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Linking plant communities on land and at sea: The effects of *Posidonia oceanica* wrack on the structure of dune vegetation

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ABSTRACT

Although terrestrial and marine ecosystems are often perceived as clearly distinct, in coastal areas biological communities on land and at sea are in fact intimately linked. One way in which terrestrial and marine systems interact is through the accumulation of seagrass wrack on beaches, which plays an important role as a nutrient input in coastal dune food webs. Here we test whether accumulated beach-cast wrack also influences the structure and diversity of coastal dune plant communities. Relying on a database of 572 vegetation surveys distributed across the island of Sardinia, we used mixed-effects models to compare the vegetation cover and species richness of plant communities exposed to different amounts of *Posidonia oceanica* beach-cast wrack. We found that beaches which receive high amounts of *P. oceanica* wrack have considerably greater vegetation cover (10% on average) than those with fewer deposits. The positive relationship between beach-cast wrack and vegetation cover was especially strong in nearshore plant communities, becoming progressively weaker along the habitat zonation. A similar pattern was found for species richness: beaches with high levels of accumulated wrack had more diverse drift line and foredune plant communities, while habitats further away from the shoreline were unaffected. Our study is the first to present evidence suggesting that activities which reduce wrack accumulation on beaches – either through direct removal of deposits or by causing P. oceanica seabeds to decline – can have effects on both the structure and diversity of coastal dune plant communities. Effective management of Mediterranean coastal dune ecosystems will require developing clear strategies for the removal and relocation of accumulated beach-cast wrack.

1. Introduction

Coastal dune systems are ecotonal habitats whose physical and biotic structure is strongly shaped by the influence of adjoining ecosystems. On the one side, coastal habitats are increasingly threatened by human disturbance, particularly in the form of land use change (Brown and McLachlan, 2002; Carboni et al., 2010; Malavasi et al., 2013). At the other end, the presence of the sea directly influences a number of abiotic parameters such as salt spray, wind intensity and sand burial, giving rise to a marked sea-inland environmental gradient which shapes vegetation features of coastal dune systems worldwide (Doing, 1985; Feola et al., 2011). Coastal habitats are also strongly linked to marine ecosystems through the supply of biotic material (Polis and Hurd, 1996). In particular, the relationship between aquatic and terrestrial systems through seagrass wrack accumulated on sandy beaches has attracted the attention of several authors. Most of this research has focused on providing qualitative and quantitative descriptions of beach-cast wrack material, as well as determining its associated macrofauna (Dugan et al., 2003; Ochieng and Erftemeijer, 1999) and its trophic contribution to the food web (Hyndes and Lavery, 2005; Ince et al., 2007). However, very few studies have directly explored the possible effects of beach-cast wrack on terrestrial vegetation.

In the Mediterranean basin, the endemic *Posidonia oceanica* is the most abundant and well-studied seagrass (Larkum et al., 2006). Following winter storms, detached leaves, rhizomes and reproductive material of *P. oceanica* are transported to beaches, where they accumulate and form considerable deposits (Balestri et al.,

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2006, 2011; Diaz-Almela et al., 2006). Previous studies have shown that the beach-cast wrack from *P. oceanica* is a critical nutrient source and nursery for coastal fauna (Colombini and Chelazzi, 2003; Colombini et al., 2009; Ince et al., 2007). It has also been suggested that beach-cast wrack is important for dune plant species. Several vegetation scientists performing coastal dune vegetation surveys have noted (as personal observations) that "*Halo-nitrophilous annuals communities colonize beaches with deposits of algae and P. oceanica wrack*", and that "*communities that grow in bays where the sand is mixed to P. oceanica wrack are enriched in halo-nitrophilous species*" (e.g. Brambilla et al., 1982; Mossa et al., 1984, 2000). Motivated by these observations, other authors have found evidence that these deposits are in fact a source of nutrients for the seagrasses meadows themselves (Mateo et al., 2003), and have shown that they contribute to the nitrogen supply of the coastal dune ecosystem, influencing a number of plant species at different stages life cycle (Cardona and García, 2008; Del Vecchio et al., 2013). Here we investigate whether beach-cast wrack can influence more than just the physiological ecology of a select number of species, and we ask whether these deposits can have an impact on the costal dune plant community as a whole.

We explore whether coastal areas that receive low vs. high volumes of *P. oceanica* beach-cast wrack develop quantifiable differences in their plant communities. Specifically, we ask whether the presence of *P. oceanica* beach-cast wrack influences the (a) vegetation cover and (b) species richness of coastal dune plant communities, and (c) whether these effects vary along the sea-inland gradient (i.e., are communities closer to the sea more affected by the accumulation of plant debris than those further inland?). To the best of our knowledge, this work is the first attempt to explore the effect of different volumes of beach-cast wrack on coastal dune vegetation at a community level. We chose to focus on species richness and vegetation cover as both have been shown to be good measures of ecosystem functionality and biotic processes, and are therefore an indicator of ecosystem degradation and conservation status (Keith et al., 2013). Furthermore, because both species richness and vegetation cover are relatively easy to measure, they are widely recorded and easily available.

2. Methods

2.1. Study area

Species richness and cover data were obtained from a comprehensive literature review of phytosociological relevés performed in coastal areas across the island of Sardinia (Italy) (Fig. 1). We focused on the island of Sardinia as a study area because (a) the coastal vegetation of the island is still relatively well conserved and has been thoroughly investigated; (b) *P. oceanica* meadows surround the island and large deposits of seagrass wrack accumulate along Sardinian coasts; (c) a *P. oceanica* beach-cast wrack distribution map, crucial for this investigation, is available for Sardinian coasts (De Falco et al., 2008).

2.2. Map of *P. oceanica* beach-cast wrack

Each spring, local municipalities across Sardinia remove accumulated beach-cast material (mainly constituted of *P. oceanica* wrack) to promote the recreational use of beaches by tourists. De Falco et al. (2008) took advantage of this and developed a map of the amount of wrack removed in different municipalities. For 34 of the 73 coastal municipalities of Sardinia, the authors were able to classify beach-cast wrack deposits into one of five volumetric classes (m^3 of removed material). Here, we used this information as a proxy of the amount of beach-cast material being deposited along the coastline. Removal operations are carried out before the beginning of the bathing season, meaning that for most of the year the beach-cast wrack is present on the beaches (De Falco et al., 2008). For the purposes of our study we aggregated the accumulation levels proposed by De Falco et al. (2008) into two classes: low volumes of beach-cast wrack ("Level 1": <1000 m^3) and high volumes of beach-cast wrack ("Level 2": >1000 m^3). Municipalities in which no removal operations were carried out were excluded from all further analyses, as it would be incorrect to assume that no wrack was deposited on these beaches (Fig. 1). In the remaining municipalities removal operation occurs once per year (a part from 10 municipalities where it is repeated more than once).

2.3. Coastal dune vegetation database

We built a database of 873 vegetation plot records (phytosociological relevés) for the Sardinian coast using the software Turboveg (Hennekens, 1996). The database was compiled through a thorough search of published literature sources reporting compositional data on the plant communities of recent (Holocenic) dunes. We only included phytosociological relevés which could be georeferenced to a precision of ca. 2 km (Prisco et al., 2012b) for further details on how the database was compiled and Appendix 1 for a complete reference list). The mean plot size (±SE) was 51.5 $m^2 \pm 2.60$ m^2, and the year in which surveys were carried out varied from 1972 to 2005. Although both plot size and survey period can affect species richness and cover, preliminary analyses of the dataset suggest that neither variable strongly influenced floristic composition (Prisco et al., 2012b). We therefore chose not to account for variation in plot size or survey year in further analyses.

For each relevé we recorded the presence of all vascular plants with their cover-abundances on the Braun-Blanquet scale (1928), geographic location as inferred from the literature source and phytosociological association, based on which we assigned each relevé to a habitat category according to the Habitats Directive 92/43 CEE. We then aggregated the different CEE habitats into four macro-categories distributed along the sea–inland ecological gradient (hereafter referred to as "habitat type"; see Table 1).

For each relevé we calculated total cover and species richness of vascular plants, which we adopted as response variables in further analyses. The georeferenced relevés were overlaid onto the beach-cast wrack map in ArcGIS 9.2 (ESRI, 2006). We removed all relevés that fell within municipalities in which data on beach-cast wrack were not available. We thus obtained a dataset of 572 relevés distributed in 23 municipalities. To avoid pseudoreplication, we pooled relevés belonging to the same municipality and habitat type by calculating mean species cover and richness. This resulted in 92 replicates for all subsequent analyses (23 municipalities with four habitat types), each associated to one of two levels of wrack accumulation ("Level 1": <1000 m^3; "Level 2": >1000 m^3).

2.4. Environmental correlates

Because any differences in floristic composition determined from a comparative study such as this could be due to spatial heterogeneity in beach characteristics other than the presence and volume of beach-cast, we also considered other determinants that may influence the vegetation at this scale of analysis. Specifically, we accounted for the effects of three potentially confounding factors: climate, land use and geographical location.

To quantify the environmental and human features of interest, we created a 2 km buffer inland for the entire coast of Sardinia in a GIS environment (Carboni et al., 2010) and then extracted the values of the selected variables in the buffer areas of each

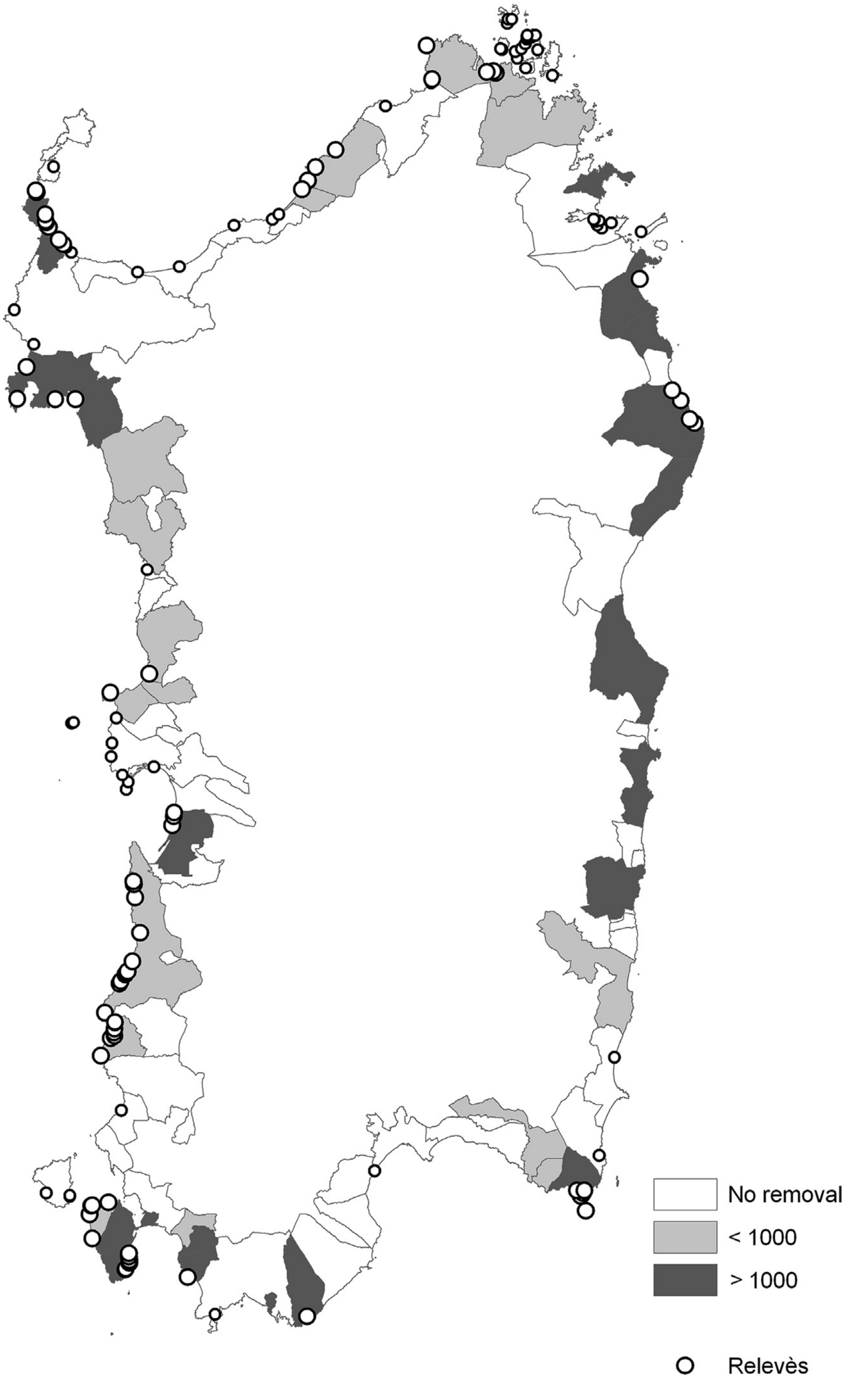

Fig. 1. Map of *P. oceanica* beach-cast wrack accumulation levels for each municipality (m^3) and distribution of phytosociological relevés. Circle size reflects number of relevés in each municipality.

municipality. To account for environmental heterogeneity we selected the following bioclimatic parameters: maximum temperature of warmest months, minimum temperature of coldest months, precipitation of wettest quarter, precipitation of driest quarter, precipitation seasonality (quantified using the coefficient of variation of monthly precipitations). Combined, these variables allow to characterize summer drought that, in arid areas such as the Mediterranean basin, is the most important stress factor for plant growth and plays a fundamental role in shaping the vegetation (Bartholomeus et al., 2012). These were obtained from mean climate grids extracted from 1 km Worldclim monthly maps (Hijmans et al., 2005). As proxies of human fruition and impact on the coast we calculated the percentage of different land use categories (urban structures, agriculture and forests) within the buffers. We decided to account for human impact because it represents a major threat for coastal environments, leading to degradation and disappearing of species and habitats (Malavasi et al., 2016). Our rationale was that coastal areas surrounded by urban settlements are accessed more easily and frequently, and therefore suffer from greater human pressure and touristic exploitation than locations surrounded by natural areas. Considering a proxy for human abundance was also important in order to correct for the fact that in

Table 1
List of habitat types assessed in the current study. Habitat types were assigned on the basis of habitat codes defined in the EU Habitats Directive (92/43 CEE). Associated phytosociological classes for each habitat type are also listed.

Habitat type	Habitat Category (Directive 92/43 CEE)	Phytosociological class
Annual vegetation of drift lines	1210 1310	*Cakiletea maritimae* *Thero-Suaedetea*
Fore dune vegetation	2110; 2120	*Ammophiletea*
Transition dune vegetation	2210	*Helichryso-Crucianelletea maritimae*
	2230	*Helianthemetea guttatae*
Fixed dune vegetation	2260; 2250; 9320	*Quercetea ilicis*

areas more densely populated municipalities might be more subject to removal operations. Percentages of land use categories were calculated from the CORINE 2000 land cover map, which was obtained from the Italian Institute for Environmental Research and Protection (ISPRA; http://www.pcn.minambiente.it/).

Finally, in order to account for any other geographically structured characteristic that may influence vegetation features (e.g. geomorphology or soil properties), we included latitude and longitude in our analysis. Before proceeding, we tested the independence of all predictors via Pearson correlation coefficient and removed the ones with correlation coefficients greater than 0.5 from further analyses. Precipitation of wettest quarter was correlated with the minimum temperature of coldest months, with precipitation seasonality and with longitude. Maximum temperature of warmest months was correlated with precipitation in driest quarter and with latitude. Agricultural areas were correlated with forest cover. Therefore, in further analyses we only included precipitation of wettest quarter, maximum temperature of warmest months, and the percentage cover of agricultural areas and urban settlements within the buffer.

2.5. *Influence of beach-cast wrack on species cover and richness*

To assess the influence of beach-cast wrack on species richness and cover, we fit separate linear mixed-effects models for each of the two response variables. Species richness and vegetation cover were modelled as a function of beach-cast wrack accumulation (factor with 2 levels). In addition to this, the model also included the effect of habitat type (factor with 4 levels) and the interaction between beach-cast wrack deposit and habitat type, allowing us to test whether the effect of beach-cast wrack varies according to habitat. Environmental covariates (precipitation of wettest quarter, maximum temperature of warmest months, percentage cover of agricultural areas and percentage cover of urban settlements) were included in the two models as continuous predictors to correct for potentially confounding influences on vegetation patterns. Lastly, to account for repeated measures determined by the fact that we compared the response of different habitats within each municipality, we included municipality as random factor in the models.

We checked for gross violations of normality through a visual inspection of the histogram of the residuals of the models. Model simplification was performed using a stepwise algorithm, through backward selection of explanatory variables. Models were compared on the basis of the small sample Akaike Information Criterion (AICc) as implemented in the R package *MASS* (Venables and Ripley, 2002), with the model having the lowest AICc being best. Linear mixed effects models were implemented in the *nlme* R package. To estimate the explained variance of the best fitting model we calculated both conditional and marginal R^2 values (R package *MuMln*). Conditional R^2 accounts for the explanatory power of both fixed and random effects, while marginal R^2 only accounts for fixed effects (Nakagawa and Schielzeth, 2013).

3. Results

Overall, our analysis revealed that coastal dune plant communities in municipalities which receive a high volume of *P. oceanica* wrack have significantly greater vegetation cover compared to those which receive <1000 m^3 of deposits each year (10% increase on average). Despite these marked changes in vegetation cover, beaches with high and low cast wrack accumulation levels did not differ markedly in terms of species richness (Fig. 2). What did emerge, instead, was that the presence of high volumes of wrack on beaches tended to have a greater impact on habitats that are closest to the sea compared to those that are found further inland along the zonation.

3.1. *Vegetation cover*

Mixed-effects modelling revealed a significant effect of beach-cast wrack on vegetation cover (Table 2). Species cover of relevés was higher in municipalities with wrack accumulation >1000 m^2, and this pattern was particularly evident in the vegetation of the drift line and the foredune (Figs. 2 and 3). This pattern of increased cover in relation to higher levels of beach-cast wrack persisted even after having accounted for the confounding effects of habitat type, climate, human fruition and geography. In fact, all the selected environmental factors and human variables were excluded from the most parsimonious model following model simplification, with the exception of habitat type and the interaction term of habitat type with wrack accumulation, which were retained in the final model. Not surprisingly, species cover varied significantly depending on habitat type (significant effect of the factor “habitat type”: Table 2) and there was a general increment in cover from the upper beach to the inland habitat types. Although the interaction term between beach-cast wrack accumulation level and habitat type was not significant, it was retained in and it enhanced the performance of the model, suggesting a difference in the effects of wrack accumulation on cover depending on the habitat type (ΔAICc between the model with and without the interaction term = −13.2). Specifically it appears that wrack accumulation is linked to greater increases in total cover in habitats closer to the sea compared to habitats found further along the zonation (Fig. 3a). The best fitting model explained a large portion of the underlying variance in vegetation cover among relevés (conditional $R^2 = 0.78$; marginal $R^2 = 0.73$).

3.2. *Species richness*

In contrast to species cover, we found no strong effect of beach-cast wrack on patterns of species richness when looking across habitats (Table 3). Climatic, human and geographical factors were also maintained in the most parsimonious model (though they had no significant effect in determining richness patterns). Instead, we found that species richness mostly depended on habitat type. As was the case for vegetation cover, species richness increased from the pioneer vegetation of the coastline to the fixed dune habitats. Although species richness varied little among the two levels of wrack accumulation when all habitats were considered together (Fig. 2), we found that habitats that are closest to the sea tended to have higher species richness in municipalities that receive high levels of stranded wrack (Fig. 3b). This is supported by the fact that the interaction between wrack and habitat type was highly significant in the model. The conditional R^2 of the best fitting model was

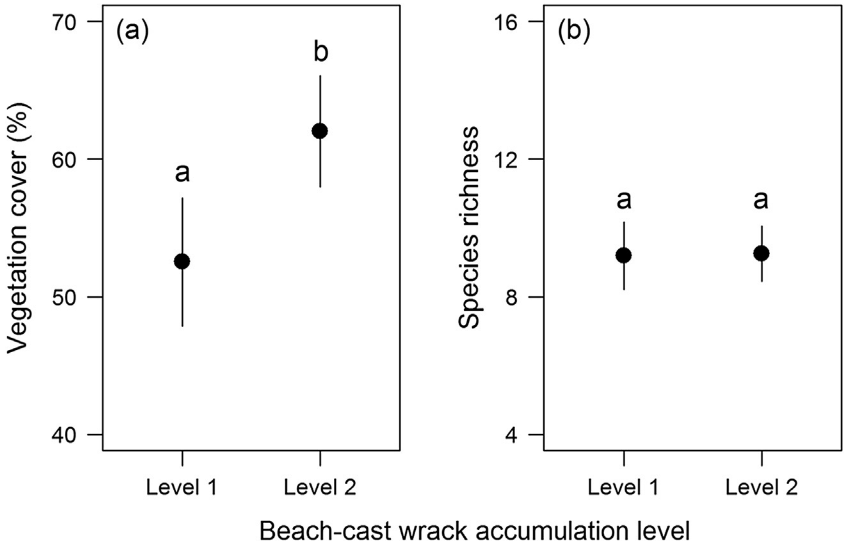

Fig. 2. Mean of (a) species cover (%) and (b) species richness in relevés with different levels of *P. oceanica* beach-cast (Low < 1000 m^3; High > 1000 m^3). Values with different capital letters are significantly different at $P < 0.05$ (linear mixed-effects model). Error bars are SE.

Table 2
Summary table of the model testing the effects of beach cast wrack on species cover. Predictors retained in the best fitting model are highlighted in bold.

Predictor	Degrees of freedom	*F*-value	*P*-value
Wrack	1	4.95	0.037
Habitat type	3	51.45	<0.001
Precipitation wettest quarter	1	0.02	0.896
Maximum temperature	1	0.04	0.842
Agricultural land	1	0.02	0.902
Urban area	1	0.01	0.963
Wrack *x* habitat type	3	1.34	0.282

Table 3
Summary table of the model testing the effects of beach cast wrack on species richness. Predictors retained in the best fitting model are highlighted in bold.

Predictor	Degrees of freedom	*F*-value	*P*-value
Wrack	1	0.46	0.508
Habitat type	3	56.06	<0.001
Precipitation wettest quarter	1	2.86	0.107
Maximum temperature	1	5.21	0.034
Agricultural land	1	2.81	0.111
Urban area	1	2.34	0.144
Wrack *x* habitat type	3	4.85	0.007

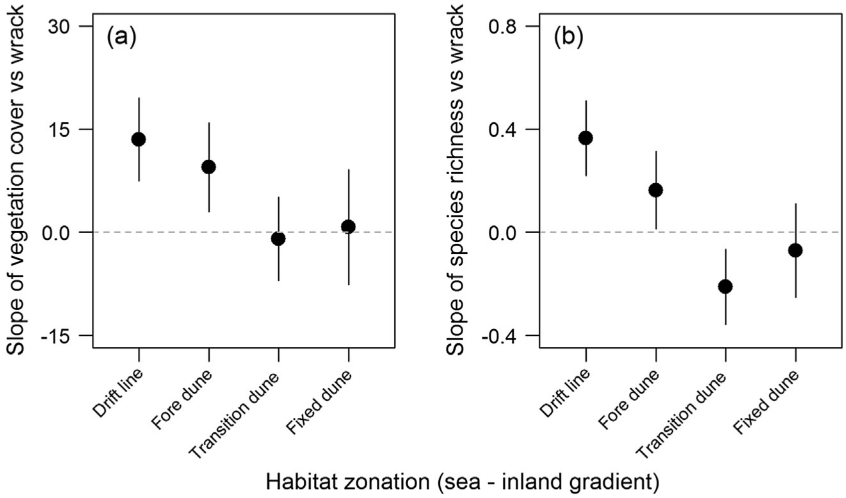

Fig. 3. Slope of (a) vegetation cover (%) and (b) species richness vs *P. oceanica* wrack level in each habitat category obtained from the “wrack x habitat” interaction term in the linear models. Error bars are SE of the model coefficients.

0.81, while the marginal R^2 was 0.73.

4. Discussion

Plant communities in coastal habitats are in a delicate balance with their surrounding environment. Coastal dune plant species are highly adapted to germinate, grow and reproduce in a narrow range of strongly limiting environmental conditions (Balestri and Cinelli, 2004; Redondo-Gomez et al., 2011). The high level of specialization which is required for plant species to inhabit and maintain viable populations in coastal ecosystems is also what makes these communities so sensitive to changes in their environment (Gilbert et al., 2008; Prisco et al., 2013; Sykes and Wilson, 1991).

Here we show that in addition to changes in climate, erosion and human disturbance, the structure of coastal dune plant communities is also shaped by the amount of *P. oceanica* beach-cast wrack which accumulates on beaches. Specifically, we find that beaches which receive less detritus during winter months tend to have lower vegetation cover and a lower richness of nearshore specialists compared to areas that receive ample beach-cast wrack.

4.1. Vegetation cover

Across the different habitat types, we found that vegetation cover on beaches that receive a high amount of beach-cast wrack was significantly greater than on beaches where only a small amount of wrack is deposited by winter storms (Fig. 2a). There are two possible ways in which abundant beach-cast wrack could promote greater vegetation cover in plant communities: by acting as a nutrient source and/or by providing shelter from the physical elements. Both observational surveys and experimental work suggest that beach-cast is an important source of key nutrients (e.g., nitrogen) in coastal dune soils (Brambilla et al., 1982; Cardona and García, 2008; Del Vecchio et al., 2013; Mossa et al., 1984). As plant growth in coastal dunes is (among other things) strongly nutrient limited (Crutsinger et al., 2013), improving the nutrient budget of these systems could promote faster plant growth and, as a result, greater vegetation cover. In addition to this, detritus accumulated on beaches can act as a barrier against the physical elements (e.g., wind, salt spray, burial), ameliorating conditions for the survival and growth of plants (Colombini et al., 2009; Elginoz et al., 2011; Ochieng and Erftemeijer, 1999), especially during the critical post-germination stage (Del Vecchio et al., 2013).

The effect of beach-cast wrack on vegetation cover was particularly strong in habitats closest to the sea, such as the drift line and foredune vegetation (Fig. 3a). This is none too surprising given that the majority of beach-cast wrack accumulates near the shore where it is deposited by waves (Balestri et al., 2006), and that the amount of detritus declines sharply further inland. In addition to this, nearshore habitats are also those most limited by abiotic stress (Tissier et al., 2013), and therefore the most likely to benefit from improved environmental conditions associated with higher levels of accumulated wrack. Stranded wrack can provide shelter during seedling development, as well as functioning as a nutrient source for select species (e.g., *Cakile maritima* and *Elymus farctus*) of the foredune vegetation (Cardona and García, 2008; Del Vecchio et al., 2013).

4.2. Species richness

Although weaker in comparison, the effects of beach-cast wrack deposits on the species richness of the community largely mimic those found for vegetation cover. When considering the dune ecosystem as a whole, species richness varied little between beaches that accumulate high versus low levels of *P. oceanica* beach-cast wrack (Fig. 2b). However, when effects are partitioned among habitats we find that communities that lie at the forefront of the sea—inland zonation do in fact harbor a greater richness of plant species on beaches that receive large amount of wrack (Fig. 3b). The fact that accumulated wrack is predominantly affecting the species richness of these nearshore habitats may explain why the overall effect (i.e., across habitats) is rather weak. Because nearshore communities are generally species-poor compared to those further inland, even a sizable increase in diversity in these habitats can be masked by background variation in species richness on fixed dunes. Our results suggest that wrack is ameliorating conditions in drift line and foredune environments, allowing a greater number of species to establish viable populations. Many of the ephemeral species that occupy these stressful environments are currently threatened by the generally declining conditions of dune habitats (Prisco et al., 2012a; Pinna et al., 2015; Fenu et al., 2015), and consequently are of high conservation priority (Fenu et al., 2016; Cogoni et al., 2015).

5. Conclusions

As human activities in coastal areas continue to expand, dune ecosystems are becoming increasingly threatened (Dugan and Hubbard, 2010). Recreational use of beaches, coastal erosion, land use change and the spread of invasive species have all been shown to drive declines in coastal dune plant communities (De Falco et al., 2008; Novoa et al., 2013; Rodgers, 2003; Vilá et al., 2011). As a result, there is increasing concern that we may be compromising the ability of these habitats to provide critical ecosystem services (e.g., protection from storms, mitigating erosion), while at the same time causing irreversible declines in a whole suite of highly specialized, and often rare or endemic plant species. In addition to previously reported drivers of disturbance, here we show that declines in the amount of wrack from seagrass beds that accumulates on beaches can have a major impact on the structure of plant communities in dune ecosystems. This previously overlooked interaction between plant communities on land and at sea has important implications for both the vegetation cover and the species richness of coastal dune plant communities, especially in habitats that develop close to the shoreline. This is concerning given that overfishing, shipping and the spread of invasive species (e.g., the alga *Caulerpa taxifolia*) continue to threaten and cause declines in *P. oceanica* seabeds across the Mediterranean basin (Duarte, 2002; Glasby, 2013; Marba et al., 1996; Marbà et al., 2006). The importance of beach-cast wrack for coastal dune plant communities needs to be accounted for when planning new management strategies for these threatened habitats. In particular, careful thought is needed when planning beach cleaning operations, such as determining when it is best to remove accumulated wrack from the shoreline and where it is most beneficial to dispose of it.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2016.10.041.

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