Colonisation patterns of supralittoral arthropods in naturally stranded wrack debris on Atlantic sandy beaches of Brazil and Spain

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Abstract. From an ecosystem perspective, wrack debris represents a key element for the maintenance of biodiversity and functioning of sandy beaches. Here, we characterised the colonisation patterns of supralittoral assemblages associated with wrack accumulations (seaweed and mangrove propagules) on multiple Atlantic sandy beaches (southern Brazil and south-western Spain). By using a manipulative field experiment, we sought to determine the temporal changes of the density, diversity and the structure of the whole community during the colonisation of wrack debris, and whether the colonisation patterns in response to the stranding of natural wrack debris were different on local (between beaches) and regional (between Atlantic regions) scales. Our results showed increases in density and diversity during the first 3 days after the stranding of seaweeds and mangrove-propagules debris. Moreover, wrack debris was promptly invaded by a wide range of species (i.e. talitrids, dipterans, coleopterans and spiders), although the colonisation pattern was slower in southern Brazil (16-day period) than in south-western Spain (3-day period). Wrack-debris characteristics (e.g. amount, degradation and composition) combined with biological strategies (e.g. trophic guilds and mobility) of supralittoral species could explain the different colonisation patterns in each Atlantic region. The temporal changes of wrack-associated fauna can have potential effects on the wrack-derived process and food-web structure on sandy beaches.

Introduction

The stranding of allochthonous organic materials (i.e. wrack) is a noteworthy process on exposed sandy beaches because of their almost complete lack of *in situ* primary production (McLachlan and Brown 2006). Once stranded on the beach, allochthonous inputs provide food or refuge to the macrofaunal community, boosting abundance and diversity of primary and secondary consumers (e.g. Ince *et al.* 2007; Crawley *et al.* 2009; Spiller *et al.* 2010). Because many of these organisms form the bottom of coastal food chains, the availability of allochthonous inputs to support their abundance and biomass is a key factor in the maintenance of biodiversity (Spiller *et al.* 2010; Harris *et al.* 2014) and the fluxes of matter and energy between marine and

terrestrial ecosystems (Polis and Hurd 1996; Spiller *et al.* 2010; Barreiro *et al.* 2013).

Wrack patches deposited on the upper beach, where they lie beyond the reach of wave action, tend to remain on the beach surface for long periods and can be colonised by supralittoral macroinvertebrates, such as talitrid amphipods, oniscoid isopods, coleopterans, arachnids, etc. (e.g. Rodil *et al.* 2008; Colombini *et al.* 2009; Ruiz-Delgado *et al.* 2015). This process could be driven by trophic or shelter needs of the different coloniser species, and might be influenced by the colonising abilities and the mobility of different taxa (Griffiths and Stenton-Dozey 1981; Marsden 1991; Colombini *et al.* 2000; Olabarria *et al.* 2007; Dufour *et al.* 2012). Therefore, faunal

colonisation (i.e. the arrivals of species to a patch of new habitat) determines the temporal changes in composition and structure of macroinvertebrates associated with wrack debris. Previous studies have evaluated the colonisation and successional dynamics in wrack patches during the decay of organic matter. Lavoie (1985) reported that the colonisation and replacement of macroinvertebrate species in stranded decaying algal patches (i.e. deposited by tides on the supralittoral zone) exhibited three successional stages: early (flies and amphipods), middle (staphylinid and hydrophylid beetles, fly larvae, spiders, etc.) and late (tenebrionids and histerids). Other studies have evaluated this process using litterbags (Inglis 1989; Jędrzejczak 2002; Dufour *et al.* 2012) or experimental algal patches (Olabarria *et al.* 2007; Rodil *et al.* 2008; Colombini *et al.* 2009). Generally, talitrid amphipods and dipterans are reported as primary colonisers of algal patches, while different insect species, mainly coleopterans (e.g. staphylinids, tenebrionids, ptiliids, histerids) and spiders, tend to colonise drift seaweed days after the initial wrack deposition. However, these studies have not found a general colonisation pattern during the decay of stranded macroalgae.

In particular, naturally stranded wrack debris is highly variable, because its habitat attributes and food value change temporally as these undergo the dynamics of the beach environment (i.e. desiccation and ageing or redeposition and re-exposure to degradation in successive tides). In this way, after the stranding of wrack debris, a directional change in assemblages could be expected: from early species associated with fresh wrack debris to early, mid and late successional species associated with patches of different states of ageing accumulated along the driftlines in successive tides. However, it is possible for the community structure to be similar at different times after the wrack accumulation, because species of different stages (i.e. early, middle and late) could colonise natural strandlines at the same time. Nevertheless, no experimental field studies have manipulated strandlines to analyse the way in which wrack accumulations deposited by tides are colonised by supralittoral arthropods. Moreover, the colonisation patterns can change locally because of the influence of environmental and morphodynamic features of beaches on the wrack supply (Barreiro *et al.* 2011) and the abundance of supralittoral species (Defeo and Gómez 2005; Baldanzi *et al.* 2013). Besides the lack of colonisation studies in natural strandlines on different morphodynamic beach states, it should be noted that no study has evaluated the colonisation patterns of supralittoral macroinvertebrates associated with mangrove-propagule debris, which represents the main organic component of the strandlines in tropical and subtropical beaches (e.g. Colombini and Chelazzi 2003; Ruiz-Delgado *et al.* 2014). Studies performed in different worldwide regions are needed to evaluate, in a general way, ecological processes, such as the colonisation of wrack debris on sandy beaches.

The aim of this study was to evaluate the colonisation patterns of supralittoral arthropods in wrack debris that had been naturally stranded in successive tides. This study was performed on four exposed sandy beaches, which differ in wrack composition and environmental features, located on the Brazilian and Spanish Atlantic coasts. For this, we manipulated the presence of stranded wrack, removing or not removing wrack debris, from areas where these had naturally stranded,

and then monitored the wrack biomass and the associated macroinvertebrates for a 47-day period. This study provides the first assessment of the effect of stranding wrack debris (i.e. seaweed and mangrove propagules) on the colonisation patterns of supralittoral arthropods on Atlantic sandy beaches using a field-based experiment. This approach allowed us to evaluate the temporal patterns of individual species and the whole community in manipulated plots during the deposition of new wrack debris and compare those with patterns of occurrence of macroinvertebrates in adjacent unmanipulated plots. Specifically, we hypothesised that: (1) density, number of species and the structure of the community will change temporarily during the deposition of wrack debris because of the life-history attributes (mobility, colonising ability) and the species-specific strategies to use wrack debris as a feeding site; (2) the temporal patterns of the communities and their timing of stabilisation, with respect to the control, will be beach dependent and thus related to the site differences in physical and environmental features; (3) different temporal patterns in response to the stranding of natural wrack debris are expected on sandy beaches located in both Atlantic regions (southern Brazil and south-western Spain) related to the differences in community composition of species and composition of wrack debris.

Materials and methods

Study area

This study was conducted on four sandy beaches located in two geographical regions – southern Brazil and south-western Spain (Fig. 1) – in order to investigate, in a general way, the effect of stranding wrack debris (i.e. seaweed and mangrove propagules) on the colonisation patterns of supralittoral macroinvertebrates. On the southern coast of Brazil two beaches (Cem and Assenodi), located in the Paraná region, were selected. This region has a humid subtropical climate with a mean annual temperature of 22.2°C and mean annual precipitation of 1890 mm. Tides on the Paraná coast are semidiurnal and microtidal, with a tidal range of 0.5–2 m (Knoppers *et al.* 1987). Cem (25°34′24″S, 48°20′13″W) located near to the mouth of the Paranaguá estuary, is a low-energy reflective beach, modified by tides. It has fine sands and a steep slope. Assenodi (25°35′24″S, 48°22′04″W), located on the Leste coastal plain, is an intermediate to dissipative, wave-dominated beach with fine sands and a gentle slope (Table 1). Both beaches are bordered by *restinga* (i.e. coastal sand dune vegetation). Wrack deposits of these beaches were composed of three types of mangrove propagules – *Laguncularia racemosa*, *Rhizophora mangle* and *Avicennia schaueriana* – as well as by terrestrial-derived vegetation. The coast of south-western Spain has a dry-summer subtropical climate with a mean annual temperature of 18.4°C and mean annual precipitation of 546.1 mm. In this geographical region two sandy beaches (Levante and Cortadura), located in the Gulf of Cadiz, were selected. The Gulf of Cadiz is a semidiurnal mesotidal environment with a tidal range between 1.1 and 3.2 m (Benavente *et al.* 2002). Levante (36°33′37″N, 6°13′27″W) located in the outer zone of Cadiz Bay, is a dune-backed, wave-dominated, and dissipative beach. It is characterised by fine sand and a gentle slope. Cortadura (36°28′58″N, 6°15′77″W), located in the south of Cadiz Bay,
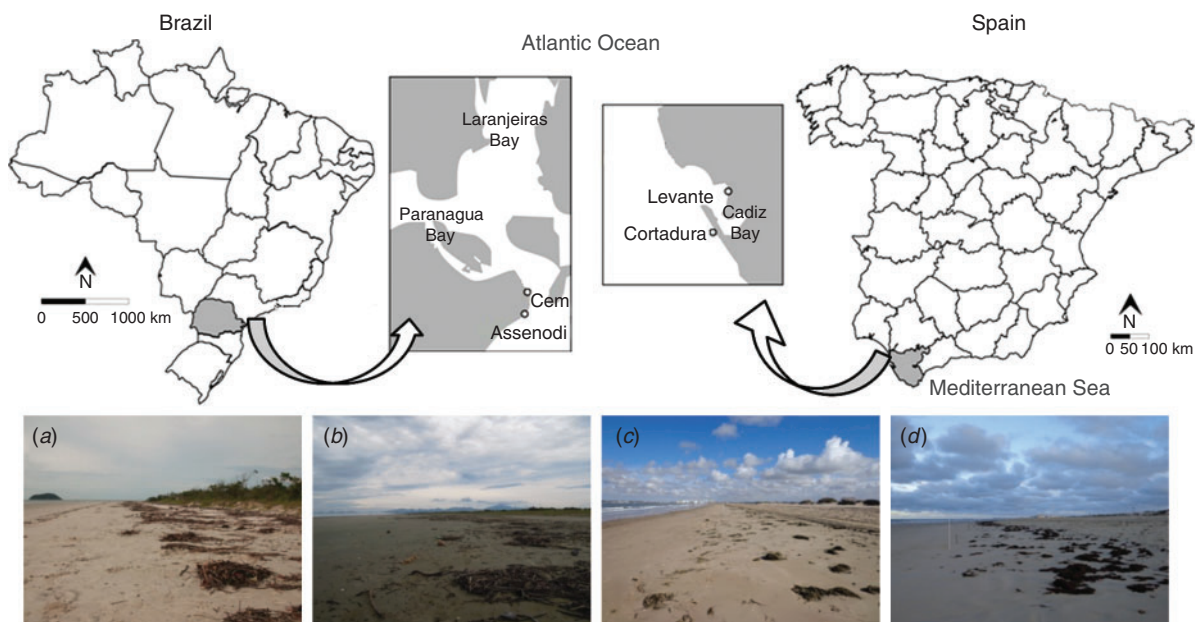
Fig. 1.　Geographic location of the study sites on the southern coast of Brazil and the south-western coast of Spain, showing the four sandy beaches sampled: Assenodi (*a*) and Cem (*b*); Levante (*c*) and Cortadura (*d*). Photo credits (*a–d*): J. V. Vieira and M. C. Ruiz-Delgado.

Table 1.　**Summary of the physical characteristics of each surveyed beach together with seasonal climate data (temperature and precipitation, mean for 1961–90) for southern Brazil (June to August) and south-western Spain (October to December)**

	Southern Brazil		South-western Spain	
Beach	Assenodi	Cem	Levante	Cortadura
Beach length (m)	2100	1000	1000	2480
Intertidal width (m)	110	53	105	85
Slope (°)	1.26	2.40	2.03	2.19
Mean sand grain size (mm)	0.27	0.23	0.18	0.23
Wave period (s)	7.00	4.90	5.00	7.00
Wave height (m)	1.00	0.25	0.75	0.65
Dean's parameter	5.53	1.76	6.20	3.37
Mean spring tide range (m)	1.70	1.70	2.00	2.00
Relative tide range (m)	1.70	6.80	5.71	3.08
Seasonal mean temperature (°C)	18.00		16.83	
Total seasonal precipitation (mm)	271.90		276.40	

is a wave-dominated and intermediate beach. This beach has fine sand and a steep slope (Table 1) and is backed by foredunes and low vegetated dune ridges. The driftlines of Levante were composed of two seagrass species: *Zostera noltii* and *Cymodocea nodosa*. Meanwhile, at Cortadura wrack deposits comprised a mixture of brown macroalgae (*Dictyopteris membranacea* and *Cladostephus spongiosus*), some species of red algae (*Halopithys incurva* and *Chondria dasyphylla*) and green algae (*Codium decorticatum* and *Codium fragile*).

Study design and sampling methods

The *in situ* colonisation of naturally accumulated wrack debris was analysed for a 47-day period from 18 June to 3 August 2012 in the Paraná region and for 28 October to 13 December 2012 in

the south-western region. During this period climatic conditions were quite similar at both regions (Table 1) and we expected a great number of species associated with wrack debris (e.g. Gonçalves and Marques 2011). An experimental stretch of 115 m (alongshore) was delimited and divided into three sampling blocks at each beach. Each block consisted of two plots, control and manipulated, each 15 m wide, extending from the base of the dune to the driftline at each beach (~30–50 m). Plots within each block were placed 5 m apart and the same distance was placed between blocks. Control plots were not manipulated and represent the unaltered condition of the wrack-associated fauna in the beach. Manipulated plots were manipulated prior to the start of the experiment (Day 1), removing all macroscopic organic material accumulated on the beach surface (i.e. supratidal and intertidal) with the aid of garden rakes. This design

allowed the evaluation of the colonisation process in naturally stranded wrack debris covering an area without previous wrack accumulation at the upper beach.

Biological responses were compared between manipulated and control plots on six sampling days (Days 1, 3, 6, 16, 32 and 47) after the deposition of new wrack debris to analyse the change in species composition associated with wrack (e.g. Lavoie 1985; Jędrzejczak 2002; Dufour *et al.* 2012). Samplings were performed during low tides, when MHWS (mean high water spring tide) varied between 1.4 and 1.6 m on beaches of southern Brazil, and between 1.2 and 1.5 m on beaches of south-western Spain and wrack debris were stranded on and above the current high tide-line of the beaches studied.

On each sampling date, wrack coverage was measured from photographs taken within six 1 × 1-m quadrats placed randomly in each plot (three controls and three manipulated). Moreover, at each plot, random samples ($n = 6$) were collected by pushing a core (15 cm in diameter and 20 cm in depth) vertically through the wrack mat into the sediment to collect wrack debris as well as wrack-associated macrofauna (non-substrate modifiers) and those underneath the wrack debris (substrate modifiers). Samples were taken within each photographed quadrat. At the free end of the core, a plastic bag was used to prevent mobile fauna (mainly insects and amphipods) from escaping. Samples were transferred into 70% alcohol. In the laboratory, the samples were washed to separate fauna and wrack debris. All macroinvertebrates retained on a sieve of 0.5 mm mesh were sorted, counted and identified to the lowest possible taxonomic level. For each biological sample, species number, density (expressed as total number of individuals per square metre of the surface covered by wrack debris) and diversity (Shannon–Wiener index) were calculated. To estimate wrack biomass, wrack debris of each sample was separated and dried to a constant weight at 60°C (g DW) (Barreiro *et al.* 2011). The coverage was estimated as the percentage of plot surface (1 × 1-m quadrat) covered by wrack debris using Image J ver. 1.45 (Abràmoff *et al.* 2004). To estimate the amount of wrack debris in each plot (g DW m^{-2}), the values of wrack biomass per core and coverage of each sampling date were used.

Data analysis

As our main goal was to search for colonisation patterns of the supralittoral assemblages in response to the stranding of wrack, univariate and multivariate analyses were performed separately for each geographic region (southern Brazil and south-western Spain). First, the effect of the stranding of wrack on the temporal and spatial variability of univariate descriptors (i.e. total density, species richness and diversity) was tested using a mixed analysis of variance (ANOVA) including four factors: treatment (two levels: control and manipulated, fixed and orthogonal), sampling times (six levels, fixed and orthogonal), beaches (two levels, fixed and orthogonal) and blocks (three levels, random and nested in each beach). Moreover, the spatial and temporal variation of wrack biomass between treatments was tested using the same mixed ANOVA as above. The analysis of variance is commonly used for the particular case of partitioning the variation in a response variable into that explained and that unexplained by one or more factors (Underwood 1997). Therefore, we performed ANOVAs to evaluate the effect of specific

factors, i.e. significant interaction Treatment × Time and Treatment × Time × Beach. This was meant to identify the temporal changes of supralittoral communities in response to the stranding of wrack debris as well as to determine whether these temporal patterns might be beach dependent. Homogeneity of variance was examined by Cochran's test while normality was analysed through visual inspection of residual and probability plots. Data were transformed when variances were significantly different at $P = 0.05$ (Underwood 1997). Significant interactions that included the above-mentioned factors (Treatment, Time or Beach) were analysed using Student–Newman–Keul (SNK) tests (Underwood 1997).

Second, the effect of wrack deposition on the temporal and spatial variability of macroinvertebrate assemblages was analysed with a permutational multivariate ANOVA (PERMANOVA: Anderson 2001) based on the same design used for the univariate analyses. A series of *a posteriori* pairwise comparisons ($P < 0.05$) were performed to investigate the temporal changes of treatments in species composition at the beaches studied. The similarity matrices were calculated using the Bray–Curtis coefficient based on fourth-root transformed data. The statistical significance of variance components was tested using 9999 permutations and a significance level of $P = 0.05$. The contribution of individual species to overall dissimilarity in assemblage structure between treatments and sampling times was determined by SIMPER analysis. Temporal variation of the mean density of the species that contributed most to the dissimilarity between treatments at each beach was analysed using the same four-factor mixed ANOVA as above. Univariate analyses were performed using the GAD package (Sandrini-Neto and Camargo 2013) in R, ver. 2.15.2 (R Foundation for Statistical Computing, Vienna, Austria, see at https://www.R-project.org/, accessed 30 September 2015) and multivariate analyses were carried out using PRIMER ver. 6 with the PERMANOVA+ add-on (PRIMER-E Ltd, Plymouth, UK).

Results

Spatio-temporal changes in stranded wrack biomass

The biomass of the stranded wrack differed between treatments and over time, although this pattern varied between beaches in each geographic region (i.e. significant Treatment × Time × Beach (Block) interaction, $F_{20,360} = 2.88$, $P < 0.001$, Table S1, southern Brazil; Treatment × Time × Beach interaction, $F_{5,360} = 12.20$, $P < 0.001$, Table S2, south-western Spain). Despite the small-scale spatial variability, an increase of wrack biomass was detected in manipulated areas between Days 1 and 3 at Cem (southern Brazil). However, these values were lower than in control plots (SNK tests, $P < 0.05$) (Fig. 2*a*). Similar values compared with controls were detected between Days 6 and 47 (Fig. 2*a*). An accumulation of wrack debris in manipulated plots was also recorded between Days 1 and 16 at Assenodi beach, although with far lower values compared with the control plots (SNK tests, $P < 0.001$) (Fig. 2*b*). Control values were reached between Days 16 and 32 (Fig. 2*b*). At Levante beach (south-western Spain), wrack debris accumulated between Days 1 and 6 in the manipulated areas, although its values were lower than in control plots (SNK tests, $P < 0.001$) (Fig. 2*c*). Values similar to those of the control areas were detected
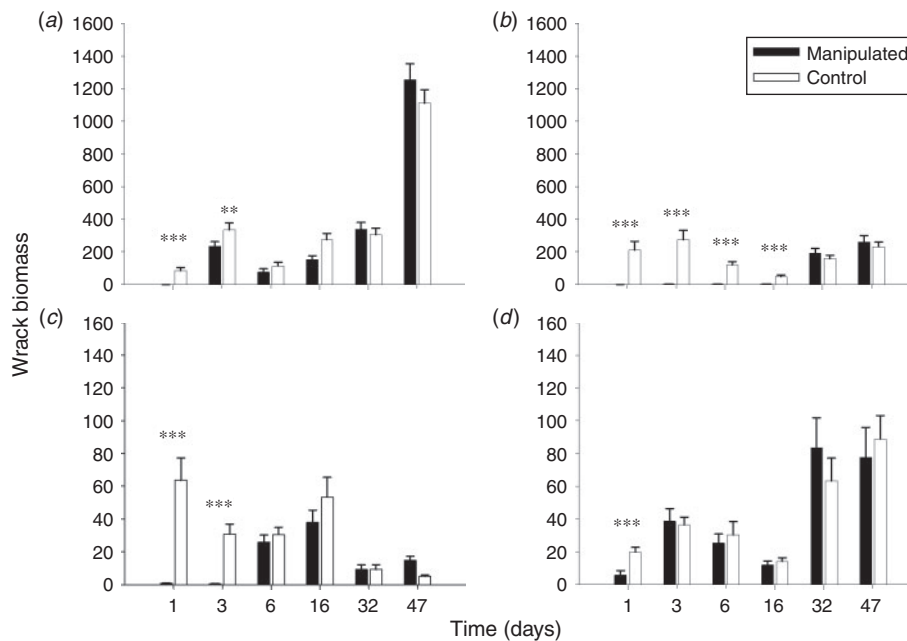
Fig. 2. Mean (±s.e., $n = 18$, average of treatment plots) of wrack biomass (g DW m^{-2}) in the control and manipulated plots at (*a*) Cem and (*b*) Assenodi (southern Brazil) and (*c*) Levante and (*d*) Cortadura (south-western Spain) over time. The significance of differences between treatments is represented as: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; no asterisk, non-significant differences.

between Days 6 and 47. At Cortadura beach, an increase of wrack biomass was detected in manipulated areas between Days 1 and 3, although with lower values compared with control plots (SNK test, $P < 0.001$) (Fig. 2*d*). Both treatments were comparable between Days 3 and 47 (Fig. 2*d*).

Colonisation patterns of supralittoral macroinvertebrates in wrack debris

Composition and univariate patterns of wrack-associated macroinvertebrates

In southern Brazil, a total of 4514 individuals and 23 taxa were sampled in wrack deposits on both beaches. The talitrid amphipod *Platorchestia monodi*, the staphylinids of the genus *Bledius* and coleopterans in the Cleridae, Nitidulidae, Carabidae and Tenebrionidae accounted for 85% of the total abundance associated with wrack debris, although the contribution of these taxa in the community structure differed at each beach (see Table S3). In south-western Spain, a total of 7193 individuals classified in 31 taxa were collected in wrack debris during the experiment. The talitrid amphipod *Talitrus saltator*, the staphylinid *Phytosus spinifer*, the tenebrionid *Phaleria bimaculata* and larvae of this family, and dipterans were the most abundant taxa (representing ~80% of the total abundance) associated with algal wrack debris. However, the contribution of these taxa in the community structure differed between beaches (see Table S4).

In southern Brazil, the mean total density differed significantly between treatments and over time, this pattern changing between beaches (i.e. significant Treatment × Time × Beach interaction, $F_{5,360} = 4.28$, $P = 0.008$, Table S1). The mean total density increased between Days 1 and 3 in the manipulated

plots, although values were significantly lower than in control plots at both beaches (SNK tests, $P < 0.05$) (Fig. 3*a, b*). Density values of manipulated plots became similar to those of control on Days 3 and 6 at Assenodi (Fig. 3*b*) and Cem (Fig. 3*a*), respectively. However, the number of species and diversity varied between treatments and over time (i.e. significant Treatment × Time interaction: $F_{5,360} = 7.21$, $P < 0.001$; $F_{5,360} = 5.73$, $P = 0.001$; Table S1). In the manipulated areas, both variables increased between Days 1 and 3, although with significantly lower values than in control areas (SNK tests, $P < 0.05$; illustrated for Cem beach, Fig. 3*c, d*). Control values were reached on Day 16 at both beaches (SNK test, $P > 0.05$). In contrast, in south-western Spain, mean total density, species richness and diversity differed significantly between treatments and over time, this trend differing between beaches (i.e. significant Treatment × Time × Beach interaction: $F_{5,360} = 3.01$, $P = 0.034$; $F_{5,360} = 4.98$, $P = 0.001$; $F_{5,360} = 3.06$, $P = 0.034$; Table S2). The mean total density increased in manipulated plots between Days 1 and 6, although values were significantly lower than in control plots until Day 6 (SNK tests, $P < 0.01$) (Fig. 3*e*). Species richness and diversity were significantly lower in manipulated than in control plots on Day 3 at Levante beach (SNK test, $P < 0.01$) (Fig. 3*g, h*) and on Days 1 and 6 at Cortadura beach (SNK test, $P < 0.05$) (Fig. 3*f*).

Multivariate patterns of wrack-associated assemblages

In southern Brazil, *P. monodi*, *B. bonariensis*, *Bledius* sp. 1, Carabidae at Assenodi, and *P. monodi*, Cleridae, Nitulidae and *P. testacea* at Cem, colonised wrack debris of manipulated plots within 1 and 3 days after wrack deposition. Moreover, coleopteran larvae, dipterans and Lycosidae occupied the wrack debris
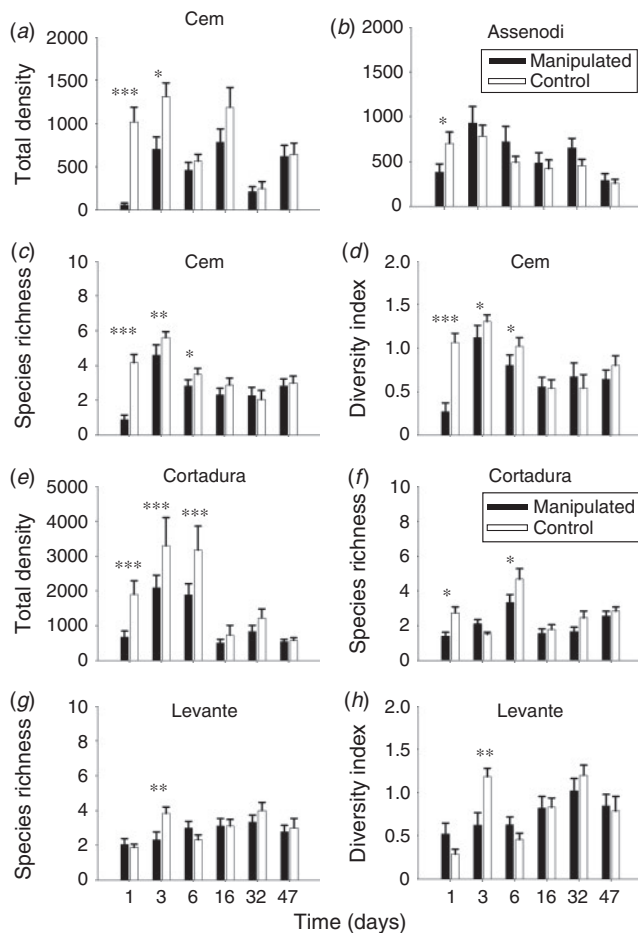
Fig. 3. Mean (±s.e., $n = 18$, average of treatment plots) of (*a*, *b*) total density (individuals m^{-2}) in the manipulated and control plots at Cem and Assenodi over time; (*c*) species richness (species m^{-2}) and (*d*) diversity index in the manipulated and control plots at Cem over time (southern Brazil); (*e*) total density in the manipulated and control plots at Cortadura over time; (*f*, *g*) species richness in the manipulated and control plots at Cortadura and Levante over time; (*h*) diversity index in the manipulated and control plots at Levante over time (south-western Spain). The significance of differences between treatments is represented as: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; no asterisk, non-significant differences.

on the first 3 days, although in low abundance. For the following days of exposure (i.e. between Days 6 and 47), *P. monodi* was the most abundant taxon in the wrack debris, followed by coleopterans (such as Cleridae, Carabidae, Nitidulidae), dipterans and Lycosidae (see Table S5). In contrast, PERMANOVA tests revealed that the wrack-associated assemblages in manipulated plots differed from those in control plots over time (i.e. significant Treatment × Time interaction, pseudo-$F_{5,360} = 9.46$, $P < 0.001$; Table S6). Pairwise comparisons of this interaction revealed that the assemblages differed between treatments on Days 1, 3 and 6 (Table S6) and this was re-established between Days 6 and 16.

SIMPER analysis showed that dissimilarities between treatments were accounted for by Talitridae (*P. monodi*), Staphylinidae (*B. bonariensis*), Tenebrionidae (*P. testacea*), and clerid and nitidulid coleopterans (see Table S7). The densities of

P. monodi and nitidulid beetles varied between treatments and over time (i.e. significant Treatment × Time interaction, $F_{5,360} = 9.71$, $P < 0.001$; $F_{5,360} = 8.18$, $P < 0.001$; Table S1). The density of *P. monodi* increased between Days 1 and 6 in the manipulated areas and the same pattern was found for nitidulid density between Days 1 and 3, although with lower values than in control plots for these days (SNK tests, $P < 0.01$) (Fig. 4*a*, *b*). Similar values compared with the control areas were detected on Day 16 for *P. monodi* (Fig. 4*a*) and on Day 6 for Nitidulidae (Fig. 4*b*). The density of *P. testacea* varied between treatments and over time, this tendency changing between beaches (i.e. significant Treatment × Time × Beach interaction, $F_{5,360} = 5.24$, $P = 0.003$; Table S1). The density of *P. testacea* increased between Days 1 and 3 in the manipulated plots (Fig. 4*c*) only at Cem beach, reaching values similar to those of the control areas on Day 3 (SNK tests, $P > 0.05$). The density of clerid beetles varied between treatments and over time, although this pattern differed between blocks within beaches (i.e. significant Treatment × Time × Beach (Block), $F_{5,360} = 1.66$, $P = 0.03$; Table S1). Despite the small-scale spatial variability, density values increased between Days 1 and 6 in manipulated plots, although with lower values than in control plots for these days (SNK tests for Cem beach, $P < 0.05$) (Fig. 4*d*). Clerids reached similar density values compared with the control areas on Day 16 (Fig. 4*d*).

In south-western Spain, *T. saltator*, *T. europaeus*, *P. bimaculata*, dipterans (adults and larvae) and staphylinid species (*P. spinifer* and *A. gregaria*) colonised the new wrack debris in the manipulated plots on the first 3 days (see Table S5). On the following days of exposure (i.e. between Days 6 and 47), *T. saltator* was the most abundant taxon in wrack debris, followed by staphylinid species (*P. spinifer*, *C. xantholoma*, *A. gregaria*), *P. bimaculata* and dipterans (adults and larvae) (Table S5). In contrast, the PERMANOVA analysis showed that wrack-associated macrofaunal assemblages in manipulated plots differed from those in controls over time and this pattern varied between beaches (i.e. significant Treatment × Beach × Time interaction, pseudo-$F_{5,360} = 2.51$, $P = 0.017$; Table S6). Pairwise comparisons on this interaction revealed that the community structure differed between treatments on Day 1 and these differences were not recorded on Day 3 at both beaches (Table S6).

SIMPER analysis indicated that Talitridae (*T. saltator*), Tenebrionidae (*P. bimaculata* adults and larvae of this family), Staphylinidae (*P. spinifer*) and Diptera were the main taxa responsible for the community-structure differences between the manipulated and control plots (see Table S7). The density of *T. saltator* varied between treatments over time (i.e. significant Treatment × Time interaction, $F_{5,360} = 3.10$, $P = 0.03$; Table S2). The density of *T. saltator* increased in manipulated plots between Days 1 and 3, although values were significantly lower than in control plots (SNK tests, $P < 0.001$) until Day 3 (Fig. 4*e*). The density of *P. bimaculata* and of tenebrionid larvae was lower in the manipulated plots than in control plots (Fig. 4*f*, *g*), although this pattern was significant only for tenebrionid larvae (i.e. significant Treatment × Time interaction, $F_{5,360} = 2.74$, $P = 0.05$; Table S2) on Day 1 (SNK tests, $P < 0.001$). This species reached values similar to control areas on Day 3 (Fig. 4*g*).
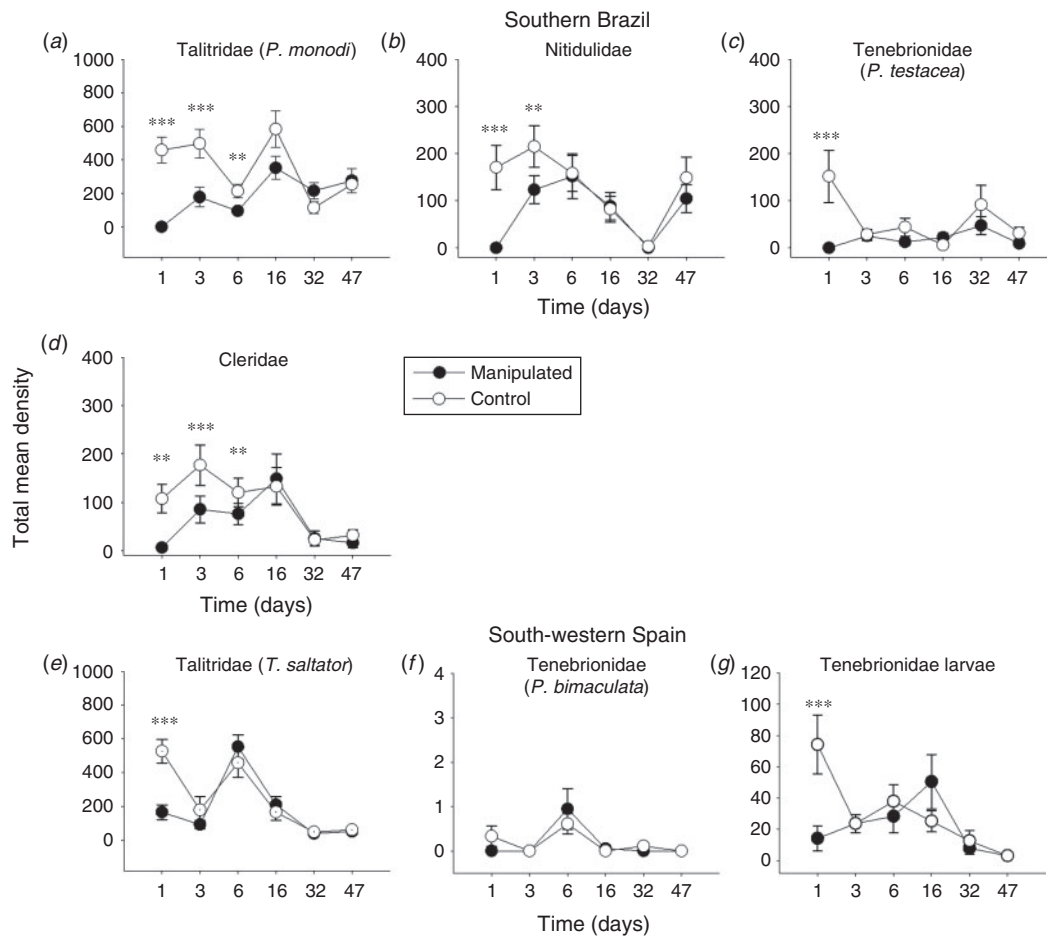
Fig. 4. Mean (±s.e., $n = 18$, average of treatment plots) density of individuals (individuals m^{-2} surface wrack-covered) in the manipulated and control plots over time. (*a*) *Platorchestia monodi*, (*b*) Nitidulidae, (*c*) *Phaleria testacea*, (*d*) Cleridae, average in the manipulated and control plots at Cem over time (southern Brazil); (*e*) *Talitrus saltator*, (*f*) *Phaleria bimaculata*, (*g*) Tenebrionidae larvae, average in the manipulated and control plots at Levante over time (south-western Spain). The significance of differences between treatments is represented as: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; no asterisk, non-significant differences.

Discussion

In this study, we experimentally manipulated stranded organic debris in supratidal areas in order to evaluate the colonisation patterns of supralittoral arthropods in wrack debris that had been naturally stranded in the successive tides. According to our results, on the first 3 days after the stranding of new wrack debris, density, species richness and diversity significantly increased in manipulated plots subsidised by seaweeds and mangrove propagules. Once the allochthonous inputs were stranded on the beach, the abundance and diversity of the supralittoral species that use these materials as food (directly or indirectly) or shelter immediately seemed to increase (Colombini *et al.* 2000; Spiller *et al.* 2010; Gonçalves and Marques 2011). This effect is reported for the first time in mangrove-propagule debris, which is the main input of organic materials in tropical and subtropical sandy beaches. During the experiment, several scavenger and detritivorous species (such as amphipods, tenebrionids and staphylinids) predominated in the wrack debris. This attracted predators, such as carnivorous

beetles (some staphylinids, carabids) and spiders in manipulated plots. Thus, on highly subsidised beaches, seaweed and mangrove-propagule debris can support several species, which could be attributed to various trophic levels (primary and secondary consumers and top predators, *sensu* Colombini *et al.* 2011). This compartmentalisation might influence the stability of food webs (Bergamino *et al.* 2013). Moreover, the diversity of trophic species associated with wrack debris might increase the acquisition of energy from these food sources and, as a result, the biomass production of the overall beach ecosystem (Lercari *et al.* 2010; Bergamino *et al.* 2011).

Beach morphodynamics interact very tightly with the amount of wrack and the density of supralittoral populations. A recent study has reported that small beaches with a low wave height and steep slope provide favourable conditions for wrack accumulation (Barreiro *et al.* 2011). In our study regions, narrow beaches with low wave heights and steep slopes (i.e. Cem of southern Brazil and Cortadura of south-western Spain) registered higher wrack-biomass values in manipulated plots than did

the other beaches (Assenodi and Levante, respectively). Moreover, the biomass of the wrack that accumulated in manipulated plots was quickly comparable (on Days 3 or 6) with those in the control plots at Cem and Cortadura beach, indicating that their physical features could favour greater accumulation of wrack. Nevertheless, the morphodynamic and physical features (such as slope, mean grain size) of beaches influence the abundance of supralittoral populations, reflective environments being safe habitats for these organisms (Defeo and Gómez 2005). Therefore, it is possible that the higher total densities and density of populations (mainly amphipods) in reflective and intermediate beaches (Cem and Cortadura, respectively) could drive the quick response of supralittoral fauna to the stranding of wrack debris. Because no two beaches are the same, local dimensions should be considered when evaluating ecosystem processes such as colonisation of wrack-debris.

Our study provides novel evidence concerning the different colonisation patterns of invertebrate assemblages in response to the stranding of seaweed and mangrove-propagule debris in two Atlantic regions. Supralittoral assemblages in manipulated plots converged quickly (i.e. within a 3-day period) with those in control areas on sandy beaches subsidised by algal wrack (in south-western Spain). Notably, the colonisation of mangrove-propagule debris (in southern Brazil) by supralittoral arthropods was slower (i.e. a 16-day period) after the stranding of the wrack debris. The temporal variability of wrack supply and the different behaviour of species with respect to the wrack resource may explain these different colonisation patterns. In southern Brazil, the slow arrival of wrack-propagules on manipulated plots (during the first 6 days) could determine the slowness (i.e. within a 16-day period) of the colonisation process by supralittoral assemblages. For instance, the protracted pattern (16-day period) of one of the most abundant species in Brazilian assemblages (*P. monodi*) might be explained by the passive transportation of individuals attached to wrack via sea currents, as has been demonstrated for other beach-hopper species (Wildish 2012; Pavesi *et al.* 2013; Fanini and Lowry 2014). Moreover, *P. monodi* (non-substrate modifiers) appears to have reduced mobility, like other beach-hopper species (e.g. Colombini *et al.* 2013), and therefore, wrack-colonisation through the movement of adults and juveniles may be slow (i.e. within a 16-day period). This is a plausible explanation for the patterns of the coleopterans, but the life-history attributes and behavioural adaptations of coleopterans inhabiting subtropical sandy beaches (such as Staphylinidae, Nitidulidae, Cleridae, etc.) are poorly understood (Defeo and McLachlan 2011), making it difficult to explain their response patterns. In contrast, in south-western Spain, the stranded biomass in the manipulated plots quickly reached values similar to those of controls (within 3- or 6-day periods), apparently enabling the rapid colonisation in the strandlines (within a 3-day period). This may be explained by the changes in talitrid density (i.e. *T. saltator*) after the stranding of the wrack. This sandhopper species (substrate modifier) is associated exclusively with sandy beaches and has less probability of passive transport via rafting (Fanini and Lowry 2014). However, *T. saltator* has high mobility owing to its effective jumping and crawling abilities, which could enable rapid colonisation of wrack.

After deposition on the beach, wrack debris undergoes many processes, including drying, *in situ* macrofaunal consumption and microbial degradation, determining its moisture and decomposition stage (Griffiths and Stenton-Dozey 1981; Inglis 1989; Jędrzejczak 2002; Orr *et al.* 2005). Since the specific fauna associated with wrack debris is regulated by the need to find an adequate food or microhabitat (e.g. Colombini *et al.* 2009) these processes could influence temporal changes of wrack-associated assemblages in each study region. In south-western Spain, algal wrack patches were rapidly colonised (within a 3-day period) by Talitridae (*T. saltator*), which used algal wrack directly (without trophic mediation) for food (Adin and Riera 2003) and refuge against harsh environmental conditions (e.g. Ruiz-Delgado *et al.* 2015). Moreover, the rapid degradation (within 1 day) of algal wrack by bacteria and macrofaunal consumption (Orr *et al.* 2005; Mews *et al.* 2006; Lastra *et al.* 2008) can attract scavengers (*P. bimaculata* and larvae), which increased in density in manipulated plots during the first 3 days after the stranding of the wrack. In southern Brazil, Nitidulidae and *P. testacea* are apparently scavengers (Caldas and Almeida 1985; Marinoni and Dutra 1997) and also increase rapidly (in the first 3 days) in density in the decaying wrack of manipulated plots. However, the indirect use of wrack-propagules as food might explain a protracted pattern (within 16 days) by other supralittoral species. For instance, clerid species, being mainly carnivorous (Marinoni and Dutra 1997), presumably feed on larvae and immature individuals associated with wrack debris. *P. monodi* feeds on microalgae or bacteria, according to gut-content analyses of individuals collected on the study beaches (unpubl. data). Therefore, *P. monodi* and Cleridae can feed on wrack, benefiting from the presence of other species (bacteria, microalgae or macroinvertebrates), which would probably result in the slow density increases (16 days) in manipulated areas. Therefore, the different use of wrack as food or shelter by the main species could determine the colonisation pattern of wrack debris in each study region.

Our results demonstrate that the colonisation of the wrack debris can be closely related to the wrack-debris characteristics (e.g. the amount, degradation and composition) combined with biological strategies (i.e. mobility and trophic guilds) of supralittoral species in each Atlantic region. Knowledge of temporal changes of densities and composition of wrack-associated fauna is key for evaluating the food-web structure on sandy beaches, despite that supralittoral fauna is not considered a biomass compartment in the trophic modelling. This study reveals that colonising assemblages of wrack debris (seaweed and mangrove propagules) are composed of abundant and diverse macroinvertebrate species, belonging to different trophic levels, which could make the structure of the food web more complex in addition to increasing the fluxes of energy and matter. These findings could be used as baseline information for evaluating the role of wrack debris in the trophic functioning of highly subsidised sandy beaches, where such debris is an essential component for ecosystem function.

Acknowledgements

References

Abràmoff, M. D., Magalhaes, P. J., and Sunanda, J. R. (2004). Image processing with ImageJ. *Biophotonics International* **11**, 36–42.

Adin, R., and Riera, P. (2003). Preferential food source utilization among stranded macroalgae by *Talitrus saltator* (Amphipoda, Talitridae): a stable isotopes study in the northern coast of Brittany (France). *Estuarine, Coastal and Shelf Science* **56**, 91–98. doi:10.1016/S0272-7714(02)00124-5

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**, 32–46.

Baldanzi, S., McQuaid, D. C., Cannicci, S., and Porri, F. (2013). Environmental domains and range-limiting mechanisms: testing the abundant centre hypothesis using southern African sandhoppers. *PLoS One* **8**(1), e54598. doi:10.1371/JOURNAL.PONE.0054598

Barreiro, F., Gómez, M., Lastra, M., López, J., and De la Huz, R. (2011). Annual cycle of wrack supply to sandy beaches: effect of the physical environment. *Marine Ecology Progress Series* **433**, 65–74. doi:10.3354/MEPS09130

Barreiro, F., Gómez, M., Lastra, M., López, J., and De la Huz, R. (2013). Coupling between macroalgal inputs and nutrients outcrop in exposed sandy beaches. *Hydrobiologia* **700**, 73–84. doi:10.1007/S10750-012-1220-Z

Benavente, J., Del Río, L., Anfuso, G., Gracia, F. J., and Reyes, J. L. (2002). Utility of morphodynamic characterisation in the prediction of beach damage by storms. *Journal of Coastal Research* **36**, 56–64.

Bergamino, L., Lercari, D., and Defeo, O. (2011). Food web structure of sandy beaches: temporal and spatial variation using stable isotope analysis. *Estuarine, Coastal and Shelf Science* **91**, 536–543. doi:10.1016/J.ECSS.2010.12.007

Bergamino, L., Gómez, J., Barboza, F. R., and Lercari, D. (2013). Major food web properties of two sandy beaches with contrasting morphodynamics, and effects on the stability. *Aquatic Ecology* **47**, 253–261. doi:10.1007/S10452-013-9440-5

Caldas, A., and Almeida, J. R. (1985). Hábitos alimentares e comportamento de *Phaleria brasiliensis* Laporte, 1840 (Coleoplera, Tenebrionidae) na praia de Bolafogo, Rio de Janeiro, RJ. *Revista Brasileira de Entomologia* **29**, 221–224.

Colombini, I., and Chelazzi, L. (2003). Influence of marine allochthonous input on sandy beach communities. *Oceanography and Marine Biology: An Annual Review* **41**, 115–159.

Colombini, I., Aloia, A., Fallaci, M., Pezzoli, G., and Chelazzi, L. (2000). Temporal and spatial use of stranded wrack by the macrofauna of a tropical sandy beach. *Marine Biology* **136**, 531–541. doi:10.1007/S002270050713

Colombini, I., Mateo, M. A., Serrano, O., Fallaci, M., Gagnarli, E., Serrano, L., and Chelazzi, L. (2009). On the role of *Posidonia oceanica* beach wrack for macroinvertebrates of a Tyrrhenian sandy shore. *Acta Oecologica* **35**, 32–44. doi:10.1016/J.ACTAO.2008.07.005

Colombini, I., Brilli, M., Fallaci, M., Gagnarli, E., and Chelazzi, L. (2011). Food webs of a sandy beach macroinvertebrate community using stable isotopes analysis. *Acta Oecologica* **37**, 422–432. doi:10.1016/J.ACTAO.2011.05.010

Colombini, I., Fallaci, M., Gagnarli, E., Rossano, C., Scapini, F., and Chelazzi, L. (2013). The behavioural ecology of two sympatric talitrid species, *Talitrus saltator* (Montagu) and *Orchestia gammarellus* (Pallas) on a Tyrrhenian sandy beach dune system. *Estuarine, Coastal and Shelf Science* **117**, 37–47. doi:10.1016/J.ECSS.2012.09.016

Crawley, K. R., Hyndes, G. A., Vanderklift, M. A., Revill, A. T., Peter, D., and Nichols, P. D. (2009). Allochthonous brown algae are the primary food source for consumers in a temperate, coastal environment. *Marine Ecology Progress Series* **376**, 33–44. doi:10.3354/MEPS07810

Defeo, O., and Gómez, J. (2005). Morphodynamics and habitat safety in sandy beaches: life-history adaptations in a supralittoral amphipod. *Marine Ecology Progress Series* **293**, 143–153. doi:10.3354/MEPS293143

Defeo, O., and McLachlan, A. (2011). Coupling between macrofauna community structure and beach type: a deconstructive meta-analysis. *Marine Ecology Progress Series* **433**, 29–41. doi:10.3354/MEPS09206

Dufour, C., Probert, P. K., and Savage, C. (2012). Macrofaunal colonisation of stranded *Durvillaea antarctica* on a southern New Zealand exposed sandy beach. *New Zealand Journal of Marine and Freshwater Research* **1**, 1–15.

Fanini, L., and Lowry, J. (2014). Coastal talitrids and connectivity between beaches: a behavioural test. *Journal of Experimental Marine Biology and Ecology* **457**, 120–127. doi:10.1016/J.JEMBE.2014.04.010

Gonçalves, S. C., and Marques, J. C. (2011). The effects of season and wrack subsidy on the community functioning of exposed sandy beaches. *Estuarine, Coastal and Shelf Science* **95**, 165–177. doi:10.1016/J.ECSS.2011.08.036

Griffiths, C. L., and Stenton-Dozey, J. M. E. (1981). The fauna and rate of degradation of stranded kelp. *Estuarine, Coastal and Shelf Science* **12**, 645–653. doi:10.1016/S0302-3524(81)80062-X

Harris, L., Campbell, E. E., Nel, R., and Schoeman, D. (2014). Rich diversity, strong endemism, but poor protection: addressing the neglect of sandy beach ecosystems in coastal conservation planning. *Diversity & Distributions* **20**, 1120–1135. doi:10.1111/DDI.12226

Ince, R., Hyndes, G. A., Lavery, P. S., and Vanderklift, M. A. (2007). Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. *Estuarine, Coastal and Shelf Science* **74**, 77–86. doi:10.1016/J.ECSS.2007.03.029

Inglis, G. (1989). The colonisation and degradation of stranded *Macrocystis pyrifera* (L.) C. Ag. by the macrofauna of a New Zealand sandy beach. *Journal of Experimental Marine Biology and Ecology* **125**, 203–217. doi:10.1016/0022-0981(89)90097-X

Jędrzejczak, M. F. (2002). Stranded *Zostera marina* L. *vs* wrack fauna community interactions on a Baltic sandy beach (Hel, Poland): a short-term pilot study. Part II. Drifline effects of succession changes and colonisation of beach fauna. *Oceanologia* **44**, 367–387.

Knoppers, B. A., Brandini, F. P., and Thamm, C. A. (1987). Ecological studies in the Bay of Paranagua. II: some physical and chemical characteristics. *Nerítica* **2**, 1–36.

Lastra, M., Page, H. M., Dugan, J. E., Hubbard, D. M., and Rodil, I. F. (2008). Processing of allochthonous macrophyte subsidies by sandy beach consumers: estimates of feeding rates and impacts on food resources. *Marine Biology* **154**, 163–174. doi:10.1007/S00227-008-0913-3

Lavoie, D. R. (1985). Population dynamics and ecology of beach wrack macroinvertebrates of the central California coast. *Bulletin of the Southern California Academy of Sciences* **84**, 1–22.

Lercari, D., Bergamino, L., and Defeo, O. (2010). Trophic models in sandy beaches with contrasting morphodynamics: comparing ecosystem structure and biomass flow. *Ecological Modelling* **221**, 2751–2759. doi:10.1016/J.ECOLMODEL.2010.08.027

Marinoni, R. C., and Dutra, R. C. (1997). Familias de coleoptera capturadas com armadilha malaise em oito localidades do estado do Paraná, Brasil, diversidades alfa e beta. *Revista Brasileira de Zoologia* **14**, 751–770. doi:10.1590/S0101-81751997000300021

Marsden, I. D. (1991). Kelp–sandhopper interactions on a sandy beach in New Zealand. I. Drift composition and distribution. *Journal of Experimental Marine Biology and Ecology* **152**, 61–74. doi:10.1016/0022-0981(91)90135-J

McLachlan, A., and Brown, A. C. (2006). 'The Ecology of Sandy Shores', 2nd edn. (Academic Press: New York.)

Mews, M., Zimmer, M., and Jelinski, D. E. (2006). Species-specific decomposition rates of beach-cast wrack in Barkley Sound, British Columbia, Canada. *Marine Ecology Progress Series* **328**, 155–160. doi:10.3354/MEPS328155

Olabarria, C., Lastra, M., and Garrido, J. (2007). Succession of macrofauna on macroalgal wrack of an exposed sandy beach: effects of patch size and site. *Marine Environmental Research* **63**, 19–40. doi:10.1016/J.MARENVRES.2006.06.001

Orr, M., Zimmer, M., Jelinski, D. E., and Mews, M. (2005). Wrack deposition on different beach type: spatial and temporal variation in the pattern of subsidy. *Ecology* **86**, 1496–1507. doi:10.1890/04-1486

Pavesi, L., Tiedemann, R., De Matthaeis, E., and Ketmaier, V. (2013). Genetic connectivity between land and sea: the case of the beachflea *Orchestia montagui* (Crustacea, Amphipoda, Talitridae) in the Mediterranean Sea. *Frontiers in Zoology* **10**, 1–19. doi:10.1186/1742-9994-10-21

Polis, G. A., and Hurd, S. D. (1996). Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small island and coastal land communities. *American Naturalist* **147**, 396–423. doi:10.1086/285858

Rodil, I. F., Olabarria, C., Lastra, M., and Lopez, J. (2008). Differential effects of native and invasive algal wrack on macrofaunal assemblages inhabiting exposed sandy beaches. *Journal of Experimental Marine Biology and Ecology* **358**, 1–13. doi:10.1016/J.JEMBE.2007.12.030

Ruiz-Delgado, M. C., Vieira, J. V., Veloso, V. G., Reyes-Martínez, M. J., Sallorenzo, A. I., Borzone, C. A., Sánchez-Moyano, J. E., and García-García, F. J. (2014). The role of wrack deposits for supralittoral arthropods: an example using Atlantic sandy beaches of Brazil and Spain. *Estuarine, Coastal and Shelf Science* **136**, 61–71. doi:10.1016/J.ECSS.2013.11.016

Ruiz-Delgado, M. C., Reyes-Martínez, M. J., Sánchez-Moyano, J. E., López-Pérez, J., and García-García, F. J. (2015). Distribution patterns of supralittoral arthropods: wrack deposits as a source of food and refuge on exposed sandy beaches (SW Spain). *Hydrobiologia* **742**, 205–219. doi:10.1007/S10750-014-1986-2

Sandrini-Neto, L., and Camargo, M. G. (2013). GAD: an R package for ANOVA designs from general principles. (Comprehensive R Archive Network.) Available at https://cran.r-project.org/ [Verified 30 September 2015].

Spiller, D. A., Piovia-Scott, A. N., Wright, L. H., Yang, G., Takimoto, T. W., and Schoener, T. I. (2010). Marine subsidies have multiple effects on coastal food webs. *Ecology* **91**, 1424–1434. doi:10.1890/09-0715.1

Underwood, A. J. (1997). 'Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance.' (Cambridge University Press: Cambridge, UK.)

Wildish, D. J. (2012). Long distance dispersal and evolution of talitrids (Crustacea: Amphipoda: Talitridae) in the northeast Atlantic islands. *Journal of Natural History* **46**, 2329–2348. doi:10.1080/00222933.2012.708458

Supplementary material

Colonisation patterns of supralittoral arthropods in naturally stranded wrack debris on Atlantic sandy beaches of Brazil and Spain

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Table S1.   Results of the mixed-model ANOVA for wrack biomass, the community structure indices (total density, species richness, Shannon–Wiener index) and the densities of the main taxa (*Platorchestia monodi*, *Phaleria testacea*, Nitidulidae and Cleridae) in southern Brazil between treatments (two levels; fixed factor), beaches (two levels; fixed factor), sampling times (six levels; fixed factor) and blocks (three levels; random factor and nested in beach)

d.f., degrees of freedom; m.s., mean square; ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$. Bold values indicate significant interactions of interest analysed by pairwise comparisons

		Wrack biomass		Total density		Species richness		Diversity		*P. monodi*		*P. testacea*		Nitidulidae		Cleridae	
Source	d.f.	m.s.	F	m.s.	F	m.s.	F	m.s.	F	m.s.	F	m.s.	F	m.s.	F	m.s.	F
Treatment (Tr)	1	1782.02	8.30*	34.65	41.75**	70.08	26.24**	4.41	16.53*	39.24	37.34**	44307.00	3.55	90.80	31.94**	47.65	49.97**
Beach (Be)	1	5255.20	107.61***	25.91	3.94	21.33	4.94	1.91	9.96*	13.55	4.47	161482.55	18.49*	366.33	39.29**	381.21	29.28**
Time (Ti)	5	3329.07	130.45***	28.46	5.35**	28.03	10.77***	1.81	11.49***	5.56	3.33*	12723.41	4.74**	36.76	8.15***	13.31	3.02*
Block (Bl)(Be)	4	48.84	3.56**	6.58	2.19	4.32	1.74	0.19	0.87	3.03	4.22**	8735.86	1.89	9.32	2.92*	13.02	4.39**
Tr × Be	1	419.25	1.95	19.32	23.28**	1.12	0.42	0.00	0.00	0.00	0.00	39823.24	3.19	0.10	0.04	16.76	17.58*
Tr × Ti	5	360.90	9.12***	19.54	10.21***	17.66	**7.21***	1.28	**5.73**	9.31	**9.71***	15915.85	5.45**	31.30	**8.18***	2.74	0.55
Be × Ti	5	957.41	37.52***	24.28	4.57**	21.84	8.39***	1.04	6.58***	12.57	7.54***	12460.36	4.64**	39.01	8.65***	27.33	6.20**
Tr × Bl(Be)	4	214.60	15.63***	0.83	0.28	2.67	1.07	0.27	1.20	1.05	1.46	12472.32	2.69*	2.84	0.89	0.95	0.32
Ti × Bl(Be)	20	25.52	1.86*	5.32	1.77*	2.60	1.05	0.16	0.71	1.67	2.32**	2682.78	0.58	4.51	1.41	4.41	1.48
Tr × Ti × Be	5	85.72	2.17	8.19	**4.28**	2.37	0.97	0.15	0.69	1.13	1.18	15270.19	**5.24**	3.00	0.79	4.97	1.01
Tr × Ti × Bl(Be)	20	39.59	**2.88***	1.91	0.64	2.45	0.99	0.22	1.01	0.96	1.33	2921.92	0.63	3.83	1.20	4.94	**1.66**
Residual	360	13.73		3.00		2.49		0.22		0.72		4625.74		3.19		2.97	
Cochran's test		C = 0.0547; n.s.		C = 0.055; n.s.		C = 0.049; n.s.		C = 0.0395; n.s.		C = 0.039; n.s.		C = 0.301; n.s		C = 0.040		C = 0.053; n.s.	
Transformation		Square root		log(*x*+1)		–		–		log(*x*+1)		–		log(*x*+1)		log(*x*+1)	

Table S2.   Results of the mixed-model ANOVA for wrack biomass, community structure indices (total density, species richness, Shannon–Wiener index) and the densities of the main taxa (*Talitrus saltator*, and Tenebrionidae larvae) in south-western Spain between treatments (two levels; fixed factor), beaches (two levels; fixed factor), sampling times (six levels; fixed factor) and blocks (three levels; random factor and nested in beach)

d.f., degrees of freedom; m.s., mean square; ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$. Bold values indicated significant interactions analysed by pairwise

comparisons

Source	d.f.	Wrack biomass		Total density		Species richness		Diversity index		*T. saltator*		Tenebrionid larvae	
		m.s.	F	m.s. × 10⁷	F	m.s.	F	m.s.	F	m.s.	F	m.s.	F
Treatment (Tr)	1	11.27	63.13**	2.20	24.36**	20.02	19.09*	0.54	5.20	19.29	27.25**	15.58	4.12
Beach (Be)	1	14.82	9.00*	10.94	217.46***	35.02	14.09*	15.14	85.27***	641.03	329.41***	3.57	4.49
Time (Ti)	5	2.22	3.17*	1.86	9.98***	14.44	6.55***	1.28	5.48**	66.60	21.60***	18.46	4.31**
Block (Bl)(Be)	4	1.65	8.26***	0.50	0.35	2.48	1.05	0.18	0.96	1.95	0.50	0.80	0.28
Tr × Be	1	4.06	22.72**	0.85	9.42*	2.52	2.40	0.06	0.59	0.29	0.41	0.01	0.00
Tr × Ti	5	5.34	24.37***	0.16	3.06*	0.95	0.47	0.18	0.86	13.99	**3.10***	9.57	**2.74***
Be × Ti	5	10.56	15.07***	1.36	7.31***	24.52	11.11***	2.68	11.51***	30.54	9.91***	43.33	10.12***
Tr × Bl(Be)	4	0.18	0.90	0.09	0.64	1.05	0.44	0.10	0.57	0.71	0.18	3.78	1.34
Ti × Bl(Be)	20	0.70	3.52***	0.19	1.32	2.21	0.93	0.23	1.26	3.08	0.79	4.28	1.52
Tr × Ti × Be	5	2.76	**12.61*****	0.16	**3.01***	10.14	**4.98****	0.65	**3.06***	2.37	0.53	1.89	0.54
Tr × Ti × Bl(Be)	20	0.22	1.10	0.05	0.38	2.04	0.86	0.21	1.16	4.51	1.15	3.49	1.24
Residual	360	0.20		0.14		2.37		0.18		3.91		2.82	
Cochran's test		C = 0.0549; n.s.		C = 0.270; n.s		C = 0.046; n.s.		C = 0.052; n.s.		C = 0.053; n.s.		C = 0.049; n.s.	
Transformation		Fourth root		–		–		–		log(x+1)		log(x+1)	

Table S3.   Total abundance (number of individuals) and percentage composition (percentage of community) of arthropods found in the wrack deposits on beaches of southern Brazil (Cem and Assenodi)

Taxa	Cem		Assenodi	
	Total abundance	Percentage of community	Total abundance	Percentage of community
Amphipoda				
Talitridae				
Platorchestia monodi	1283	53.10	771	37.00
Isopoda				
Tylidae				
Tylos niveus	1	0.04	1	0.05
Coleoptera				
sp. 1	5	0.20	9	0.43
larvae sp. 1	44	1.82	106	5.09
Tenebrionidae				
Phaleria testacea	149	6.17	2	0.10
Tenebrionid larvae	51	2.11	1	0.05
Staphylinidae				
Bledius bonariensis	17	0.70	678	32.53
Bledius hermani	22	0.91	–	–
Bledius sp. 1	16	0.66	35	1.68
Bledius sp. 2	–	–	19	0.24
Gabronthus sp. 1	5	0.20	–	–
Heteroceridae				
Efflagitatus freudei	–	–	6	0.29
E. freudei larvae	–	–	50	2.40
Cleridae	300	12.41	31	1.49
Carabidae	–	–	280	13.44
Nitidulidae	394	16.30	55	2.64
Scarabeidae				
Aphodinae sp. 1	9	0.36	4	0.19
Curculionidae	2	0.08	–	–
Araneae				
Allocosa brasiliensis	9	0.37	20	0.96
Araneae sp. 1	19	0.78	8	0.39
Araneae sp. 2	6	0.25	–	–
Araneae sp. 3	–	–	3	0.14
Araneae sp. 4	–	–	–	–
Araneae sp. 5	1	0.04	–	–
Diptera	83	3.44	19	0.91
Total density	2416		2084	
Total number of species	19		17	

Table S4. Total abundance (number of individuals) and percentage composition (percentage of community) of arthropods found in the wrack deposits on beaches of south-western Spain (Levante and Cortadura)

Taxa not collected on the beach are represented by en-dashes

Taxa	Levante		Cortadura	
	Total abundance	Percentage of community	Total abundance	Percentage of community
Amphipoda				
Talitridae				
Talitrus saltator	813	48.25	4569	74.23
Isopoda				
Armadillidae				
Armadillium sp. 1	4	0.24	–	–
Tylidae				
Tylos europaeus	–•	–	40	0.65
Coleoptera				
Tenebrionidae				
Phaleria bimaculata	33	1.96	37	0.60
Tenebrionid larvae	69	4.09	125	2.03
Staphylinidae				
Myrmecopora sulcata	1	0.06	2	0.03
Hydrosmecta thinobioides	7	0.42	–	–
Tachyporus pusillus	1	0.06	1	0.02
Aleochara bipustulata	1	0.18	–	–
Acrotona orbata	17	1.00	17	0.27
Aloconota gregaria	27	1.60	14	0.22
Phytosus spinifer	52	3.09	571	9.27
Carpelimus rivularis	13	0.77	8	0.13
Anotylus nitidulus	24	1.42	6	0.10
Remus sericeus	2	0.12	12	0.19
Cafius xantholoma	11	0.65	14	0.23
Curculionidae	7	0.42	6	0.11
Carabidae	15	0.89	5	0.09
Chrysomelidae	8	0.47	1	0.02
Elateroidae	2	0.12	–	–
Scarabidae	3	0.18	–	–
Histeridae	8	0.47	6	0.11
Araneae				
Lyniphiidae	37	2.20	9	0.16
Agelinidae	1	0.06	–	–
Salticidae	2	0.12	–	–
Diptera				
Adults	276	16.38	49	0.89
Larvae sp. 1	153	9.08	9	0.16
Pupae sp. 1	24	1.42	5	0.09
Hymenoptera				
Pteromalidae	15	0.89	–	–
Hemiptera				
Psylloidea	39	2.31	2	0.04
Saldidae				
Saldula saltoria	15	0.89	–	–
Thysanoptera	2	0.12	–	–
Total abundance	1685		5508	
Total number of species	29		20	

Table S5.   Temporal variation of macroinvertebrate taxa based on abundance classes (4th root transformed) for manipulated plots on sandy beaches on both studied regions

Pla, *Platorchestia monodi*; Pha, *Phaleria testacea*; Dip, Diptera; Tal, *Talitrus saltator*; Tyl, *Tylos europaeus*; Dip, Diptera; Bon, *Bledius bonariensis*; Her, *Bledius hermani*; Cle, Cleridae; Pha, *Phaleria bimaculata*; DipLv, dipteran larvae; Nit, Nitidulidae; TenLv, tenebrionid larvae; Ble, *Bledius* sp. 1; Alo, *Aloconota gregaria*; ColLv, coleopteran larvae sp. 1; Allo, *Allocosa brasiliensis*; Phy, *Phytosus spinifer*; Caf, *Cafius xantholoma*; Lyn, Lyniphiidae; Ara, Arachnidae sp. 1; Eff, *Efflagitatus* larvae; Car, Carabidae; Acro, *Acrotona orbata*; Psy, Psylloidea; Car, Carabidae. Bold names relate to Assenodi Beach and Cortadura Beach

Abundance class	Southern Brazil Manipulated (days)						South-western Spain Manipulated (days)					
	1	3	6	16	32	47	1	3	6	16	32	47
4.5–5.0							**Tal**	**Tal**				
4.0–4.5												
3.5–4.0		**Bon**		Pla			**Tal**		Tal		**Tal**	
3.0–3.5		Pla	**Bon**		**Pla**	Pla			**Phy**	**Tal**		**Tal**
2.5–3.0	**Bon**	**Car**	Pla Nit **Car**	Cle **Pla**			**Pla**	Tal		Tal		
2.0–2.5	**Eff**	Cle Nit	Cle	Nit **Bon** **ColLv** **Car**	**Bon** **ColLv**	ColLv Nit		Tal Dip		**Phy**	Dip **Phy**	Tal Lyn
1.5–2.0	**Ble** **ColLv** **Car**	Pha TenLv Dip **Pla**	**Ble** **Pla**	Pha **Eff**	Pla Cle Pha Dip Ble **Car**	Dip **Car**	Pha TenLv **TenLv** **Phy**	TenLv	Dip **Pha** **TenLv**	DipLv Phy TenLv **TenLv**	Tal Phy Psy	Dip Phy Psy **Dip** **Phy**
1.0–1.5	Cle TenLv Her	Bon Ble Ara ColLv **Eff**	Pha TenLv Dip Allo	Dip **Dip**	Her TenLv **Cle** **Nit** **Eff** **Allo** **Dip**	Cle Pha **Nit** **Bon** **Dip** **ColLv**	Dip DipLv Alo Dip	Pha **Dip** **Tyl** **Alo** **Phy** **DipLv**	Alo **Dip** **Tyl** **Alo** **Caf**	Dip Pha Alo Caf **Pha** **DipLv**	Alo Ano **Lavt** **Caf**	Ano **Tyl** **TenLv** **Car** **Lyn**
0.5–1.0	Bon ColLv **Pla**	Her Allo **Ble** **Allo** **Dip** **ColLv**	Ara **ColLv** **Eff**	**Cle** **Allo**	ColLv Allo	Bon Ble TenLv **Ble** **Allo**	Ano	DipLv Phy Lyn **TenLv** **Lyn** **Car** **Caf**	DipLv TenLv	**DipLv**	Caf Lyn **Acro** **Lyn**	Pha Alo Caf

Table S6. PERMANOVA results and pairwise comparisons performed to compare macroinvertebrates assemblages for each geographical region (southern Brazil and south-western Spain)

Degrees of freedom (d.f.), mean square (m.s.) and pseudo-*F* are shown. Pairwise test: C, Control; T, Treatment. Bold values indicate significant results. The data were fourth-root-transformed.

Source	d.f.	South-western Spain		Southern Brazil	
		m.s.	Pseudo-*F*	m.s.	Pseudo-*F*
Treatment (Tr)	1	2242.00	5.63*	22956.00	22.43**
Beach (Be)	1	44534.00	202.49***	105740.00	70.10***
Time (Ti)	5	7407.90	9.77***	9762.00	11.96***
Block (Bl)(Be)	4	398.24	0.73	1508.60	2.15*
Tr × Be	1	1110.40	5.05*	4012.50	3.92*
Tr × Ti	5	920.26	1.21	5758.00	**9.46***
Be × Ti	5	9281.90	17.77***	11075.00	13.56***
Tr × Bl(Be)	4	219.93	0.41	1023.70	1.46
Ti × Bl(Be)	20	758.16	1.40*	816.54	1.16
Tr × Ti × Be	5	1313.20	**2.51**	711.85	1.17
Tr × Ti × Bl(Be)	20	522.18	0.96	608.87	0.87
Residual	360	540.34		703.15	

Pairwise test	Time (T)	Condition (C)	*P* (MC)		Condition	*P* (MC)
Tr × Ti × Be	T1	Lev × C *v*. T	**0.0090**	Tr × Ti	C *v*. T	**0.0002**
		Cort × C *v*. T	**0.0077**			
	T3	Lev × C *v*. T	0.1103		C *v*. T	**0.0094**
		Cort × C *v*. T	0.8303			
	T6	Lev × C *v*. T	0.5265		C *v*. T	**0.0238**
		Cort × C *v*. T	0.3123			
	T16	Lev × C *v*. T	0.4613		C *v*. T	0.2019
		Cort × C *v*. T	0.9243			
	T32	Lev × C *v*. T	0.3778		C *v*. T	0.7199
		Cort × C *v*. T	0.3911			
	T47	Lev × C *v*. T	0.1551		C *v*. T	0.2023
		Cort × C *v*. T	0.3857			

Table S7. SIMPER (Similarity Percentage) analysis listing species that contribute collectively to at least 70% of total assemblage dissimilarity between treatments (control and manipulated) at the sampling times (T1–T16)

Codes for higher taxa: AMP, Amphipods; COL, Coleoptera

(a) Southern Brazil		Average abundance		Contrib.	
		Manipulated	Control	%	Cum.%
T1: 90.19% dissimilarity					
P. monodi	AMP	0.03	1.38	35.53	35.53
B. bonariensis	COL	0.59	0.46	21.05	57.09
Nitidulidae	COL	0.00	0.85	20.07	77.16
Cleridae	COL	0.06	0.39	9.42	83.19
P. testacea	COL	0.00	0.36	6.43	93.01
T3: 60.01% dissimilarity					
P. monodi	AMP	0.69	1.44	26.99	26.99
B. bonariensis	COL	0.99	0.80	24.69	51.68
Nitidulidae	COL	0.45	0.82	17.71	69.38
Cleridae	COL	0.32	0.52	12.38	81.76
P. testacea	COL	0.28	0.35	9.93	91.69
T6: 68.48% dissimilarity					
P. monodi	AMP	0.56	1.17	28.33	28.33
B. bonariensis	COL	0.72	0.44	25.80	54.14
Nitidulidae	COL	0.42	0.64	19.27	73.41
Cleridae	COL	0.34	0.43	13.69	87.09
P. testacea	COL	0.09	0.24	7.21	94.30
T16: 66.85% dissimilarity					
P. monodi	AMP	0.98	1.27	31.37	31.37
B. bonariensis	COL	0.37	0.21	20.45	51.83
Cleridae	COL	0.39	0.51	19.18	71.01
Nitidulidae	COL	0.32	0.31	14.94	85.95
P. testacea	COL	0.24	0.13	7.54	93.49
(b) South-western Spain		Average abundance		Contrib.	
		Manipulated	Control	%	Cum.%
T1 – Levante: 53.58% dissimilarity					
T. saltator	AMP	0.98	1.69	43.18	43.18
Tenebrionid larvae	COL	0.53	0.00	22.69	65.88
Diptera	DIP	0.18	0.17	10.89	76.76
P. bimaculata	COL	0.25	0.00	9.10	85.86
T3 – Levante: 51.95% dissimilarity					
Diptera	DIP	0.54	1.23	28.34	28.34
T. saltator	AMP	0.76	0.82	22.73	51.07
Tenebrionid larvae	COL	0.59	0.65	18.09	69.16
P. bimaculata	COL	0.12	0.32	9.28	78.44
P. spinifer	COL	0.06	0.22	7.10	85.54
T1 – Cortadura: 44.32% dissimilarity					
T. saltator	AMP	1.49	2.12	39.51	39.51
Tenebrionid larvae	COL	0.22	0.62	22.05	61.57
P. spinifer	COL	0.21	0.56	19.29	80.86
Diptera	DIP	0.11	0.33	13.16	94.02
T3 – Cortadura: 44.32% dissimilarity					
T. saltator	AMP	2.26	2.46	42.17	42.17
Diptera	DIP	0.28	0.17	17.42	59.59
P. spinifer	COL	0.17	0.19	13.71	73.30