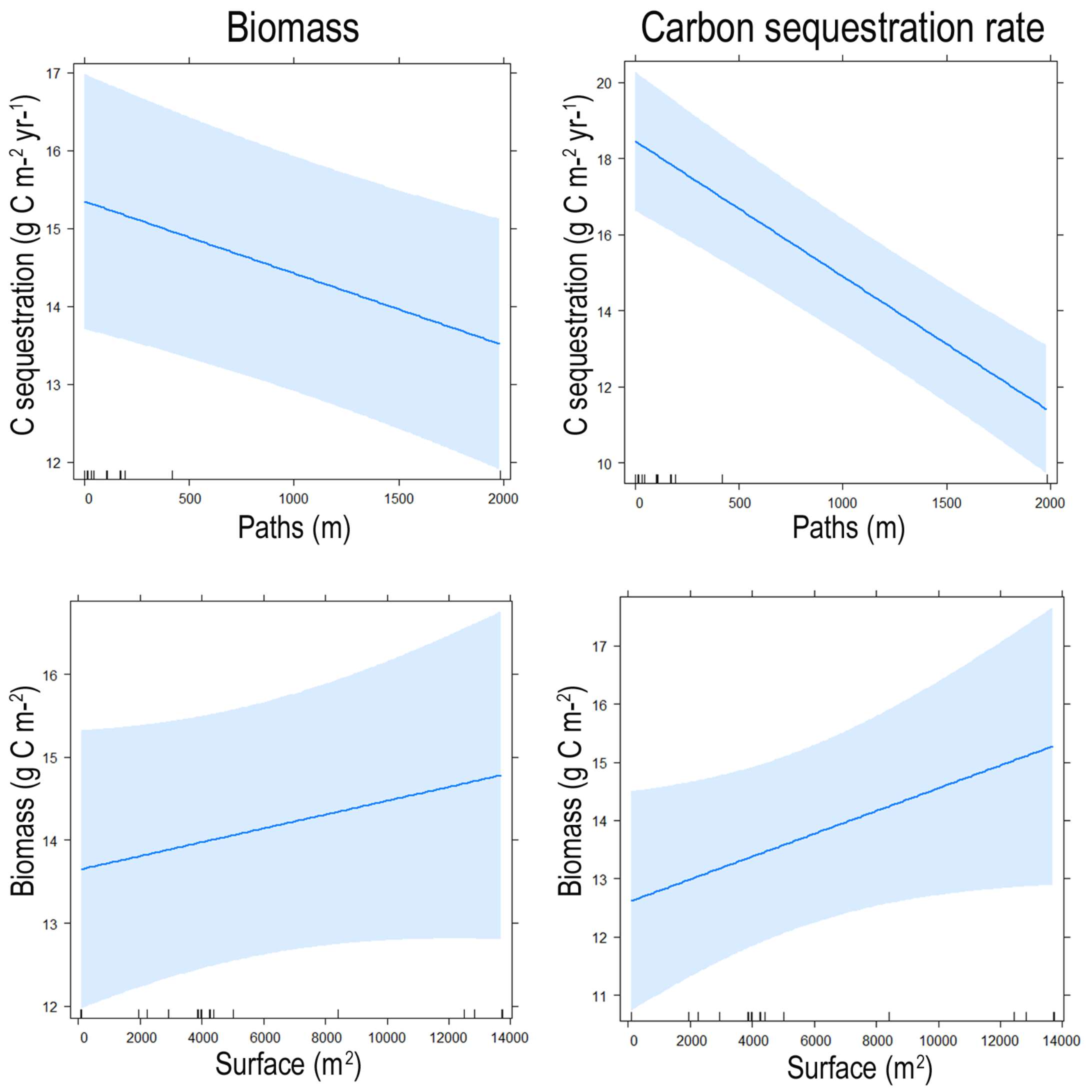

Figure 3. Trends of biomass and carbon sequestration rate against the tested variables. Blue bounds represent the 95% confidence interval.

the protection action exerted by foredune ridges (Del Vecchio et al. 2018, Buffa et al. 2021). Their standing biomass is mainly determined by dwarf shrubs and herbaceous perennial species, and a thick carpet of mosses and, sometimes, lichens (Silan et al. 2017). Being less exposed to limiting abiotic factors, they normally have a higher vegetation cover compared to foredune vegetation (Houston 2008, Del Vecchio et al. 2018). While herbaceous perennial species contribute to produce a high quantity of biomass thanks to a well-developed root system (taproot), or below-ground storage organs (Berg et al. 1998, Provoost et al. 2004), evergreen, slow-growing dwarf shrubs, with partially lignified stems, contribute to the carbon sequestration rate due to their slow biomass turnover (Silan et al. 2017).

The analyses at patch level revealed a negative effect of disturbance in the form of trampling on both standing biomass and carbon sequestration rate. In line with previous studies (Martínez et al. 2006, Delgado-Fernandez et al. 2019), our results showed that the contribution to the climate regulation service is reduced where dune habitats are degraded by human disturbance, with a decrease in the carbon sequestration rate that can be as high as 60% in high trampled areas. Human trampling has already been identified as one of the most detrimental threats to sand dune ecosystems worldwide. Trampling mostly acts at local scale by reducing individual plant fitness of less tolerant species (e.g., slow-growing species; Silan et al. 2017), thereby selectively filtering susceptible species. By increasing sand movements, human trampling also influences seed germination patterns, thus affecting resident species that require seed burial for germination (Del Vecchio et al. 2021). Trampling has been also identified as a crucial factor in facilitating the establishment of alien and opportunistic species, many of which show an annual life cycle, and therefore do not contribute to the medium-long term carbon sequestration (Rose and Hermanutz 2004, Jørgensen and Kollmann 2009, Del Vecchio et al. 2015, Smith and Kraaij 2020). All these local processes synergistically lead to species replacement and species loss and gain, and/or variation in species density, that have repercussions at the community level, altering community structure and function. Changes in these vegetation features may have substantial impacts on the habitat quality of individual sand dune patches within the landscape, ultimately hindering the provision of the climate regulation service.

Disturbance affects sand dune vegetation at local scales through changes in plant community composition and complexity, and at regional/landscape scales through changes in habitat extent and configuration. Interestingly, we did not find a significant relation between patch surface and both standing biomass and the carbon sequestration rate. The process of carbon sequestration as measured here can be considered as a population-based ecosystem service (Lindborg et al. 2017) that depends on the population and community dynamics, which in turn are driven by historical land-use and disturbance (Barford et al. 2001). The lack of significance could depend on the up-scaling from the plot to the patch level. At plot scale, carbon sequestration depends on several parameters, including individual plant growth forms, resource acquisition strategy, the decomposition rate of organic matter, which typically are highly spatially variable, especially in sand dune systems. This in turn leads to non-linear responses when small scale average values are scaled up to larger patches (Dendoncker et al. 2008).

Management of ecological processes promoting ecosystem services can be undertaken at different spatial scales from local to global (Lindborg et al. 2017). Our study suggests that, when different plant communities are spatially interconnected, the approach at the landscape scale results in a better understanding of ecosystem dynamics, functioning and resistance to perturbations and allows to plan coherent management strategies. Ecosystem service science has already identified management at different spatial scales as a crucial issue (Carpenter et al. 2006, Prager et al. 2012). In sand dune ecosystems, management plans should address the local scale, to secure plant community composition and complexity, and the landscape scale to assure the integrity of the natural turnover of vegetation types across the sea-inland gradient. Only this multi-scale approach will allow a successful biodiversity conservation (Del Vecchio et al. 2019, Torca et al. 2019), and an appropriate dune system functioning (Malavasi et al. 2016, Drius et al. 2019), and also guarantee an efficient provision of ecosystem services.

Conclusions

Our research provided new insights on the importance of vegetation and the influence of landscape spatial patterns on coastal ecosystem services, focusing on biomass and carbon sequestration rate of herbaceous vegetation types.

We acknowledge that our measurements have a certain degree of approximation, due to having limited as much as possible the detrimental effects of biomass removal. However, we could provide an estimation of carbon storage and carbon sequestration rate of dune vegetation, thereby contributing with crucial knowledge to this still open research field through the least invasive sampling method. To improve measurement accuracy, total biomass or plant growth rate could be figured out by growing plants in common gardens or in experimental field. Although time-consuming, and possibly demanding in terms of available structures and costs, such an approach would increase accuracy, at the same time assuring a low impact on plant communities and on the entire dune system.

By linking landscape features to ecosystem services, we contributed to the understanding of the relationship between the disturbance on coastal systems and their functioning. Assessment of the effect of landscape spatial pattern on ecosystem services such as this carried out in our research also provides important insight for prioritizing conservation actions.

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Competing interests

The authors have declared that no competing interests exist.

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Supplementary material

Table S1

Authors: Silvia Del Vecchio, Silvia Rova, Edy Fantinato, Fabio Pranovi, Gabriella Buffa

Data type: table

Explanation note: List of selected species of the dataset.

Link: https://doi.org/10.3897/pls2022591/04.suppl1