Biodiversity effects on macroalgal productivity: exploring the roles of richness, evenness and species traits

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ABSTRACT: In the last 2 decades, concerns regarding the effects of global loss of diversity have prompted considerable research on the functional consequences of biodiversity. In this context, a new perception of biodiversity as a major regulator of the functioning of ecosystems has emerged. The concept of biodiversity has a wide meaning and includes not only the number of species, but also the number of traits, relative species and trait abundances, etc. Understanding how these different components of biodiversity influence the functioning of communities is required in order to improve our ability to project the future consequences of the current rate of diversity loss. We used a short term manipulative experiment to disentangle the effects of species numbers, species traits (identity) and species relative abundance (evenness) on the primary productivity rates of intertidal macroalgal assemblages. We also examined the ability of functional identity and diversity indices to predict the magnitude of primary productivity and overyielding. Results suggested that the intense identity effects, derived from species traits, drove the response of the experimental assemblages. The relevance of species traits was confirmed by the significant effects of the community-level functional identity descriptors on the functioning of the assemblages. Also, weak but consistently positive effects were detected for evenness. Finally, the interaction between species richness and evenness suggested that the negative effect of high dominance by single species (i.e. low evenness) was more intense on those assemblages with reduced species richness. Thus, understanding potential interactions between richness, evenness and functional identity among other biodiversity components is critical to identify present and project future consequences of anthropogenic disturbances.

KEY WORDS: Biodiversity · Ecosystem functioning · Species number · Evenness · Functional diversity · Functional identity · Seaweeds

INTRODUCTION

Every day, organisms on Earth move hundreds of thousands of tons of elements and compounds through their biochemical activity. For more than 50 yr, ecologists have investigated these biologically driven processes that are occurring in ecosystems. Good examples are the conceptual models developed by Odum in the 1950s and 1960s characterizing how energy and matter flow through ecosystems (Odum 1969). However in the last 2 decades, renewed interest in the functional attributes of ecosystems has emerged from the recognition that under the current rates of biodiversity loss, the functioning of the Earth's natural ecosystems and the services they sustain are under threat (Hooper et al. 2005,

Stachowicz et al. 2007, Reiss et al. 2009, Cardinale et al. 2012). These research efforts have demonstrated that biodiversity can directly control the functioning of ecosystems in terms of nutrient cycling and biomass production. Ecosystem functions are broadly defined as an amalgamation of processes that control the fluxes of energy, nutrients and organic matter through the environment (Cardinale et al. 2012).

Despite initial controversy regarding the mechanism underlying the relationship between biodiversity and ecosystem functioning (Huston et al. 2000, Mittelbach et al. 2001), research in the last 2 decades has reached similar conclusions (Loreau et al. 2001, Cardinale et al. 2006, Tilman et al. 2006, Reiss et al. 2009): that a minimum number of species is necessary to maintain the basic functioning of ecosystems, and a larger number of species is required to maintain both the structure and functioning of ecosystems (Loreau et al. 2001). Furthermore, biodiversity not only influences ecosystem processes such as biogeochemical cycles, but is also relevant for other ecosystem properties such as stability (Tilman et al. 2006), resistance to the establishment of introduced species (Stachowicz & Byrnes 2006) and temporal and spatial predictability (McGrady-Steed et al. 1997). Three main mechanisms have been proposed as driving the positive effect of diversity on ecosystem processes: (1) resource partitioning, resulting from the complementary use of resources by different species; (2) facilitation, used here as synonymous with positive interactions, representing benefits provided by one species that can increase the effective niche of other species (Bruno et al. 2003); and (3) sampling effect, a simple probabilistic effect that occurs when increasing the number of species in any assemblage increases the probability of including highly productive species (Spaekova & Leps 2001, Aarssen et al. 2003). Resource partitioning and facilitation are often known together as niche complementarity (Flombaum et al. 2014), however, the relative importance of these mechanisms in natural systems is very much unknown (Cardinale et al. 2012, Flombaum et al. 2014).

To date, most of the knowledge on the relationship between biodiversity and ecosystem functioning has been derived from theoretical models and experimental systems in which the number, identity and functional traits of species have been highly controlled at local scales (Solan et al. 2006). Few studies have included evenness in their design, i.e. how similar abundances are across species in a community. In natural systems, the abundance of species is usually highly uneven, with the majority of species occurring in low abundance and only a few being extremely common (Schläpfer & Schmid 1999). Thus, including only the richness of species or traits in experiments ignores the influence of relative species abundances on intra- and inter-specific interactions, which ultimately drive the functional effects of biodiversity (Hillebrand et al. 2008, Zhang et al. 2012). Also, understanding how changes in species evenness can modify ecosystem functioning is highly relevant in the context of the decline in global biodiversity. Evenness usually changes more rapidly in response to anthropogenic stressors than does species richness (Chapin et al. 2000). Species that are at risk or on the way to extirpation probably go through a low-abundance stage before disappearing completely, and hence evenness may decline long before species richness does (Chapin et al. 2000, Mulder et al. 2004). Additionally, evenness and species richness are not always correlated, and both positive and negative relationships have been described in terrestrial systems (Stirling & Wilsey 2001). Finally, richness and evenness may respond differently to environmental drivers and a deeper understanding of the relationships between species richness and evenness along geographical gradients and across the biological and trophic hierarchies is required (Soininen et al. 2012).

Species functional traits are increasingly recognized as playing a major role in determining ecosystem functioning. Functional traits are the features (morphological, physiological, phenological, etc.) that determine how species respond to environmental factors, interact with other species and/or influence ecosystem properties (Pérez-Harguindeguy et al. 2013). Hence, community functional diversity, defined as the value and range of species traits that influence ecosystem functioning in a given system, potentially provides greater explanatory power than species richness because it links organisms with the functions they mediate (Griffin et al. 2009).

The importance of understanding the functional effects of biodiversity components is particularly relevant in the context of the emergent communities, with novel species and traits composition a consequence of global anthropogenic disturbances like climate change or invasions (Grimm et al. 2013). For example, the arrival of introduced species is considered to have a global impact with large effects on the diversity of native assemblages. Thus, non-native species with single functional traits are often highly dominant in their host assemblages, displacing native species and modifying the structure and functioning of host communities (Ruesink et al. 2006, Wallentinus & Nyberg 2007).

Theories on the relationship between biodiversity and ecosystem functioning have been largely derived from ecological studies in terrestrial systems. However, the number of studies conducted in marine systems has rapidly increased in recent years (Gamfeldt et al. 2015). In marine macroalgal communities, studies on biodiversity–ecosystem functioning have focused on the effects of species richness on primary production and on the stability of natural communities (Bruno et al. 2003, Stachowicz et al. 2008, Boyer et al. 2009, Kraufvelin et al. 2010, Bracken & Williams 2013). Macroalgal communities present high rates of benthic primary production, fuelling highly diverse animal assemblages in coastal areas (Middelboe et al. 2006). Most of the studies performed to date describe significant effects of species richness on primary productivity and stability (see a recent review by Gamfeldt et al. 2015). However, richness alone may be an incomplete surrogate for communities' biodiversity (Soininen et al. 2012); evenness should also be assessed. Arenas et al. (2009) carried out an observational study in natural macroalgal assemblages and found positive effects of species richness and evenness on the primary productivity of the assemblages. However, observational approaches have several limitations, such as the impossibility of establishing causality and identifying underlying mechanisms. In fact, only manipulative experimental approaches allow the creation of causal connections (Benedetti-Cecchi 2004), helping to understand how these structural diversity components interact to shape the ecosystem functioning of communities (Arenas et al. 2009, Maestre et al. 2012).

In this study, we evaluated the potential interactions between species richness and evenness in driving primary productivity of synthetic macroalgal assemblages. We created artificial macroalgal assemblages and used a modification of the design proposed by Benedetti-Cecchi (2004), which explicitly included diversity and evenness as factors while controlling the effect of identity. Based on previous research, our initial hypotheses were that both evenness and species richness would have positive effects on the assemblages' performance, with potential interactions between both factors, basically resulting from strong identity effects. We expected highly productive species to drive the response of assemblages predominantly in those assemblages with low evenness levels as a consequence of the dominance of these highly productive species. Functional diversity indices aim to better summarize the extent of functional differences in a community (Ricotta 2005) and thus should have a closer relationship to the produc-

tivity of the assemblages than other diversity descriptors such as species richness. Thus, to further explore the potential relationship between the different components of diversity and productivity, we also examined the relationships between several functional diversity and identity descriptors and the productivity proxies of the assemblages.

MATERIALS AND METHODS

We conducted an experiment using artificial assemblages made with 8 species of macroalgae collected in coastal areas of northern Portugal. Four brown seaweeds: *Stypocaulon scoparium* (Linnaeus) Kützing, *Bifurcaria bifurcata* R. Ross, *Fucus vesiculosus* Linnaeus, *Sargassum muticum* (Yendo) Fensholt, and 4 red seaweeds: *Chondracanthus acicularis* (Roth) Fredericq, *Mastocarpus stellatus* (Stackhouse) Guiry, *Chondracanthus teedei* (Mertens ex Roth) Kützing, and *Osmundea pinnatifida* (Hudson) Stackhouse were used. All of these species are abundant, perennial seaweeds at the collection sites, represent different morphologies and are suitable for the manipulation procedures used to create the synthetic assemblages.

Algal fronds were collected in April and May 2013 from rocky shores at Praia Norte, (41° 41′ 27″ N, 8° 50′ 57″ W) and Praia de Moledo (41° 50′ 22″ N, 8° 52′ 30″ W), Portugal. Both sites are exposed rocky intertidal shores with large granite and slate platforms and abundant rock-pools. They have a semi-diurnal tidal regime, with the largest tidal range close to 4 m during spring tides. At the collection dates, healthy fronds from the 8 different target species were cut or scraped from the rock and transferred to the laboratory in plastic bags and cool boxes. Once in the laboratory, seaweeds were sorted by species and rinsed in a bath of freshwater (about 30 s) to remove herbivores (Arenas et al. 2009). Fronds were then placed in separate, continuously aerated 80 l seawater tanks.

Our experiment was designed to examine the relationships between 3 different components of diversity (species richness, species identity and evenness) with several proxies of primary productivity as indicators of community performance. We used a 3-factor mixed experimental design, adapting the design proposed by Benedetti-Cecchi (2004) (Fig. 1). We considered the 3 components of diversity cited above as factors of the experimental design: (1) species richness (SR) as a fixed factor with 2 levels (2 or 4 species), (2) evenness (Ev) as a fixed factor with 2 levels (low and high) and (3) identity (Id) as a random factor
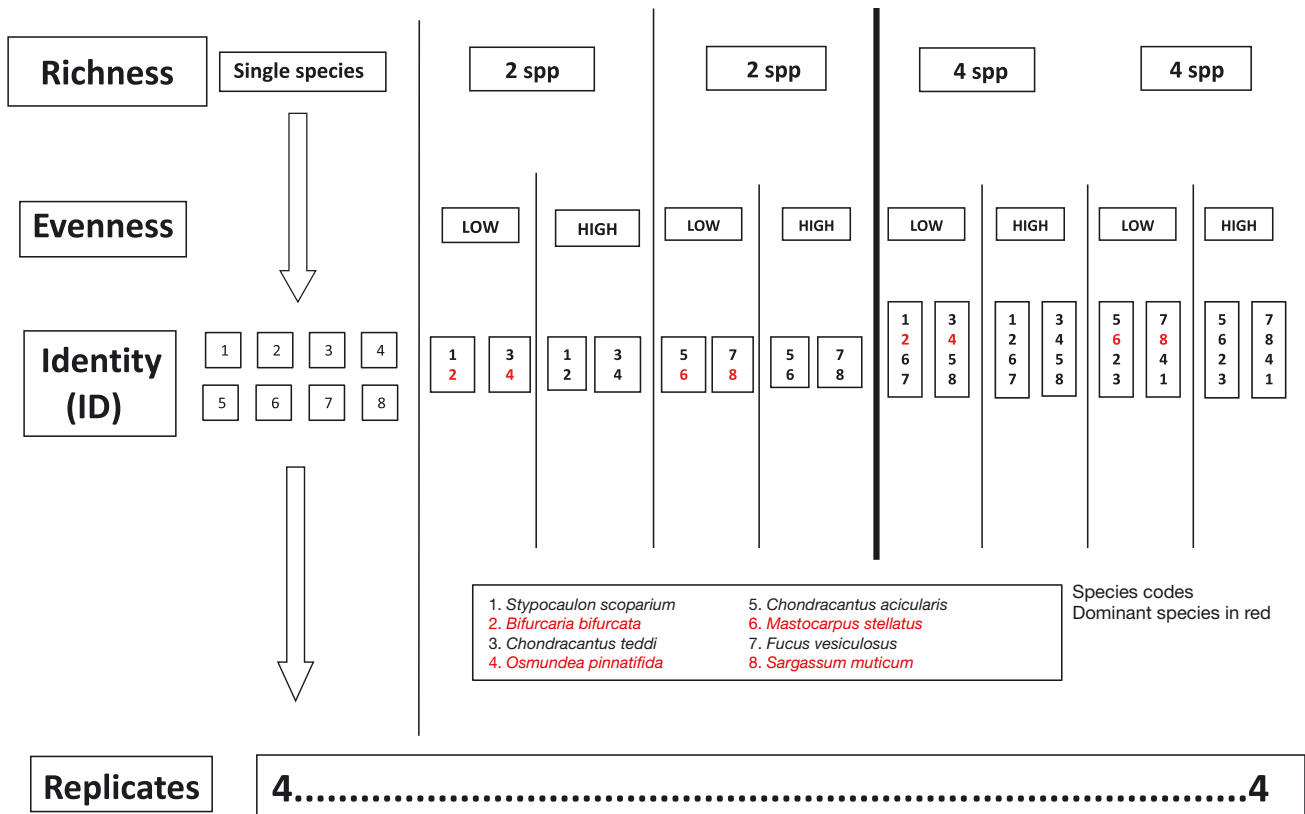
Adapted from Benedetti-Cecchi (2004)

Fig. 1. Experimental design used to disentangle the effects of species richness, identity and evenness (distribution of biomass) using assemblages built with 8 macroalgal species. Species that occur at a high richness level also occur in treatments with low richness treatments. Dominant species in the low evenness treatments are in red

nested in diversity with 4 levels, i.e. we included 4 different combinations of 2 and 4 species (ID1, ID2, ID3, ID4; Fig. 1). Species were randomly selected from our species pool to create the 2 assemblages; 2 additional random species were then added to those initial ones to produce the 4 species assemblages. Identities were (1) ID1, including the species *S. scoparium* and *B. bifurcata* in the 2-species richness treatment along with 2 more species, randomly selected from the pool, in the 4-species richness treatment (*F. vesiculosus* and *S. muticum*); (2) ID2, including the species *C. teedei* and *O. pinnatifida* in the 2-species richness treatment and 2 more species in the 4-species richness treatment (*C. acicularis* and *S. muticum*), (3) ID3, with *C. acicularis* and *M. stellatus* in the 2-species richness treatment and *B. bifurcata* and *C. teedei* in the 4-species assemblages and (4) ID4, which included the species *F. vesiculosus* and *S. muticum* in the 2-species richness treatment; *O. pinnatifida* and *S. scoparium* completed the 4 species required for the high diversity treatment. In the low species richness assemblage, our design incorpo-

rated all the species from the 4-species richness assemblages, preventing any confounding effects between richness and identity effects (Bulling et al. 2006, Stachowicz et al. 2007). We created 4 replicates per identity assemblage and built a total of 64 multi-species assemblages.

The evenness treatment was implemented by considering 2 different levels of species biomass distribution in the assemblages (i.e. high and low evenness treatments). Thus, high evenness had equal amount of biomass per species in the assemblage, while low evenness had a 'dominant' species with higher biomass than the other species in the assemblage. Dominant species, randomly selected from the species pool, were *B. bifurcata*, *O. pinnatifida*, *M. stellatus* and *S. muticum*. In the 2-species assemblages and low evenness treatment, the dominant species included 75 g fresh weight (FW) biomass and the non-dominant, 25 g FW, resulting in a Pielou's evenness index of 0.80 ± 0.003 (n = 16). In 2-species assemblages with high evenness, each species was represented by 50 g of FW biomass with a Pielou's

evenness index of 0.99 ± 0.0001 (n = 16). A similar biomass distribution was done in the case of the 4-species assemblage – low evenness treatment; the dominant species contributed 62.5 g FW and the other 3 species 12.5 g FW each, with Pielou's evenness index of 0.77 ± 0.003 (n = 16). Finally, in the case of the high evenness treatment, each species included 25 g FW, with Pielou's evenness index of 0.99 ± 0.0001 (n = 16). Wet weights were estimated after removing excess water from the algae using a salad spinner and a dry cloth (Bruno et al. 2005). Balance precision was ±0.01 g.

Additionally, we built single species assemblages for each of the 8 seaweed species used in the experiment. These assemblages, with 4 replicates per species, allowed us to examine the existence of overyielding, i.e. increased productivity in species mixtures relative to monocultures (Hooper & Dukes 2003). A total of 96 assemblages were created for the experiment (Fig. 1).

To assemble the 96 synthetic communities, each with an area of 196 cm^2, we used the collected seaweed (see above). Small groups of fronds were secured with small cable ties to a 5 mm plastic mesh, keeping the fronds upright. Groups of fronds were regularly distributed throughout the mesh with a distance among groups of around 2 cm. Overall biomass in the assemblages was 100 g FW of seaweeds, which was within the range of biomass found in rock-pools with erect seaweeds at the collection sites (authors' pers. obs.). Seaweeds and mesh were then secured to PVC plates to increase strength and ensure negative buoyancy. Once constructed, the assemblages were submerged in four 600 l (40 cm depth) outdoor tanks filled with filtered seawater (salinity ~35‰) with continuous aeration to create turbulence. Plates were haphazardly rearranged between tanks twice per week to prevent any tank or position effect. The temperature of the seawater in the tanks was controlled at 16°C using Aqua Medic® Titan 2000 cooler units. To avoid nutrient limitation, seawater was enriched every 2 d by adding inorganic nitrogen (NaNO$_3$) and phosphorus (NaH$_3$PO$_4$) to a final concentration of approx. 50 µM N and 5 µM P, respectively. Salinity was regularly monitored and tanks were regularly refilled with freshwater to compensate for water evaporation.

Incubation procedures and ecosystem functioning surrogates

To allow some adjustment of the seaweeds within the assemblages, the incubations were carried out 2 wk after their construction. Incubations were performed sequentially in the same order that the plates were assembled. Productivity–irradiance (P–I) curves were estimated by measuring oxygen fluxes within incubation chambers at 7 successive irradiance intensities (0 µmol photons m^{-2} s^{-1} [dark period], 24, 164, 262, 345, 417 and 1578 µmol photons m^{-2} s^{-1}). Maximum irradiance levels in the chamber were lower than those recorded in the field at sea surface level where, during sunny days in winter, irradiance can reach around 2000 µmol photons m^{-2} s^{-1} (Arenas et al. 2009, authors' pers. obs. using a scalar quantum sensor). The light source in the chamber was composed of 64 fluorescent tubes, 30 W (Osram L® 965 Biolux). Irradiance inside the chamber was measured using a photosynthetically active radiation (PAR) sensor (Walz® ULM500 Universal Light Meter). For each P–I incubation, the successive irradiance periods lasted around 20 min, the time necessary for the fluorescent tubes to warm up and the assemblages to reach linear rates of oxygen flux (Migné et al. 2002). Timing of the light system was controlled using Aqua Medic® AT Control System controllers. The entire set of incubations took around 2 h 30 min per assemblage. The incubation chambers consisted of 12.5 l sealed Plexiglas chambers partially submersed in a larger, temperature-controlled cooling tank. Mean temperature inside the incubation chamber was 16.5 ± 0.06°C. We used 1 µm-filtered seawater, and the water movement inside the incubation chambers was maintained through a submersible pump (300 l h^{-1}) equipped with diffusers to reduce turbulence. Changes in oxygen concentration through time were measured using a luminescent dissolved oxygen probe connected to a data-logger (Hach® HQ40) that registered a new measurement every 30 s. To reduce possible effects of circadian rhythms on algal productivity, incubations were always carried out during daylight hours (between 08:00 and 18:00 h). Productivity related measures were estimated through oxygen fluxes by regressing oxygen concentration (µmol O$_2$ l^{-1}) through time (s^{-1}) during dark and light periods of increasing intensities. Estimations were corrected by seawater volume inside the chamber.

The variables respiration (Resp), maximum gross and net primary productivity (GPP, NPP) and photosynthetic efficiency at low light irradiance (α) were used as surrogates for the assemblages' functioning (Arenas et al. 2009). Respiration of the assemblages (mg O$_2$ assemblage^{-1} h^{-1}) and NPP (mg O$_2$ assemblage^{-1} h^{-1}) were estimated from oxygen fluxes at

different irradiance intensities (dark period for respiration rates). Both variables were calculated by plotting oxygen concentration over incubation time and fitting a linear regression line to calculate rates of oxygen change. α (mg O_2 assemblage^{-1} h^{-1} / μmol photons m^{-2} s^{-1}) was estimated as the slope of the *P–I* relationship at light-limited irradiances through linear regressions. GPP was calculated as the sum of NPP and the absolute value of respiration (i.e. |Resp|) (Migné et al. 2002).

Overyielding, assemblages' functional identity and diversity calculations

The relative performance of mixtures versus monospecific assemblages for each response variable was examined using log response ratios (LRR) as ln(*O/E*), where *O* is the observed response value and *E* is the expected value (Orwin et al. 2014, Matias et al. 2015). Expected values were calculated based on monoculture responses and the relative proportion of each species within the mixed communities. This ratio is an indicator of overyielding, and reveals whether the functioning of a given mixture differs from the expected functioning based on the performance of the constituent species in monospecific assemblages. Thus, if LRR > 0, there is a positive diversity effect, whereas if LRR < 0 there is a negative diversity effect. Our experiment used a substitutive design since the biomass in the assemblages was always the same irrespective of the richness and evenness treatments. Thus, the overyielding indices were always calculated in this substitutive setting.

To functionally characterize each species and estimate different functional indices for each assemblage, we used a similar procedure to that used by Griffin et al. (2009) for seaweeds. For all species, 4 functional traits related to photosynthesis and resource use were measured: (1) specific thallus area (STA), expressed in mm^2 mg^{-1}; (2) thallus dry mass content (TDMC) in mg g^{-1}; (3) thallus thickness (TT) in mm; and (4) a proxy for vertical space use, i.e. frond length (VS). Measures were made on 10 fronds, identical to those used to build the assemblages and collected from the same sites.

Functional diversity indices aim to better summarize the extent of functional differences in a species pool (Ricotta 2005), and thus should have a closer relationship to the productivity of the assemblages than other diversity descriptors like species richness. Several functional indices have been proposed by researchers in the last several years (see Petchey & Gaston 2002, Laliberté & Legendre 2010, Ricotta & Moretti 2011). Thus, we calculated the functional diversity index (FD) from Petchey & Gaston (2002), defined by the authors as the total branch length of a functional dendrogram based on Euclidean distances. We also estimated for each assemblage the functional dispersion index (FDis), which measures the dispersion or variation of species traits within an assemblage. This index accounts for species abundance and is unaffected by species richness (Laliberté & Legendre 2010). Finally, we calculated the community-weighted mean (CWM) trait for each assemblage and functional trait. CWMs assess the functional structure of the assemblages using mean trait indices within communities. CWM indices are not actually functional diversity indices, but rather a measure of the dominant trait value within an assemblage, and are calculated as the averaged trait value in the community weighted by the species abundance (Sydenham et al. 2016).

Statistical analyses

Analysis of variance (ANOVA) was used to test the hypotheses that both evenness and species richness have positive and interactive effects on the assemblages' performance. Changes in GPP, NPP, Resp and α were analyzed using a 3-factor nested ANOVA. Diversity (2 levels) and evenness (2 levels) were considered fixed and orthogonal factors and identity (4 levels) was considered a random factor nested in diversity. Before each analysis, the homogeneity of variances was evaluated using Cochran's test. Variances were not heterogeneous and data transformation was not necessary. *A posteriori* multiple comparisons were done using Student-Newman-Keuls (SNK) tests ($\alpha = 0.05$). GMAV v.5 for Windows was used for these analyses (Underwood 1997).

To further assess how the traits of each assemblage may define their performance, we followed, in part, the methodological framework proposed by Díaz et al. (2007). Thus, we used pairwise regressions to examine the relationships between the functional traits (i.e. CWMs) and diversity descriptors mentioned above and the different productivity proxies measured in the experimental assemblages. We also examined the potential idiosyncratic effects of the seaweed species by examining the pairwise associations between species abundances and the proxies of productivity. Pairwise analyses were carried out using R (R Core Team 2015).

RESULTS

Functional performance of single-species assemblages

Assemblages with a single species served to characterize the functional performance of each species, and were used for the estimations of the LRRs of multiple species assemblages. All 4 functional parameters estimated throughout incubations (i.e. GPP, NPP, Resp and α) showed significant differences among the species (ANOVA, p < 0.05 in all the response variable models), i.e. identity effects were obvious among the selected species. *Sargassum muticum* had the highest values of GPP, NPP, Resp and light photosynthetic efficiency (i.e. α) compared to all the other species. *Fucus vesiculosus*, *Chondracanthus acicularis* and *Stypocaulon scoparium* exhibited intermediate performances. *Bifurcaria bifurcata* was the seaweed with the lowest overall performance (Fig. 2).

Functional performance of multiple species assemblages: richness, evenness and identity effects

Functional performance of the macroalgal assemblages revealed some significant effects. The consis-

tent effect of seaweed identities on the performance of assemblages was supported by the significant effect of identity for all the functional proxies measured (Table 1). Additionally, the interaction richness × evenness was significant for GPP and marginally not significant for the other 3 functional proxies (p = 0.052, 0.09 and 0.05 for NPP, Resp and α, respectively). This interaction resulted from a positive effect of evenness on gross productivity at low richness treatments but no effects on those assemblages with higher species richness. Similar patterns were found for NPP, Resp and α (Fig. 3).

Functional performance of multiple species assemblages: overyielding

LRR ratios of GPP and NPP were significantly affected by the interaction between species richness and evenness (SR × Ev) and by the identity (Id) predictors (Table 2). The interaction SR × Ev in terms of the overyielding ratios suggested that the effect of evenness varied with diversity levels. Thus at low diversity, higher evenness improved the performance of the assemblages relative to their expected performance from monocultures (Fig. 4), but in as-
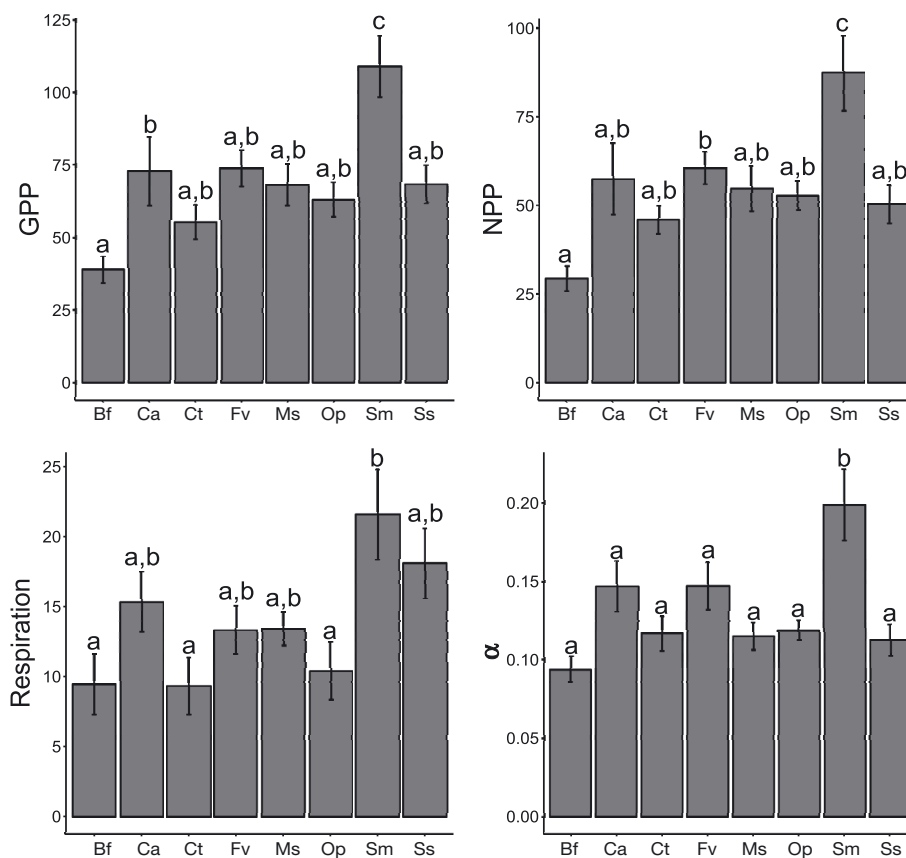

Fig. 2. Mean (+SE; n = 4) (a) gross primary productivity (GPP), (b) net primary productivity (NPP), (c) Respiration and (d) α (photosynthetic efficiency at low intensity levels) for single-species assemblages for the 8 seaweeds used in our experiment. Ss: *Stypocaulon scoparium*; Bb: *Bifurcaria bifurcata*; Ct: *Chondracanthus teedei*; Op: *Osmundea pinnatifida*; Ca: *Chondracanthus acicularis*; Ms: *Mastocarpus stellatus*; Fv: *Fucus vesiculosus*; Sm: *Sargassum muticum*. All measures refer to the whole assemblage. Units for the ordinate *y*-axis (GPP, NPP and Respiration): mg O_2 assemblage^{-1} h^{-1}; for α: mg O_2 assemblage^{-1} h^{-1} / μmol photons m^{-2} s^{-1}

Table 1. Summary of ANOVA analyses of the effects of species richness (SR), evenness (Ev), identity (Id) and their corresponding interactions on gross primary production (GPP), net primary production (NPP), respiration rates (Resp) and photosynthetic efficiency at low intensity levels (α). Numbers in **bold** indicate significant effects (p < 0.05)

Source	df	GPP		NPP		Resp		α	
		F	p	*F*	P	*F*	p	*F*	p
SR	1,6	0.09	0.770	0.06	0.816	0.29	0.606	0.05	0.823
Ev	1,6	2.16	0.191	1.54	0.273	2.6	0.154	1.11	0.336
Id (SR)	6,48	**4.79**	**<0.001**	**4.44**	**0.002**	**2.4**	**0.041**	**3.31**	**0.008**
SR × Ev	1,6	**7.09**	**0.037**	5.82	0.052	4.07	0.090	5.93	0.050
Ev × Id (SR)	6,48	1.52	0.192	1.73	0.135	1.09	0.382	1.97	0.088

semblages with 4 species the effect was negligible. It is worth noting that average LRRs at high diversity were positive, suggesting better productivity than expected from monocultures.

Functional performance of multiple species assemblages: pairwise relationships between continuous metrics

Pairwise analyses showed that neither species richness nor evenness were significant predictors of the assemblages' productivity-related responses or overyielding (i.e. LRR). The same was true for the 2 functional diversity indices examined (FD and FDis). Conversely, CWM indices did explain significant proportions of variation in the functioning of the assemblages, supporting the importance of species trait effects. Thus, assemblages with larger CWM.STA (i.e. larger overall specific thallus area) were more productive. Conversely, assemblages with overall thicker fronds (larger CWM.TT) were less productive (Table 3). In the case of LRR (overyielding in-

dicator), the significant community mean traits predictors were CWM.TDMC (thallus dry mass content) with a positive effect and CWM.VS with a negative effect on the overyielding indices (Table 4).

Furthermore, the presence of certain species seemed to have significant effects on the performance of the assemblages. Particularly intense were the negative effects of *B. bifurcata* and the positive effects of *Chondracanthus teedei* and *S. muticum* on the productivity of the assemblages (Table 3). *S. muticum* effects reversed in the case of overyielding, suggesting negative interactions with the other species. The same occurred with *Fucus vesiculosis* (Table 4).

DISCUSSION

In our experimental study, we examined how several diversity-related traits affected the functional performance of synthetic macroalgal assemblages, using primary productivity as a proxy for ecosystem function. We used an experimental design derived from Benedetti-Cecchi (2004) to separate the influence of species richness, evenness and identity. Additionally, we calculated indices of functional diversity and community mean traits and examined their ability as continuous predictors to estimate the productivity and overyielding indices in the assemblages.

Our findings showed the prevalence of species traits, i.e. identity effects, as the main driver of the performance of the assemblages. Species traits effects
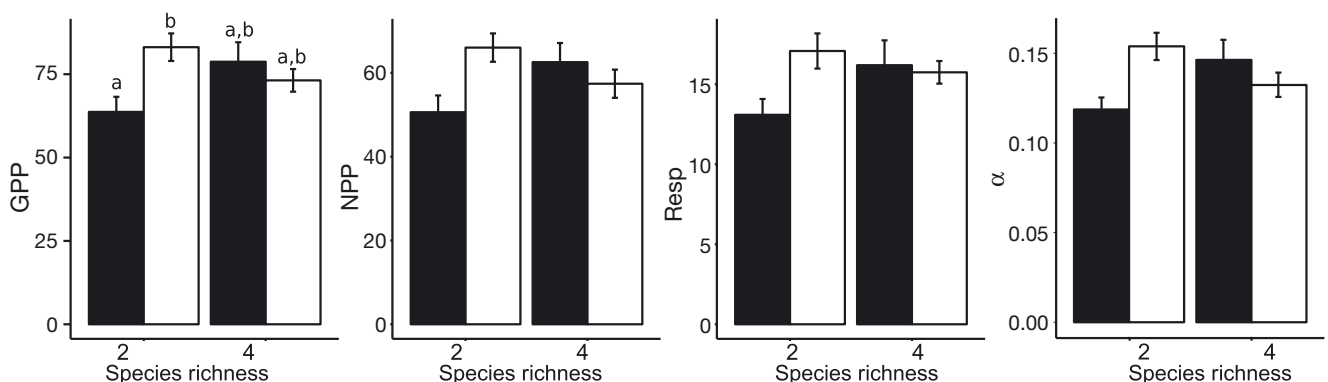

Fig. 3. Mean (+SE; n = 16) values of gross primary productivity (GPP), net primary productivity (NPP), respiration rate (Resp) and photosynthetic efficiency at low intensity levels (α) for each richness and evenness treatment. Filled bars: low evenness treatments; white bars: high evenness treatments. Units are as in Fig. 2. Bars sharing the same letters did not differ in *a posteriori* Student-Newman-Keuls (SNK) test (p > 0.05)

Table 2. Summary of ANOVA analyses of the effects of species richness (SR), evenness (Ev) and identity (Id) on the log response ratios (LRR) for gross primary production (GPP) net primary production (NPP) and respiration rates (Resp) after 15 d of the experiment. Numbers in **bold** indicate significant effects (p < 0.05)

Source	df	LRR GPP		LRR NPP		LRR Resp	
		F	p	F	p	F	p
SR	1, 6	0.03	0.864	0.02	0.893	0.04	0.848
Ev	1, 6	**12.36**	**0.012**	**6.83**	**0.040**	2.31	0.517
Id (SR)	6, 48	**7.23**	**<0.001**	**6.11**	**<0.001**	6.79	**<0.001**
SR × Ev	1, 6	**34.28**	**0.001**	**24.92**	**0.002**	2.20	0.188
Ev × Id (SR)	6, 48	0.31	0.927	0.43	0.855	1.45	0.216

were apparent in the analyses of variance, where the identity factor was significant for all analyses performed. They were also supported by the consistency as significant predictors in the linear models of some community-weighted mean functional traits (i.e. communities' functional identity) and species biomass. Furthermore, and despite the limitations of this type of manipulative experiment (i.e. artificial assemblages, short duration and small spatial scale; Gamfeldt et al. 2015), we found that the effects of species identities were not always additive, and species interactions partially modified their functional performance when coexisting in a community. Thus, relative species abundance (evenness) promoted productivity in low diversity treatments but not in high diversity treatments.

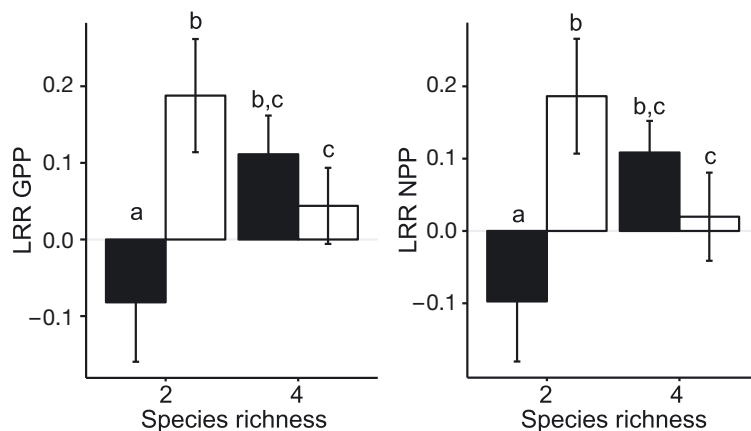The confirmation that species identity and the functional identity (i.e. CWMs) explained a larger proportion of variation in community productivity than species richness and functional diversity supports the general consensus that ecosystem processes are governed by functional traits of species (i.e. identity) and dominance effects (Roscher et al. 2012, Enquist et al. 2015). Hence, the results are largely in agreement with Grime's Mass Ratio Hypothesis (MRH). The MRH states that ecosystem functioning is determined by the characteristics or traits of the dominant (largest biomass) species (Grime 1998). In a removal experiment performed in 3 different marine systems (including macroalgal communities), Davies et al. (2011) found that the functional contribution of species was directly proportional to their contribution to community biomass in a 1:1 ratio. This relationship was consistent across the 3 marine ecosystems examined and 3 ecosystem processes measured (gross primary productivity, nutrient uptake and filtration rate). We also found evidence of biomass effects, but always mediated by species traits. Only in some species was biomass significantly related to assemblages' performance, suggesting the preponderance of species traits effects.

In fact, strong species traits effects are a frequent outcome of biodiversity-functioning experiments, particularly those performed at small local spatiotemporal scales (Cardinale et al. 2006). Previous research on seaweed assemblages also found strong species identity effects (Bruno et al. 2005, 2006, Griffin et al. 2009). In our study, for example, assemblages including the brown seaweed *Sargassum muticum* generally showed high productivity and respiration ratios with increasing effects at higher biomasses. This species was also the best-performing species in the experiments carried out by Griffin et al. (2009). The effect of this species was opposite regarding the LRR ratio for two of the productivity proxies, suggesting the existence of negative interactions with other species. Interestingly, *S. muticum* is a Japanese invasive species in the European Atlantic shores and in certain areas the species has displaced the very abundant native *Bifurcaria bifurcata*, severely modifying primary productivity patterns in invaded areas (Vaz-Pinto et al. 2014). Not surprisingly, *B. bifurcata* was the species with lower overall performance in our experience. Thus, our assemblages seem to mimic patterns that have already been described in other studies from natural systems. Species traits or identity ef-

Fig. 4. Mean (+SE; n = 16) values of log response ratios for gross primary productivity (LRR GPP) and net primary productivity (LRR NPP) for each richness and evenness treatment. Filled bars: low evenness treatments; white bars: high evenness treatments. Bars sharing the same letters did not differ in *a posteriori* Student-Newman-Keuls (SNK) test (p > 0.05)

Table 3. Slope parameter estimations of the pairwise relationships (OLS) between species richness (SR), evenness (Ev), functional diversity and functional dispersion (FD and FDis), community-weighted mean traits (CWM) for specific thallus area (STA), thallus dry mass content (TDMC), thallus thickness (TT) and frond length (VS) (CWM.STA, CWM.TDMC, CWM.TT and CWM.VS) and abundance of the different species with the different proxies of assemblages functioning used in our study (gross primary production, GPP; net primary production, NPP; Respiration, Resp; and photosynthetic efficiency at low intensity levels, Alpha). Positive and negative symbols reflect the sign of the effect. *p < 0.05; **p < 0.01; ***p < 0.001. Significant predictors are in **bold**

Predictors	GPP	NPP	Resp	α
SR	1.27	0.83	−0.44	0.001
Ev	29.09	21.95	−7.14	0.04
FD	−5.81	−4.89	0.99	−0.008
FDis	−4.33	−3.15	−1.18	−0.005
CWM.STA	**29.05****	**21.48***	**7.56****	0.03
CWM.TDMC	2.01	3.25	−1.11	0.006
CWM.TT	**−40.1****	**−30.6***	**−9.58****	**−0.05***
CWM.VS	7.36	8.36	−1.00	0.01
S. scoparium biomass	−0.2	−0.15	−0.04	0.0008
B. bifurcata biomass	**−0.31*****	**−0.25***	**−0.06****	0.0008
C. teedei biomass	**0.42****	**0.33***	**0.09***	**0.006***
O. pinnatifida biomass	0.18	0.12	**0.05***	0.0002
C. acicularis biomass	−0.07	−0.06	−0.008	0.00006
M. stellatus biomass	−0.18	−0.15	−0.008	−0.0003
F. vesiculosis biomass	0.13	0.11	0.02	0.0002
S. muticum biomass	**0.24****	**0.22****	0.02	**0.0004***

Table 4. Slope parameter estimations of the pairwise relationships (OLS) between species richness (SR), evenness (Ev), functional diversity and dispersion (FD and FDis), community-weighted mean traits and abundance of the different species with the log response ratios (LRR) for the productivity proxies GPP, NPP and Resp. Positive and negative symbols reflect the sign of the effect. *p < 0.05; **p < 0.01; ***p < 0.001. Significant predictors are in **bold**; abbreviations and genus names as in Table 3

Predictors	LRR GPP	LRR NPP	LRR Resp
SR	0.028	0.009	−0.01
Ev	0.39	0.38	−0.48
FD	0.03	0.07	0.13
FDis	0.06	0.09	0.10
CW.STA	−0.02	−0.16	**−0.59****
CWM.TDMC	**−0.40****	**−0.34***	**0.66****
CWM.TT	0.19	0.33	0.47
CWM.VS	**−0.39****	**−0.33***	**0.7*****
S. scoparium biomass	0.002	0.004	0.003
B. bifurcata biomass	0.002	**0.003***	0.002
C. teedei biomass	**0.008*****	**0.007****	**−0.013****
O. pinnatifida biomass	0.002	0.001	**−0.006*****
C. acicularis biomass	−0.001	−0.001	−0.0005
M. stellatus biomass	−0.001	−0.001	0.0008
F. vesiculosis biomass	−0.005	**−0.005***	**0.006***
S. muticum biomass	−0.004	**−0.003****	**0.004****

fects have also been identified as very relevant when considering other community-level processes in macroalgal assemblages such as resistance to invasion (Arenas et al. 2006, Vaz-Pinto et al. 2014).

In addition to the preponderance of traits or identity effects, our experiment revealed the existence of other diversity-related effects. Thus, we found a positive effect of evenness on the productivity of assemblages in low diversity treatments, but this effect was absent at high diversity. Positive effects of evenness on primary production in terrestrial systems have been recorded in several experimental studies (Stevens & Carson 2001, Kirwan et al. 2007), although dominance by large species may alter this effect (Mulder et al. 2004, Orwin et al. 2014). In marine studies, evenness has also been suggested as a potential mechanism promoting primary productivity in natural seaweed communities (Arenas et al. 2009). However, our study is among the first to experimentally examine species richness and evenness using seaweed assemblages (see also Lemieux & Cusson 2014). The mechanisms behind the positive effect of evenness could be the enhancement of resource use complementarity with increasing evenness, boosting ecosystem performance (Polley et al. 2007) and generating positive overyielding indices. The intensity of evenness effects could be stronger in low diversity treatments because when the assemblages are built with few species, the dominance of a single species may largely reduce the relevance of potential complementary interactions among the few remaining non-dominant species.

We did not find strong evidence supporting the positive effects of richness, but obviously it should not be ruled out as a driver. Short term experiments like our study frequently fail to find species richness effects (van Ruijven & Berendse 2005, Cardinale et al. 2007). In out experiment, we did not use a large richness gradient, and when doubling the number of species in the assemblages (i.e. from 2 to 4 spp.), GPP only increased by around 3% (average GGP for 2 spp. = 73.41 ± 3.48 mg O_2 h^{-1}, 4 spp. = 75.95 ± 3.36 mg O_2 h^{-1}; n = 32). This effect seems far from the estimated effect of richness found in the literature. In a recent review, Hooper et al. (2012) estimated that a 50% species loss would mean a reduction in biomass production of around 13%. If we consider assemblages with only one functional group, our results were closer to the findings reported by Hooper et al.

(2012). Thus, including single species assemblages, the average GPP in monospecific assemblages was 68.69 ± 4.11 mg O_2 h^{-1}, i.e. a value almost 10 % lower than the high diversity assemblage. Bruno et al. (2005) found that relative yields in multispecies assemblages of seaweeds were 13 % greater than monocultures, but results were not significant. Furthermore, in our study, species richness effects were always positive as suggested by the sign of the LRR ratios, except in the case of low richness and evenness treatments.

In the literature it is possible to find experiments reporting positive effects of species richness on the performance of macroalgal assemblages irrespective of the response measured. Middelboe & Binzer (2004) found positive effects of richness on macroalgal photosynthetic rates. Bruno et al. (2005, 2006) reported higher biomass accumulation in richer assemblages and Bracken & Stachowicz (2006) noticed positive richness effects on community nutrient uptake. However, whenever the experimental design allowed disentangling the mechanisms behind the positive relationship, species traits (i.e. identity effects) were identified as the dominant effect (Bruno et al. 2006).

The approach used in this study allowed us to create the experimental treatments required to examine direct additive and synergistic effects of species richness, evenness and community traits on the productivity of marine macroalgae assemblages. These direct and interactive effects are almost impossible to examine in natural assemblages. Furthermore, observational studies cannot establish causality among drivers and effects. The type of experimental approach applied here generally suffers from a lack of strict realism, but it does provide tests for specific predictions. Our approach was able to detect some of the interactive effects of species richness and evenness suggested in the literature. However, the intensity of these effects was overridden by the strong effects of species functional traits. To fully understand the role of biodiversity on the ecosystem functioning of natural communities, future studies should explicitly consider manipulations of species' relative abundances and densities, mimicking the distribution of species in natural communities. Also, next generation experiments should examine the role of diversity-generating and coexistence mechanisms on the functioning of systems at multiple trophic levels. Such research is essential for more realistically predicting the functional consequences of species extinctions in natural communities.

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