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Expanded view of the local–regional richness relationship by incorporating functional richness and time: a large-scale perspective

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ABSTRACT

Aim We investigate the relationship between local and regional richness in marine fouling assemblages using an expanded and globally replicated approach by incorporating two dimensions of diversity (taxonomic and functional) and different successional stages.

Location Global.

Methods In eight different biogeographic regions (Australia, Brazil, Chile, England, Italy, Japan, Portugal and Sweden) 68 polyvinylchloride (PVC) panels (15 × 15 × 0.3 cm) were deployed for colonization. Communities colonizing panels were analysed by measuring percentage cover at each of four different successional ages: 2, 4, 6 and 8 months. Local richness was assessed as the average number of species and functional groups (FGs) per panel and regional richness was evaluated as the estimated (Jack2) asymptote of the sample-accumulation curves for species and FG on experimental panels.

Results We found that the shape of the relationship between local and regional richness depended on successional stage and the type of richness considered, i.e. taxonomic or functional richness. Hardly any relationship was detectable between local taxonomic richness and regional taxonomic richness at any successional stage. In contrast, the relation between local functional and regional functional richness shows a unimodal pattern of change during succession, passing through the stages ‘independent’, ‘unsaturated rising’, ‘saturated rising’ and once again ‘independent’.

Main conclusions The relationship between local and regional richness, whether taxonomic or functional, frequently displays independence of the two scales, particularly in early and late phases of the successional process.

Keywords

Fouling assemblages, functional richness, jackknife estimator, spatial scales, species richness, saturation, succession.

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INTRODUCTION

The number of species in one location has been reported to depend on both local and regional processes (Ricklefs, 1987; Caley & Schluter, 1997; Ricklefs, 2004; Shurin & Srivastava, 2005). Plots of local species richness against regional species richness have been used to compare the presumed contributions of local processes (e.g. disturbance, competition) and regional factors (e.g. speciation, migration) on local assemblages (e.g.

Cornell & Lawton, 1992; Hillebrand & Blenckner, 2002; Witman *et al.*, 2004; Freestone & Harrison, 2006; Russell *et al.*, 2006; Cornell *et al.*, 2008). Theoretically, if regional species richness drives local species richness, a positive and linear relationship is expected, and we would expect more species to coexist in a given area or volume in more species-rich regions. Such local communities are referred to as ‘unsaturated’ or ‘type I’. In contrast, if local species richness levels off at intermediate regional richness because of local limitation and does not increase further with

increasing regional richness, such communities are referred to as 'saturated' or 'type II' (Cornell, 1985; Cornell & Lawton, 1992). 'Type I' communities have been reported more frequently, suggesting that the regional availability of species controls the number of species in local communities (see reviews by Lawton, 1999; Srivastava, 1999; Shurin & Srivastava, 2005). In the context of the progressive loss of global biodiversity, we would expect that the ongoing regional biodiversity loss would be accompanied by an impoverishment of local communities. In contrast, if the relationship were saturated, local communities could be affected only below a certain threshold of regional richness or by species composition and turnover.

In recent years, the use of the local–regional richness plots to examine species saturation has been criticized for various reasons including statistical issues, the relative size of the local and regional spatial scales and theoretical problems with the interpretation of the shape of the plots (Srivastava, 1999; Hillebrand & Blenckner, 2002; He *et al.*, 2005; Hillebrand, 2005; Shurin & Srivastava, 2005). As a consequence, several of these pitfalls have been addressed and suggestions to improve the analysis of the local–regional richness relationship have been made (Harrison & Cornell, 2008). One of the statistical problems arises when local diversity is underestimated and/or regional diversity overestimated, a phenomenon identified as *pseudosaturation* (Cornell, 1993; Srivastava, 1999). The underestimation of true local richness can be corrected using indices that take into account the presence/absence of infrequent species (e.g. nonparametric estimators), and regional overestimation can be avoided by including in regional richness only those species capable of recruiting into the local habitat (Harrison & Cornell, 2008). Moreover, the relationship between local and regional species richness was recognized to be sensitive to the definition of the two spatial scales (Hillebrand & Blenckner, 2002). If the area of the local habitat is large compared to the area of the region, the majority of species in the regional pool would also be present in the local community, producing linear relationships caused by autocorrelation between the two scales (Hillebrand & Blenckner, 2002). This problem can be avoided using independent data sets to measure local and regional richness (Srivastava, 1999) as well as by selecting scales for sampling local richness that are sufficiently small, to reduce internal environmental heterogeneity (Harrison & Cornell, 2008).

In view of the fact that the number of species coexisting in a limited area or volume of habitat may be affected by factors other than competition or predation and that the relationship may, on theoretical grounds, be expected to change during succession of a community (community assembly time; Mouquet *et al.*, 2003) or with functional diversity, several authors (Russell *et al.*, 2006; Cornell *et al.*, 2008) have recently cautioned that the plotted relationship alone should be used rather as a starting point for more thorough investigations.

To date, numerous studies have addressed the relationship between local and regional richness in different habitats, taxonomic groups and spatial scales (see Srivastava, 1999; Hillebrand & Blenckner, 2002). However, only a limited number of

theoretical and observational studies have explored whether this pattern changes in the course of community assembly (Mouquet *et al.*, 2003; Munguia, 2004; Starzomski *et al.*, 2008). In their theoretical model (2003), Mouquet *et al.* predicted 'saturation' at early stages of the assembly process as the typically low number of early colonizers represents only a small subset of the regional species pool. At intermediate stages of assembly time, when competition has not yet reduced the number of coexisting species, a positive linear relationship is expected. Finally, when communities are at competitive equilibrium, competitive exclusion produces a curvilinear relationship (Mouquet *et al.*, 2003). In a succession survey of marine benthic communities on pen shells in independent regions of St Joe Bay in Florida, Munguia (2004) showed that both motile and sessile species richness increased over time. In addition, the local–regional species richness plots changed shape through time: motile species exhibited saturation while sessile species showed an unsaturated pattern. The author further suggested that the level of species saturation should depend on the successional stage of a community (Munguia, 2004).

The significance of function has been recognized for the relationship between diversity and ecosystem functioning and sustainability (Hooper & Dukes, 2004; Petchey *et al.*, 2004). Functional characterization based on several ecologically relevant criteria as done in the present study better describes the ecological dissimilarity between species. Species, which are functionally more similar with regard to limiting resources, should compete more intensely. Therefore, several authors have recommended using functional richness in diversity studies instead of or in addition to taxonomic richness (e.g. Hooper *et al.*, 2005; Arenas *et al.*, 2006; Britton-Simmons, 2006; Raffaelli, 2006; Poos *et al.*, 2009; Valdivia *et al.*, 2009). If the number of coexisting forms (species or functional groups, FGs) is to some degree controlled by interactions within the community, the relationship between local and regional richness should be more meaningful when using functional richness instead of species richness, because the former more closely defines ecological roles. Thus, with increasing regional species richness, the probability arises that two recruits belong to different species. But only when regional functional richness increases in parallel with regional species richness does the probability arise that two recruits belong to different FGs and have a greater chance to coexist (Micheli & Halpern, 2005).

Local–regional richness relationships at a global scale were studied by Witman *et al.* (2004) for epifaunal invertebrate assemblages. To test for saturation, they estimated the slopes of this relationship in a log–log analysis. A steady rise of local species richness with increasing regional species richness is indicated by a slope of 1 in a log–log plot, while local saturation (an asymptote) shows a slope significantly smaller than 1 (Witman *et al.*, 2004). They found that the slopes did not differ from 1, indicating that the number of species coexisting in local communities was not limited (i.e. 'type I' community). However, Witman *et al.* (2004) did not test the local–regional relationship for functional diversity or at different successional stages as we do here.

In the present study, we report a large-scale experiment using marine hard-bottom assemblages colonizing and growing on highly replicated artificial substrates in eight different biogeographic regions. At four different successional ages we quantified the number and relative abundance of all sessile species present in our experimental units, the availability of resources (measured as percentage cover of unoccupied substratum) and functional richness. We used this information to address the following questions. (1) Does the relationship between local and regional species richness in fouling assemblages display a linear or curvilinear shape at a global scale? (2) Is this relationship sensitive to community assembly time (i.e. successional stage)? (3) Does local functional richness relate to regional functional richness in a similar way as local species richness relates to regional species richness? (4) Is the diversity of local communities affected by parameters other than regional richness, such as number of FGs or availability of resources?

MATERIALS AND METHODS

Study system and definition of spatial scales

To analyse the relationship between local and regional diversity during the succession process of fouling assemblages, we use

data from a modular global experiment – Global Approach by Modular Experiments (GAME, 2000) – performed during 2003 and 2005 in eight different biogeographic regions (Fig. 1; more detailed methods can be found in Sugden *et al.*, 2008, and Canning-Clode *et al.*, 2008a, for example). In each region, 68 polyvinylchloride (PVC) panels ($15 \times 15 \times 0.3$ cm) distributed in 12 moorings were submerged for colonization for an 8-month period. Each mooring consisted of a ground weight and a buoy that held a ring (60 cm diameter) made from stripes of grey PVC ($210 \times 25 \times 0.4$ cm) at a water depth of approximately 0.5 m. The panel size used on our system did not restrict the number of individuals so severely that saturation could result simply from limits on the number of individuals. The minimum distance between rings was 5 m. Panels were mechanically disturbed (removal of biomass from a randomly selected 20% of the panel area) at seven different frequencies: undisturbed (control) and disturbed every second, fourth, sixth, eighth, tenth and twelfth week. This disturbance regime was intended to span the typical range of locally occurring natural disturbances (e.g. grazing, predation) and to allow new species to recruit at all times. Communities colonizing all experimental units were analysed by measuring the percentage cover of each sessile species > 1 mm diameter at each of four different successional ages: 2, 4, 6 and 8 months. Total percentage cover could



Figure 1 Location of the sampling sites used for species and functional richness in fouling assemblages. Region codes are as follows: Aus, Australia ($35^{\circ}36' S$, $138^{\circ}35' E$); Bra, Brazil ($22^{\circ}02' S$, $43^{\circ}08' W$); Chi, Chile ($29^{\circ}58' S$, $71^{\circ}22' W$); Eng, England ($54^{\circ}41' N$, $01^{\circ}12' W$); Ita, Italy ($43^{\circ}30' N$, $10^{\circ}20' E$); Jap, Japan ($38^{\circ}20' N$, $141^{\circ}05' E$); Por, Portugal ($32^{\circ}38' N$, $16^{\circ}53' W$); Swe, Sweden ($58^{\circ}52' N$, $11^{\circ}08' E$).

exceed 100% in case of multi-strata growth. In addition, the percentage cover of unoccupied substratum ('availability of resources') was recorded. Local species richness in a given region was assessed at each successional age as the average species number on the undisturbed panels ($n = 8$).

In the present study, we assessed regional species richness as the total number of species observed on any panel, disturbed and undisturbed, during any of the four surveys within each of the eight regions. Undisturbed panels used for the regional richness assessment were not considered for the local analysis. We used the entire range of disturbance frequencies in order to 'sample' the regional pool as completely as possible. For each of the four surveys, 15 randomly chosen panels were assessed ($n = 15 + 15 + 15 + 15 = 60$). Each panel was only used once to avoid carry-over effects between surveys. In this way, we obtained the number of regional species colonizing a given substrate at the given depth at any time during the experiment. Regional species richness was estimated as the asymptote of the species accumulation curves using the second-order jackknife estimator (Jack2; Smith & Van Belle, 1984) which was identified as the best performing estimator (Canning-Clode *et al.*, 2008b). This nonparametric estimator takes into account the distribution of species amongst samples, i.e. considers both the number of species found in one sample only ('infrequent species') and in exactly two samples. Species accumulation curves were generated from 999 permutations of the 60 panels reserved for this estimation in each region using PRIMER software (Clarke & Gorley, 2006). To avoid autocorrelation between local and regional scales, panels used for taxonomic local richness assessment were not considered for the regional species pool.

Functional richness description

FGs comprise all species that share traits linked to ecological functions (Raghukumar & Anil, 2003), and are normally defined according to the way in which they use and compete for resources (Arenas *et al.*, 2006). In the present study, FGs were classified using five traits that we considered the most relevant to competition in fouling communities (see Table 1, Wahl, 2009) and that comprise a subsample of the traits suggested by Bremner *et al.* (2006). As our study focuses only on sessile hard-bottom assemblages on suspended substrates, only the 'attached' type in the trait category 'motility' and all species recruited via water-borne propagules were considered. After recruitment, the capacity for asexual reproduction ('modularity'), 'body size' and

'growth form' determined how the physical space a given organism occupies (and exploits) is shaped. Which energy resources are exploited within this physical space (and the water body passing through it) was identified by the trait 'trophic type'. All of the sessile species in these fouling communities may compete for substrate space when cumulative cover approaches or exceeds 100% at some advanced stage of community assembly. In addition, they may compete for light, nutrients and dissolved or particulate organic matter. Additional interactions such as allelopathy or attraction/repulsion of shared consumers are possible but were not considered here. Species were allocated to FGs based upon the five traits exhibited by the adult stages. We did not consider ontogenetic shifts of functional traits since larvae and juveniles constituted a relatively small portion of the individuals. In the fouling communities of this study the following five traits were considered: body size (small, medium, large, very large), growth form (encrusting, massive, bushy, filamentous), trophic type (autotroph, suspension feeder, deposit feeder), modularity (solitary, colonial) and motility (attached), which could theoretically produce $4 \times 4 \times 3 \times 2 \times 1 = 96$ FGs. Functional richness (local and regional) was assessed in the same way as taxonomic richness.

Statistical analysis

'Type I' and 'type II' curves were differentiated by regressing log local diversity ('dependent') against log regional diversity ('independent') (in terms of both taxonomic and functional diversity). The slope (b) of this regression indicates the degree of curvilinearity of the relationship. Linear plots (unsaturated relationships) are represented by a slope of 1 while local saturation is represented by a slope significantly < 1 but > 0 (Griffiths, 1997). Complete independence of local richness from regional richness should result in a slope = 0. For statistical grounds, and because the correct outline of a saturation function has not been theoretically defined, this method seems superior to the common linear and nonlinear regressions and has been used before (e.g. Griffiths, 1997; Witman *et al.*, 2004). Its slope can be used for more consistent meta-analytical comparisons (Hillebrand & Blenckner, 2002).

To examine the effects of open space (OS) and both regional richness measures on local taxonomic richness (LTR) and local functional richness (LFR), we used multi-level generalized linear models (i.e. generalized linear mixed models) in order to account for the hierarchical structure of the data (i.e. plate

Trait 1	Trait 2	Trait 3	Trait 4	Trait 5
Body size	Growth form	Trophic type	Modularity	Motility
S (< 1 mm)	B (bushy)	A (autotroph)	C (colonial)	A (attached)
M (1 mm – < 10 mm)	E (encrusting)	D (deposit feeder)	S (solitary)	B (burrowing)
L (10 mm – < 100 mm)	F (filamentous)	G (grazers)		C (crawling)
X (100 mm – 1000 mm)	M (massive)	P (predator)		D (drifting)
XX (> 1000 mm)		S (suspension feeder)		S (swimming)

Table 1 Dimensions used for the determination of the functional local and regional richness.

within region) (McMahon & Diez, 2007). We developed models for each of these response variables with each successional stage independently because plates from different regions had varied successional responses, and we wanted to understand successional dynamics independently. A Poisson link function was used because the response variable, local taxonomic or functional richness, was a count variable. Open space and both regional richness variables were standardized prior to entry into models to indicate the individual contribution of each predictor (Gelman & Hill, 2007). We also tested for two-way interactions between both regional richness variables and open space. These interactions allow open space to be a predictor in the regression for the slopes. Model intercepts and slopes of regional richness values were allowed to vary among regions. Multi-level models were analysed in the R platform (R Development Core Team, 2009) with the lme4 package (Bates & Maechler, 2009).

The regression equation has two levels, one for the 'local' or 'plate' scale (subscript $i = 1, \dots, n$ plates) and another for the 'regional' or 'country' scale ($j = 1, \dots, J$ regions). The regression equation for the local scale is

$$\log(\text{LTR}_{ij}) = \alpha_j + \beta_{1j} \text{OS}_{ij} \quad (1)$$

where α is the intercept of the logged LTR values within each region and β_1 is the regression coefficient that relates open space on every plate i in every region j to logged local taxonomic richness. The regional scale equations take the right-hand side of (1) and regress those coefficients given all countries

$$\alpha_j = \gamma_{00} + \gamma_{01} \text{RTR}_j + \gamma_{02} \text{RFR}_j + u_j, \quad (2a)$$

and

$$\beta_{1j} = \gamma_{10} + \gamma_{11} \text{RTR}_j + \gamma_{12} \text{RFR}_j + r_j. \quad (2b)$$

Equation 2a describes how the intercept of (1), or the average $\log(\text{LTR})$ of all plates within a region, given their open space, relates to regional taxonomic richness (RTR) and regional functional richness (RFR). Equation 2b describes how the relationship between $\log(\text{LTR})$ and open space within a region differs across regions, and relates to RTR and RFR. u and r are distributed $N(0, \sigma^2)$ where σ^2 is the variance of u and r in their respective equations. Equation 2b operates as the interaction between OS and the regional variables. Functional richness regressions were structurally identical, and need no repetition of the notation.

RESULTS

By the second month of recruitment, panels were already densely covered (average cover in month 2: $105 \pm 21\%$ SE) suggesting that competition for space (and possibly other factors) occurred for at least 6 months. Thus one important prerequisite for Mouquet's model was met.

Estimated taxonomic regional richness was highest in Australia and Sweden (55 species each) followed by Japan (54 species),

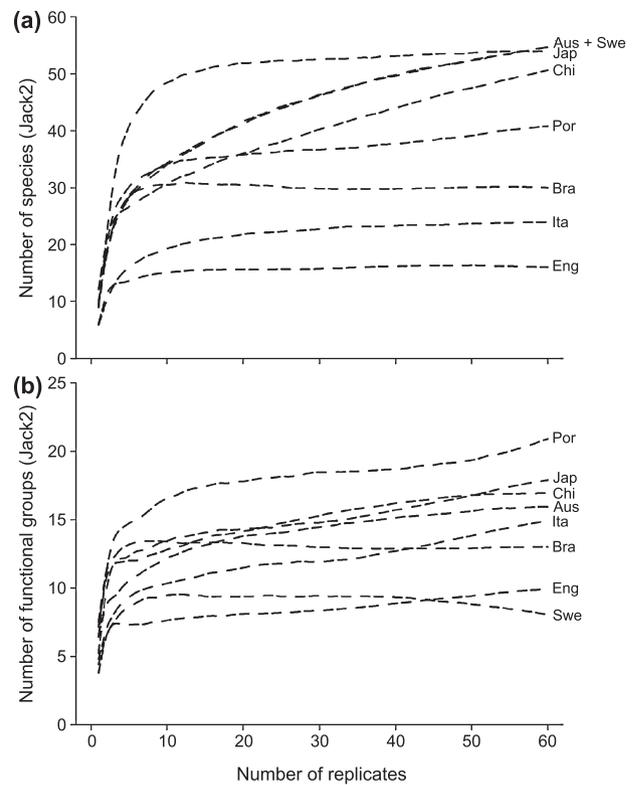


Figure 2 Species (a) and functional group (b) accumulation curves for eight regions as a function of number of replicates by using the Jack2 estimator of species richness. The endpoint of each curve (Jack2) was used as regional richness in the log–log regression of local–regional richness. Region codes as in Fig. 1.

Chile (51 species), Portugal (41 species), Brazil (30 species), Italy (24 species) and England (16 species). The slopes of the Jack2 curves for species richness were steeper for Australia, Chile and Sweden, probably due to the effect of rare species in those regions (Fig. 2a). In general, the observed richness obtained by pooling the samples used to estimate local richness was exceeded by the jackknife estimate of regional richness. (see Fig. 2a and Appendix S1 in Supporting Information). In contrast, functional regional richness ranked in a slightly different order, with Portugal containing the most FGs (21) followed by Japan (18), Chile (17), Australia (16), Italy (15), Brazil (13), England (10) and Sweden (8) (Fig. 2b). The number of species present in each FG varied for each region at both spatial scales (see Appendices S1 & S2).

The theoretical metacommunity analysis by Mouquet *et al.* (2003) predicts a unimodal relationship between local species richness and time. In the present investigation, similar relationships were only found in Portugal (Fig. 3e) and to a lesser extent in Sweden and Chile (Fig. 3b,d). In Australia and Brazil, species and functional richness reached a maximum by the first successional stage (Fig. 3a,f). Japan, Italy and England displayed a monotonic increase of species richness (and FG) toward equilibrium (Fig. 3c,g–h). Average percentage cover of local fouling species exceeded 100% at almost all stages of succession in

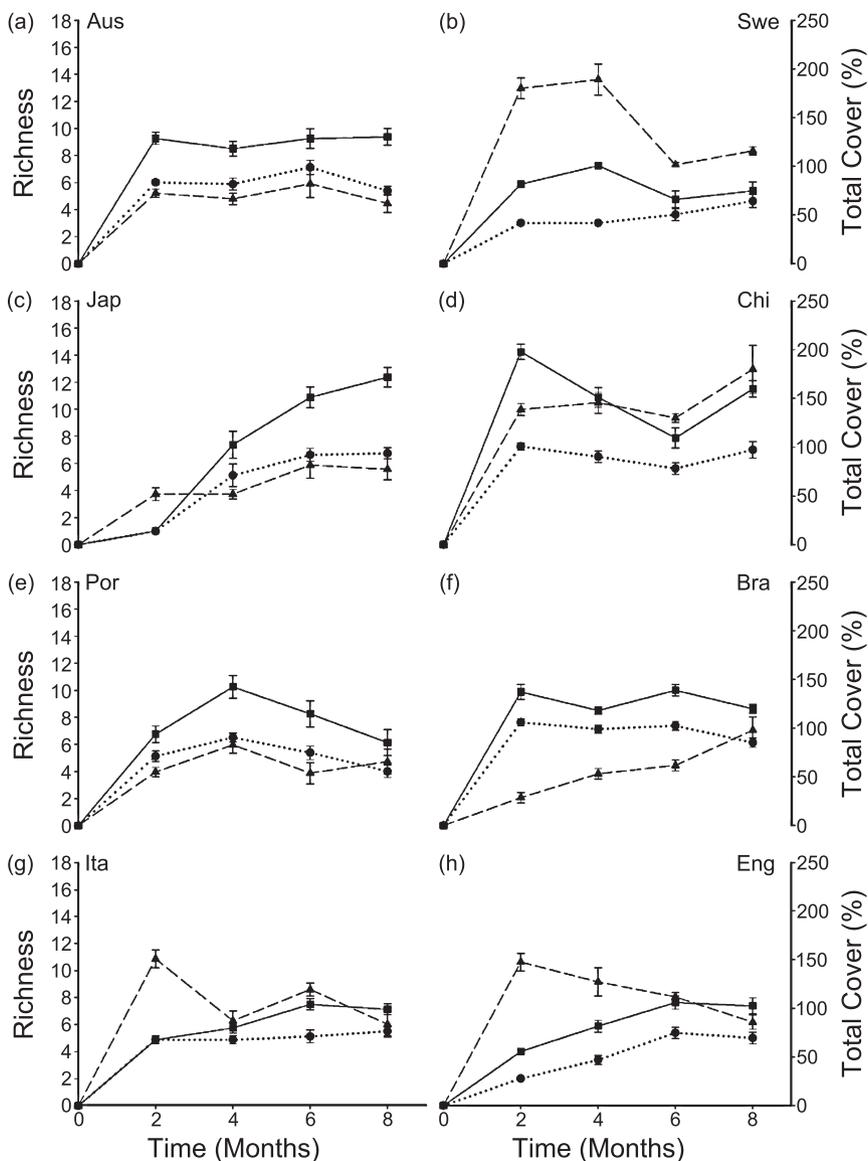


Figure 3 Community assembly over 8 months for each of the eight regions. Regions arranged by regional species richness. Region codes as in Fig. 1. Solid line indicates species richness; dotted line indicates functional richness and dashed line indicates total percentage cover. Means and standard error are indicated ($n = 8$).

Sweden, Chile, Italy and England (Fig. 3b,d,g–h), suggesting a large potential for competition for space. Average percentage cover of local fouling species did not reach 100% at any successional stage in the remaining regions. The fact that species richness was not decreasing even after 100% occupancy was reached in some regions indicates that competitive exclusion was not (yet) eliminating more species than were newly recruiting. In addition, average percentage cover at the local scale after 2 months of colonization – a proxy for fouling pressure – decreases significantly with latitude (Fig. 4, $P > 0.05$; $R^2 = 0.59$).

To distinguish between unsaturated and saturated communities we used the slope of a double log regression for both taxonomic and functional richness. At all successional ages, the relation between local and regional species richness was significantly less than 1, i.e. the number of species in a community did not rise proportionately with regional richness (Fig. 5a). In fact, at community ages of 2, 6 and 8 months, the slope of the relationship was not significantly different from 0, suggest-

ing complete independence of local and regional species richness. Only transitionally, at the age of 4 months, did local species richness rise significantly with regional richness, but nevertheless exhibited saturation at high regional richness (Fig. 5a).

For functional richness, the slope of the log–log regression exhibited a unimodal pattern of change during succession. At early (2 months) and late stages (8 months) of succession, local functional richness did not significantly depend on regional functional richness (95% CI includes 0; Fig. 5b). At the early intermediate stage (4 months), the slope was steepest, not different from 1, and local functional richness related closely and linearly to regional functional richness ('unsaturated'). At 6 months, local functional richness reached saturation, i.e. it did not increase beyond a threshold even when the number of regionally available FGs continued to rise. The gradual decrease of slope from 'unsaturated' to 'saturated' to 'independent' between 4 and 8 months could indicate that the latter should be

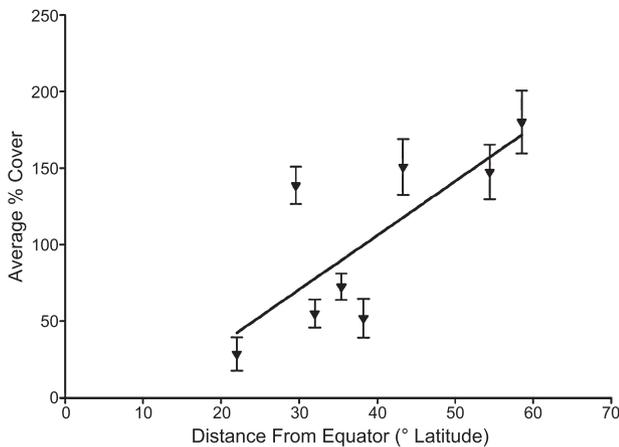


Figure 4 Relationship between average percentage cover at the local scale and latitude after 2 months of colonization. The amount of space covered within the first 2 months gives an impression of fouling pressure. Means and 95% confidence intervals are indicated.

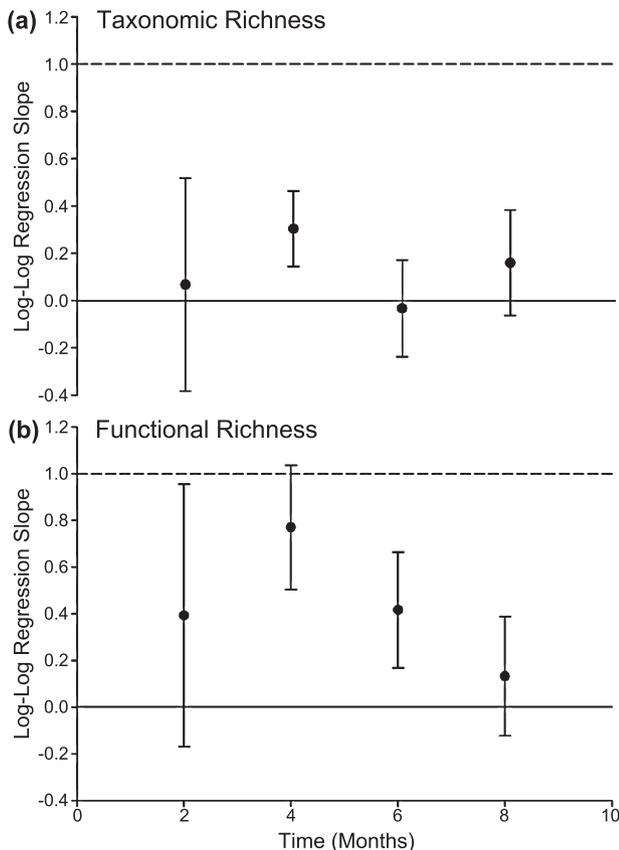


Figure 5 Slopes of the double log regression analysis over time for taxonomic richness (a) and functional richness (b). Slopes and 95% confidence intervals are indicated. Dashed line indicates a slope of 1. A slope that does not differ from 1 is indicative of unsaturation while local saturation is represented by a slope significantly smaller than 1 but larger than 0 (the latter value indicating independence) ($n = 8$).

considered as pseudo-independence and might be the result of less rich regions taking longer than richer regions to reach the functional richness plateau. This possibility is illustrated by the fact that the functionally richest region (Portugal, Fig. 3e) reaches a functional richness peak after 4 months, whereas in the functionally poorest region (England, Fig. 3h) functional richness did not reach a peak after 8 months. While the time taken to reach a functional richness peak varies between regions and perhaps with regional functional richness, the mean final functional richness at the local scale seems to converge to a range between four and seven FGs (mean \pm SE: 5.55 ± 0.42).

The interaction effects between open space and regional functional richness played a key role in driving taxonomic local richness as the generalized linear mixed models have identified this interaction as the most statistically significant predictor at later stages of succession, with its contribution ($-0.57 > \beta > -0.78$) slightly decreasing with time (Table 2a). This probably reflects the gradual filling of available space by new species from the regional pool – instead of by species already present on the panels. This mechanism, in turn, varies among regions. In a similar way, the difference between competition and regional richness of FGs negatively affects local functional richness after month 2 (Table 2b).

DISCUSSION

In this study, we examined the relationship between local and regional richness in marine fouling assemblages using an expanded approach: this is the first global-scale study to simultaneously incorporate time and functional richness. We found that the shape of the relationship depended on the successional stage and the type of richness measured. Whether taxonomic or functional richness is considered, local richness often shows independence of regional richness, particularly in early and late stages of the successional process. At intermediate successional ages, local richness displayed an unsaturated or saturated increase with regional richness.

The responses of species and functional richness at local scales to an increasing regional richness show similarities and differences. Both response variables are independent of regional richness during early and late succession. At intermediate stages (month 4), local richness relates positively with regional richness. The difference between the two response variables is that functional richness tends to relate more closely to regional richness than species richness, and that during intermediate succession species richness reaches a ceiling (with increasing regional richness), while functional richness does not. This difference may be interpreted on the basis that risk of enhanced competition at the local scale (and consequently saturation) increases more with increasing number of species (which may belong to few FGs) than with increasing number of FGs (which by definition differ ecologically to a certain degree).

Although regressing local diversity against regional diversity to examine the consequences of regional processes on local assemblages has frequently been used for different habitats, taxonomic groups or spatial scales (e.g. Valone & Hoffman,

Time	Predictors	(a) Taxonomic local richness				(b) Functional local richness			
		β	Std. Err.	z value	P-value	β	Std. Err.	z value	P-value
2 months	(Intercept)	1.89	0.22	8.69	< 0.001	1.51	0.15	9.81	< 0.001
	RTR	-0.09	0.51	-0.17	0.865	-0.31	0.36	-0.86	0.389
	RFR	0.10	0.31	0.31	0.758	0.34	0.24	1.38	0.169
	OS	-0.08	0.20	-0.40	0.689	-0.04	0.21	-0.22	0.830
	OS \times RTR	-0.08	0.50	-0.17	0.864	-0.64	0.56	-1.15	0.250
4 months	(Intercept)	2.09	0.05	43.56	< 0.001	1.68	0.06	28.68	< 0.001
	RTR	<i>0.21</i>	<i>0.11</i>	<i>1.88</i>	<i>0.060</i>	0.07	0.14	0.54	0.591
	RFR	0.17	0.13	1.36	0.175	0.24	0.15	1.57	0.116
	OS	-0.05	0.11	-0.42	0.676	<i>0.25</i>	<i>0.13</i>	<i>1.88</i>	<i>0.060</i>
	OS \times RFR	-0.48	0.35	-1.40	0.162	-0.93	0.42	-2.21	0.027
6 months	(Intercept)	2.17	0.05	46.87	< 0.001	1.81	0.06	32.86	< 0.001
	RTR	-0.05	0.11	-0.50	0.615	-0.07	0.13	-0.55	0.585
	RFR	0.25	0.10	2.43	0.015	0.17	0.12	1.37	0.170
	OS	0.24	0.11	2.24	0.025	0.17	0.13	1.35	0.177
	OS \times RFR	0.31	0.26	1.18	0.237	0.07	0.32	0.20	0.839
8 months	(Intercept)	2.18	0.06	35.03	< 0.001	1.74	0.06	30.42	< 0.001
	RTR	<i>0.24</i>	<i>0.14</i>	<i>1.66</i>	<i>0.096</i>	0.04	0.12	0.33	0.744
	RFR	0.21	0.21	1.03	0.303	0.06	0.12	0.52	0.605
	OS	0.02	0.11	0.19	0.849	-0.04	0.13	-0.35	0.728
	OS \times RTR	<i>0.47</i>	<i>0.25</i>	<i>1.90</i>	<i>0.057</i>	0.23	0.29	0.80	0.426
OS \times RFR	-0.57	0.23	-2.45	0.014	-0.60	0.25	-2.37	0.018	

Significant results ($P > 0.05$) highlighted in bold. Marginally significant results ($P \approx 0.05$) italicized ($n = 64$).

2002; Witman *et al.*, 2004; Freestone & Harrison, 2006; Cornell *et al.*, 2008), it has recently been criticized for a range of statistical and theoretical shortcomings (e.g. Hillebrand, 2005; Shurin & Srivastava, 2005). We avoided these shortcomings by following recent recommendations such as: (1) a proportional characterization of local and regional scales to avoid circularity between scales, i.e. our local scale was sufficiently small (225 cm²) to reduce internal environmental heterogeneity and we used independent data sets for the measurement of local and regional richness; (2) the inclusion in the regional species/functional pool of only those species or FGs capable of occupying the local habitat to avoid *pseudosaturation* caused by overestimation of regional richness; (3) the use of the double-log regression to distinguish between 'type I' and 'type II' curves; and (4) generalized linear mixed models of local and regional influences on local diversity for improved inferences (Hillebrand & Blenckner, 2002; Witman *et al.*, 2004; Freestone & Harrison, 2006; Harrison & Cornell, 2008). Furthermore, we believe that our regional richness assessment did not underestimate the regional species pool in this system. In each region, we surveyed 60 disturbed and undisturbed experimental units at four different successional ages over 8 months, at the same depth on identical substrates. We thus ensured that a substantial fraction of the potential founlers colonizing local communities (i.e. the relevant richness) during different seasons were inventoried.

In a simulation model originally developed for plant communities, Mouquet *et al.* (2003) predicted 'saturation' at early stages of succession, 'unsaturation' at intermediate stages and once again 'saturation' when communities reach a competitive equilibrium at later stages of succession. It should be noted, that 'independence' – when local diversity cannot exceed regional diversity – was not a predicted outcome of their model. 'Independence', i.e. when the slope in the log–log representation is not significantly different from zero, indicates that local richness of species or FGs does not increase with regional richness. Our results, with respect to species richness, do not correspond to Mouquet's prediction. While in most regions, local species and functional richness per panel do not increase after month 4, we cannot exclude the possibility that at 8 months our communities have not yet reached late-successional status. According to the model we should have observed initial (pseudo-)saturation followed by transitory unsaturation and possibly blending into mature saturation. Instead, for species richness the relationship between local and regional richness did not show any clear pattern in time. With the exception of the transitory 4-month saturation, local species richness seems independent of regional species richness. Mouquet *et al.* (2003) did not make a prediction for the development of the regional–local functional richness relationship in the course of succession. However, during succession in our communities the local–regional functional

Table 2 Results of the generalized linear mixed models with a Poisson link function for each of the four successional ages between local diversity (dependent variable (a) taxonomic local richness or (b) functional local richness) and the following predictors: regional taxonomic richness (RTR), regional functional richness (RFR), open space (OS). We also accounted for two interactions: OS and RTR (OS \times RTR) and OS and RFR (OS \times RFR).

richness relationship seems to behave almost as Mouquet *et al.* predicted for species richness. An initial ‘independence’ was followed by a conspicuous ‘unsaturation’ at the age of 4 months, then by ‘saturation’ at 6 months and by a second apparent ‘independence’ at 8 months. Apparently, the number of FGs per community is initially limited by the speed of colonization and not by the regional availability of FGs, hence ‘independence’. In an intermediate phase, when competition is not yet intense we find more FGs at the local scale where more FGs are present regionally, hence ‘unsaturation’. Subsequently, local functional richness tends to reach a maximum earlier in FG-rich regions because they cluster at lower latitudes with a more permanent availability of the regional FGs producing a pattern of ‘saturation’. Finally, when succession in the species-poorer regions has proceeded further, local functional richness approaches the values of the FG-richer regions, producing a new pattern of ‘independence’. Thus, initial and final ‘independence’ between regional and local functional richness are the product of different processes. It should be noted that the time-scales of successional dynamics are not defined in the theoretical model by Mouquet *et al.* (2003) and may have differed among the biogeographical regions investigated herein.

Most studies report local assemblages to be unsaturated (‘type I’ or linear plot) in respect to species richness, with regional diversity being a good predictor of local diversity. Similarly, a study by Witman *et al.* (2004), on the same study system and also conducted across a global scale, indicated slopes of log–log plots that do not differ from 1. Therefore, their results reported for the most similar community types are not in agreement with the results presented here.

Recent studies have also highlighted that local–regional richness plots should be used only as a starting point for interpreting the influence of local and regional processes in local communities (Russell *et al.*, 2006; Cornell *et al.*, 2008). By employing generalized linear mixed models we were able to test the relation of other parameters to species and functional richness at the local scale. We found that values of both response variables (local taxonomic and local functional richness) decrease with a complex mechanism, which incorporates open space and regional functional richness, particularly at later stages of succession. An increase in competition for available space by new species from the regional pool might explain this pattern. Furthermore, the combination of available space for colonization and a functionally diverse regional pool should facilitate the establishment of new species not yet present in the community.

Competition for space in fouling assemblages is well documented as a prominent limiting resource (Stachowicz *et al.*, 2002). Theoretically, if space is nearly filled after being colonized by a relatively small number of individuals (e.g. England), then additional species can only recruit after the death of local foulers, and species saturation is more likely to occur. Understanding how the cover at the local scale changes with latitude may ease the interpretation of whether this mechanism operates more strongly in particular regions. For example, after deployment of the panels (2 months), the rate of colonization maps to latitude and the rate of species recruitment does not. This

matches the expectation that in the tropics many species of the regional pool persist at moderate numbers, maintaining colonization at a moderate level. In contrast, during spring and early summer in high latitudes, high fouling rates can be found for seasonally available species.

We conclude that the relationship between local and regional richness, whether taxonomic or functional, surprisingly often shows independence of the two scales. This is particularly pronounced in early and late phases of the successional run investigated. In an intermediate phase local richness relates more closely to regional richness, particularly so when functional richness is considered. We suggest that early ‘independence’ is caused by scatter while late independence reflects a convergence of richness, especially functional richness, to a narrow range possibly typical for this type of community and for this size of patch. Finally, functional richness may be a better ecological metric and it reflects better than taxonomic richness the pattern predicted by Mouquet *et al.* This could be due to the observed ‘saturation’ of local functional richness: high regional species richness is not a good predictor for high functional diversity and – thus – low competition. However, although we consider that our FGs were classified according to traits that are crucial for fouling assemblages, we cannot exclude that other traits could result in a different pattern.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Number of species per functional group in each region at the regional scale

Appendix S2 Number of species per functional group in each region at the local scale for each successional stage

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BIOSKETCH

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