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Relationships between biodiversity and the stability of marine ecosystems: Comparisons at a European scale using meta-analysis

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ABSTRACT

The relationship between biodiversity and stability of marine benthic assemblages was investigated through meta-analyses using existing data sets (n = 28) covering various spatial (m–km) and temporal (1973–2006; ranging from 5 to >250 months) scales in different benthic habitats (emergent rock, rock pools and sedimentary habitats) over different European marine systems (North Atlantic and western Mediterranean). Stability was measured by a lower variability in time, and variability was estimated as temporal variance of species richness, total abundance (density or % cover) and community structure (using Bray–Curtis dissimilarities on species composition and abundance). Stability generally decreased with species richness. Temporal variability in species richness increased with the number of species at both quadrat (<1 m^2) and site (~100 m^2) scales, while no relationship was observed by multivariate analyses. Positive relationships were also observed at the scale of site between temporal variability in species richness and variability in community structure with evenness estimates. This implies that the relationship between species richness or evenness and species richness variability is slightly positive and depends on the scale of observation. Thus, species richness does not stabilize temporal fluctuations in species number, rather species rich assemblages are those most likely to undergo the largest fluctuations in species numbers and abundance from time to time. Changes within community assemblages in terms of structure are, however, generally independent of biodiversity. Except for sedimentary and rock pool habitats, no relationship was observed between temporal variation of total abundances and diversity at either scale. Overall, our results emphasize that the relation between species richness and species-level measures of temporal variability depends on scale of measurements, type of habitats and the marine system (North Atlantic and Mediterranean) considered.

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1. Introduction

For a long time, ecologists (e.g. Elton, 1958; MacArthur, 1955) have suggested that more diverse communities are more stable and diversity–stability relationships have been explored using various theoretical models (e.g. Loreau and de Mazancourt, 2013; May, 1974; Raffaelli, 2004; Solan et al., 2004), laboratory and field studies (e.g. McGrady-Steed and Morin, 2000; Petchey et al., 2002; Tilman and Downing, 1994). Interest in these relationships has resurged in recent years due to concern about the potential consequences of changing biodiversity for ecosystem functioning (e.g. Donohue et al., 2013; Stachowicz et al., 2007). Many of the theoretical and experimental studies have produced idiosyncratic results (Balvanera et al., 2006; Cottingham et al., 2001). Empirical support for relationships between biodiversity and stability across different ecological systems and spatial scales is still limited and contrasting, partly because of the practical limitations of empirical studies in encompassing long-term community dynamics. Indeed, individual studies have shown that increasing diversity may reduce (Ives and Hughes, 2002; Li and Charnov, 2001; Loreau and de Mazancourt, 2013), increase (e.g. Isbell et al., 2009; McCann, 2000; Tilman, 1996), or have little or no effect on the stability of some community attributes (e.g. McGrady-Steed and Morin, 2000). While no widespread consensus has been reached in the literature on which mechanisms are important in relating stability to biodiversity, a number of factors are known to affect the relationship. Among others, these include the scale of observation, historical effects of sites and species' life-histories, direct and indirect effects of disturbance (e.g. Bertocci et al., 2005; including speed and asynchrony of responses: Loreau and de Mazancourt, 2013), biodiversity and productivity (Kondoh, 2001). Other factors that may prevent determining relationships are pitfalls in experimental design (e.g. Hector et al., 2007; Loreau et al., 2001), calculation method and bias in estimating temporal variability (Cottingham et al., 2001; McArdle et al., 1990) and unappreciated statistical properties of these variables (Doak et al., 1998).

Studies on diversity and stability relationships have focussed largely on community aggregated variables (i.e. total biomass, production) or population abundances (see also Mykrä et al., 2011). Conversely, the analysis of stability of diversity per se within assemblage has received less attention. Temporal stability (inversely proportional to variability) in richness is expected to decrease with increasing average in number of taxa due to a pure statistic argument (positive scaling relationship between mean and variance). On the other hand, temporal variability in richness and changes in species structure within assemblages are important properties of communities. Disturbance regimes (Connell, 1978; Hughes et al., 2007) and resource availability may contribute to maintain high and relatively stable numbers of taxa at certain temporal and spatial scales. Several studies have shown that rich assemblages are locally organized in complex networks with varying interaction strengths and are prone to be generally more resistant to compositional turnover than less complex systems (Frank and McNaughton, 1991; Levine and D'Antonio, 1999; Shurin et al., 2007). If assemblage complexity begets stability via increased networks of interactions that prevent local extinctions, then rich (or more generally, diverse) assemblages should be compositionally more stable through time as compared with less diverse assemblages, despite the expected positive relationship between mean and variance. Also, intrinsic community properties such as negative covariance in species occurrence could lead to lower temporal variation at the more diverse sites offsetting the mean–variance scaling effect.

The role of evenness in diversity–stability relationships is not well understood (Hillebrand et al., 2008) and its use can provide different information not considered in the other diversity indices (Wilsey et al., 2005). Evenness within assemblages may enhance compositional stability (Frank and McNaughton, 1991) and reduce the risk of local extinction and invasion provided that no strong dominant can prevent further colonization. Polley et al. (2013) have shown that, in some circumstances, evenness in plant abundances and functional traits contributes as much as species richness to reduce temporal variability in productivity. Moreover, low dominance intensifies the stabilizing effect of richness on aggregated variables (e.g. total abundance): their variability becomes less affected by the scaling coefficient, *z*, determining the strength of the relationship between the mean and the variance (Doak et al., 1998; Vogt et al., 2006).

Ecological mechanisms that govern diversity, resource availability and species interactions are scale-dependent, so the prevalence of one mechanism at a given scale does not exclude the potential influence of other mechanisms at other scales (e.g. Raffaelli, 2006; Whittaker et al., 2001). This justifies the need to examine diversity–stability relationships at multiple scales. In this study, existing data sets were used to examine diversity–stability relationships and test whether they were different among habitats and between different European marine systems. This approach tests the general hypothesis that diversity measures (species richness and evenness) can be used as predictors of temporal stability within assemblages. Temporal stability implies lower variability that was measured as temporal variance in total community abundance, taxa number and community structure. Our specific hypotheses are that temporal variability in univariate and multivariate measures reflecting changes in species (or higher taxa) abundance and composition within assemblages is related to biodiversity measures (i) at the scale of small patches (quadrats or grabs; ~0.10 m^2); and (ii) at the scale of shores (site; ~100 s of m^2); and (iii) relationships between temporal variability and biodiversity at either scale vary according to the type of habitats and regions (marine systems). We are aware that the above hypotheses tested with observational data sets remain strictly correlative, not causal.

2. Methods

2.1. Data base description

Existing data sets of macrobenthic communities ($n = 28$) have been compiled (see list in Table 1). Each data set consists of multi-site temporal series (6 minimum) of macrobenthic community abundances (densities or % cover) of algae and fauna and covered most European regions (Fig. 1). Data sets had median values of 12 sites per data set, 4 sampling dates and 6 samples per date. The data sets cover diverse marine benthic habitats (emergent rock: $n = 20$; rock pool: $n = 3$; sediment: $n = 4$) with the addition of one data set using subsurface artificial panels (discarded for categorical habitat analyses).

2.2. Estimation of temporal variation

The temporal variability in species richness (number of species/taxa within quadrats/grabs) and total abundance (as density or % cover, within quadrats/grabs) of macrobenthic algae and fauna were used as surrogate measures of the community stability (where low variability corresponds to high stability). Due to differences in sampling design among data sets, the temporal variability was estimated as follows: (i) For randomized spatial samples at each sampling date, temporal variability (σ_t^2) in targeted variables was estimated using the Mean Squares (MS) obtained from a one-way ANOVA with time as independent factor, as $\sigma_t^2 \cong (MS_{\text{time}} - MS_{\text{residual}})/n$, where n is the number of replicate quadrats/grabs at each sampling date. (ii) In the case of unbalanced data, the variance component was estimated by a restricted maximum likelihood method (MIXED procedure in SAS, SAS, 1999). (iii) For fixed quadrat samples (i.e. repeated measures through time), temporal variability was assessed as the variance (over time) of response variables from individual quadrats. Multivariate temporal variability was estimated from the same linear model as for the univariate case using Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson, 2005). For fixed quadrats the average Bray–Curtis dissimilarity for each replicate quadrat over time was used. For analyses of variation in community

Table 1
List of data sets included in the meta-analysis. Number of time series refers to the number site for which samples were taken over many dates. Number of date refers to number of sampling occasion. Region category: NA: North Atlantic; Med: Mediterranean.

Data set #	Country	Location	Number of time series	Number of date	Temporal range	Samples per date	Range of taxa number		Habitat	Region	Organization
							Quadrat scale	Site scale			
1	Estonia	Gulf of Finland, Gulf of Riga, Tallinn Bay	8	7 to 18	1993–2001	2 to 3	3.9–8.5	13–38	Sediment	Baltic	EMI
2	France	Baie de Seine, Wimereux, Roscoff, Baie de Somme	7	9 to 20	2000–2003	1 to 3	2.2–10.4	4–29	Sediment	NA	CNRS-Roscoff
3	Germany	Helgoland Island	18	5	2005–2006	6	1.9–7.5	11–18	Artificial	NA	AWI
4	Germany	Sylt Island	6	2	2005	10	8.5–10.2	15–18	Sediment	NA	USTAN
5	Ireland	Northern Irish Sea	8	2 to 4	2004–2005	4	6.6–14.3	17–25	Emergent rock	Med	UCD
6	Ireland	South Western Celtic Sea	10	2 to 4	2004–2005	4	7.1–18.8	18–39	Emergent rock	Med	UCD
7	Italy	Lecce region	12	3	2002	10	6.1–13.3	24–45	Emergent rock	Med	CoNISMa
8	Italy	Lecce region	12	3	2002	10	9.5–15.9	34–42	Emergent rock	Med	CoNISMa
9	Italy	Lecce region	12	4	2002	10	9.5–12	36–51	Emergent rock	Med	CoNISMa
10	Italy	Lecce region	12	4	2002	10	5.7–9.9	31–48	Emergent rock	Med	CoNISMa
11	Italy	Lecce region	12	4	2002	10	6.6–8.9	34–51	Emergent rock	Med	CoNISMa
12	Italy	Lecce region	12	4	2002	10	8.6–12.5	33–42	Emergent rock	Med	CoNISMa
13	Italy	Lecce region	12	4	2002	10	10–13.8	38–46	Emergent rock	Med	CoNISMa
14	Italy	Lecce region	12	4	2002	10	8.8–11.7	31–43	Emergent rock	Med	CoNISMa
15	Italy	Lecce region	12	4	2002	10	3.9–6.6	22–30	Emergent rock	Med	CoNISMa
16	Italy	Pisa region	12	3	2003–2004	5	8.1–11.3	22–37	Emergent rock	Med	UP
17	Italy	Pisa region	12	4	1999–2001	5	7.5–10	16–20	Emergent rock	Med	UP
18	Italy	Pisa region	12	4	1999–2001	5	7.9–11.3	21–27	Emergent rock	Med	UP
19	Italy	Pisa region	8	3	2003–2004	5	8–11.3	20–32	Emergent rock	Med	UP
20	Italy	Pisa region	12	6	1994–1995	6	3.6–6.3	9–10	Emergent rock	Med	UP
21	Italy	Pisa region	9	3	1996–1998	3	4.3–6.9	8–11	Emergent rock	Med	UP
22	Italy	Pisa region	12	10	1998–2001	8	5.8–11	17–26	Emergent rock	Med	UP
23	Portugal	Porto region	40	2	2003	4	.8–12.6	2–36	Rock pool	NA	CIIMAR
24	Portugal	Porto region	12	2	2003	20	3.9–10.9	20–63	Emergent rock	NA	CIIMAR
25	England	Plymouth region	12	5	2002–2004	2	4.9–24.2	16–68	Rock pool	NA	MBA
26	England	Plymouth region	12	5	2002–2004	2	3.5–7.9	7–26	Emergent rock	NA	MBA
27	England	Plymouth region	6	5	2002–2004	6	22.4–33.4	99–120	Rock pool	NA	MBA
28	England	Tees Bay and Estuary	13	22–32	1973–1996	3 to 5	11.4–23.3	117–166	Sediment	NA	PML

Only algal cover: data set #27.
Intertidal zone: #2, 4–6, 17–27.

structure, all abundances were square-root transformed while for variation in community composition, data was transformed to presence–absence.

2.3. Diversity estimates

In each region, organisms were identified to the lowest taxonomic level possible in the field or in the lab (usually species). Organisms were identified at the same level of taxonomic resolution across data sets. Diversity was quantified in terms of species richness (S, number of species, taxa, or morphological groups) and Pielou's evenness (J'). Separate analyses were done using estimates from two different scales of observation: at the scale of the quadrat/grab ($\sim$0.10 m^2) and at the scale of the site ($\sim$100 s m^2). Estimates at the scale of the quadrat refer to the average values of variables within quadrats (i.e. all dates pooled) while estimates at scale of the site (i.e. all dates and quadrats pooled) refer to the total number of species and to the evenness of species densities averaged by site. Analyses were also performed using the rarefaction index $E(S\text{n})$ (Sanders, 1968, as modified by Hurlbert, 1971) in order to address the comparability of richness by standardizing abundances (Gotelli and Colwell, 2001; see Appendix 1 for details).

2.4. Data analysis

All relationships between dependent (univariate and multivariate measures of temporal variability) and independent variables (diversity measures: S and J') were separately investigated using linear regression. Specifically, it was examined if average species richness could be a predictor of temporal variations (as a response variable) in: *a*) species richness; *b*) community structure; and *c*) composition. Average evenness was also used as a predictor of temporal variation in: *d*) average species richness; *e*) community structure; and *f*) composition. Finally, it was tested if *h*) average species richness and *i*) average evenness were potential predictors of temporal variation in community abundance. It is worth noting that the analysis in *a*) represents a test for mean–variance relationship of species richness and this is discussed further in the text. The rarefaction index $E(S\text{n})$ was also used as a predictor of temporal variation in average species richness, community structure and composition (see supplementary results in Appendix 1). The correlation coefficient (r) and the slope parameter (β), reflecting the strength and steepness of the relationship between dependent and independent variables, respectively, were used in meta-analyses (see Table A1 in supplemental material, appendix 2). A standard meta-analytical effect size was used to determine whether there is a significant general trend in the strength of the relationship among all the data sets (Gurevitch et al., 2001; Hedges and Olkin, 1985). Fisher Z-transformed correlation coefficients $r_z = 0.5 \times \ln(1 + r)/(1 - r)$ were used, with sampling variance $\nu_z = 1 / (N - 3)$, where r is the correlation coefficient from the linear regression and N is the sample size. The slope parameter (β) along with its variance estimate SE$_\beta$ was used as size effect (Hillebrand et al., 2001; see also Hillebrand, 2004) to test for general trends. It was also investigated with categorical meta-analyses if the results were significant when aggregated within habitats (emergent rock; rock pool; and sediment) or regions (North Atlantic and Mediterranean locations; no test for Baltic region) and to test whether categories differ from each other. Sediment habitat includes both subtidal and shore soft sediment. The analysis of heterogeneity (Q-statistic) of effect sizes for different groups was also tested (Q-statistic Hedges and Olkin, 1985). This test discriminates between the total heterogeneity (Q_T) into heterogeneity between and within categories (respectively Q_B and

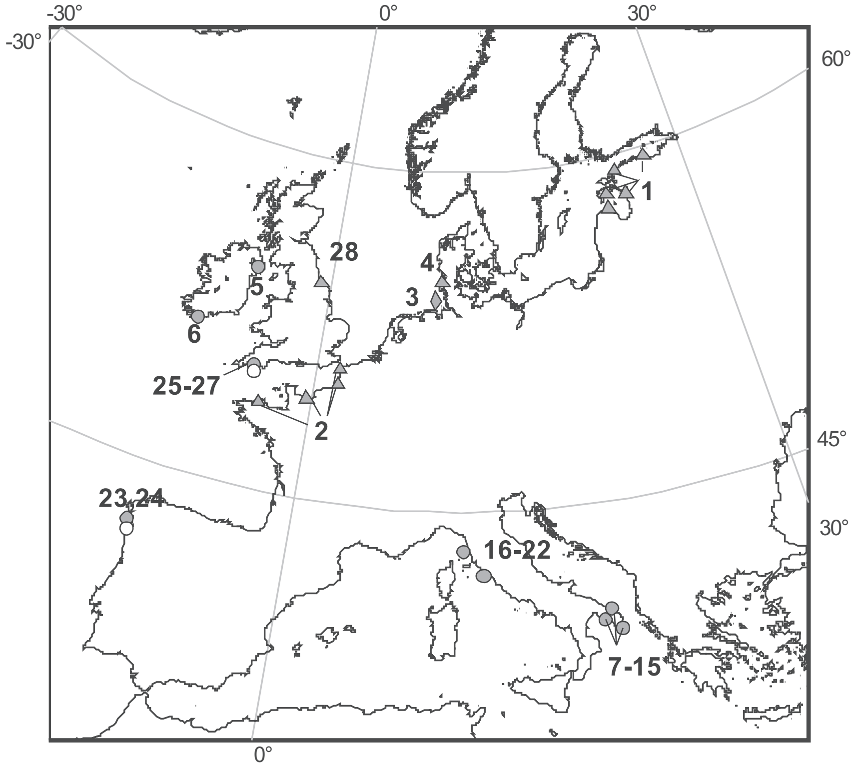

Fig. 1. Approximate location of sampling areas (with data set number, see Table 1) included in this study. Multiple sites were sampled in each area. Full circle: emergent rock habitat; open circle: rock pool; triangle: soft sediment; diamond: artificial substrata (PVC-panels).

Q_W) that are comparable to the SS terms in a standard ANOVA. Mixed model meta-analyses were used (with MetaWin 2 Rosenberg et al., 2000) and effect sizes were considered significant if their confidence interval did not bracket zero. Bootstrap 95% confidence intervals were built using 999 iterations. Potential effects of the duration (average in month) of sampling at each study site as well as the sampling effort (composite variable of averaged number of dates and samples per date for each data set sites) on effect sizes r_z and β were examined by continuous model meta-analysis (Rosenberg et al., 2000). A significance level α of 0.05 was adopted for all tests.

3. Results

3.1. Analyses of species richness variations

3.1.1. Species richness as independent variable

Significant positive correlation coefficients were observed between temporal variation in species richness and species richness levels at both quadrat (~0.10 m^2) and site (~100 s m^2) scales as the overall effect sizes (grand means) were positive and did not bracket zero (Fig. 2A, B). However, no significant trends were observed for emerged rock (ER) habitat and western Mediterranean (ME) region at both scales. At the scale of the site, the relationship strength r_z values were significantly higher for rock pool (RP) than ER habitat and significantly higher in North Atlantic (NA) than in ME region (Fig. 2B). No difference of ER effect sizes between NA ($n = 4$) and ME ($n = 16$) regions was observed in all tests (results not shown). No significant overall size effects or relationship between temporal changes in community structure and composition within assemblages with species richness was found (Fig. 2C–F). The strength and the slope of the relationships followed similar patterns for these analyses. Relationship analyses using expected species richness $E(Sn)$ (or rarefaction index) at the scale of the site as an independent variable depicted some differences with observed species richness (see Fig. A1 in Supplemental materials).

3.1.2. Evenness as independent variable

Overall, positive r_z effect size of the relationship between temporal variation in species number and evenness was observed only at the scale of the site (Fig. 3A, B). Positive strength r_z values were observed for soft sediment (SD) habitats and NA region at the quadrat scale, while at the scale of the site, positive r_z-values were observed for ER habitats and for both NA and ME regions. Slope β of the relationships followed similar trends as for the strength r_z, except from the NA region where β values were not significantly different from zero (Fig. 3A, B). When considering relationships between temporal changes within assemblages with evenness values, positive overall r_z was only observed with community structure analyses at the scale of the site (Fig. 3C–F). ER habitats as well as the ME region showed positive r_z for the latter analysis (Fig. 3D) while data from SD habitats always showed positive r_z values for all multivariate analyses (both in structure and composition data at both scales; Fig. 3C–F). Inversely, temporal changes in community composition were negatively related to evenness for ER habitat and ME region (Fig. 3E). All multivariate analyses for r_z and β followed the same trends (Fig. 3C–F) with an exception for SD habitats at the scale of the quadrat (Fig. 3C), where r_z was positive but β was not.

3.2. Analyses of total community abundance variations

Diversity was not linked to temporal variation in total community abundance (total % cover or density). Overall strength r_z and slope β effect sizes of relationships between temporal variations in community total abundance (density or % cover) and both species richness (S) and evenness (J') were not significant (Fig. 4A–D) at all scales. Positive strength r_z and slope β with S were however observed for SD habitat (both scales) and NA region (scale of the site only) (Fig. 4A, B). Temporal variation in total abundance was positively correlated with J' for rock pool habitat at both scales (Fig. 4C, D) as shown by positive r_z and slope β effect sizes.

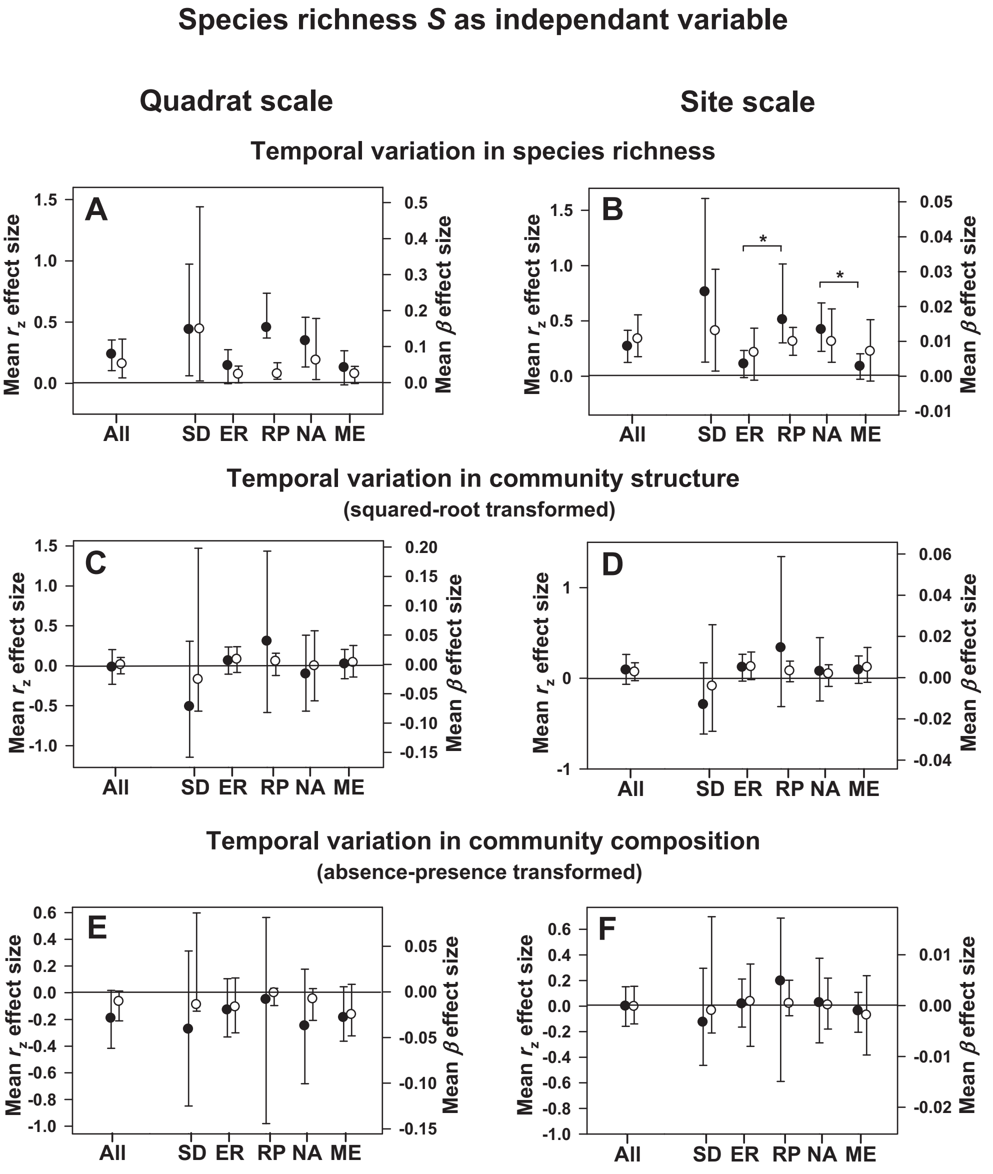

Fig. 2. Mean effect size (±95% CI) for overall effect (all data: all), by habitat (sediment: SD; emergent rock: ER; rock pool: RP), and by region (North Atlantic: NA; Mediterranean: ME) of the relationship strength r_z (black circle) and slope β (open circle) between temporal variability and species richness. Effect sizes are displayed by type of analyses (species richness variability: A, B; community assemblage variability in: structure C, D and composition E, F) and scale of richness measure (average by patch scale as quadrat: A, C, E; total by shore as site: B, D, F). Brackets with * indicate significant ($p < 0.05$) heterogeneity of effect sizes among categories. Significant effects where CIs do not overlap with zero line. Note that negative values indicate a positive stability–diversity relationship while positive values do the opposite.

3.3. Heterogeneity among data set (sampling effort and duration effect)

The duration of the studies did not affect the values of strength r_z and slope β in any of the analyses (see Supplemental material, Appendix 3). The sampling effort, determined as composite variable of number of dates and samples per date, negatively affected r_z from analyses of temporal changes in community structure (quadrat: p-value $= 0.0255$) and composition (quadrat: $p = 0.0114$; site: $p = 0.0049$) that used species richness as an independent variable. Sampling effort did not affect effect sizes in analyses of temporal variation in richness with evenness as the independent variable and all analyses of temporal variation in total abundance. Slope β-values were not affected by sampling effort in any of the analyses (results not shown).

Diversity indices measured at the scale of the quadrat versus indices measured at that of the site were correlated (average ± SE of Pearson's r coefficient per data set: species richness: 0.71 ± 0.04; evenness: 0.71 ± 0.07). However, richness and evenness measures were weakly positively correlated at the scale of quadrat ($r = 0.36 \pm 0.08$) and at the scale of the site ($r = 0.11 \pm 0.08$).

4. Discussion

This study has highlighted that, in most cases, temporal variability in the number of taxa is positively related to diversity measures in marine benthic coastal assemblages. These results suggest that greater diversity leads to less stability (inversely related to temporal variability). Variations in species abundance and composition within communities and temporal variation in total community abundance were, however, generally not linked to species richness and evenness. In addition, the diversity–stability relationships were scale dependent and varied across type of habitats and regions considered. The potential underlying mechanisms linking diversity measurements to stability are discussed below.

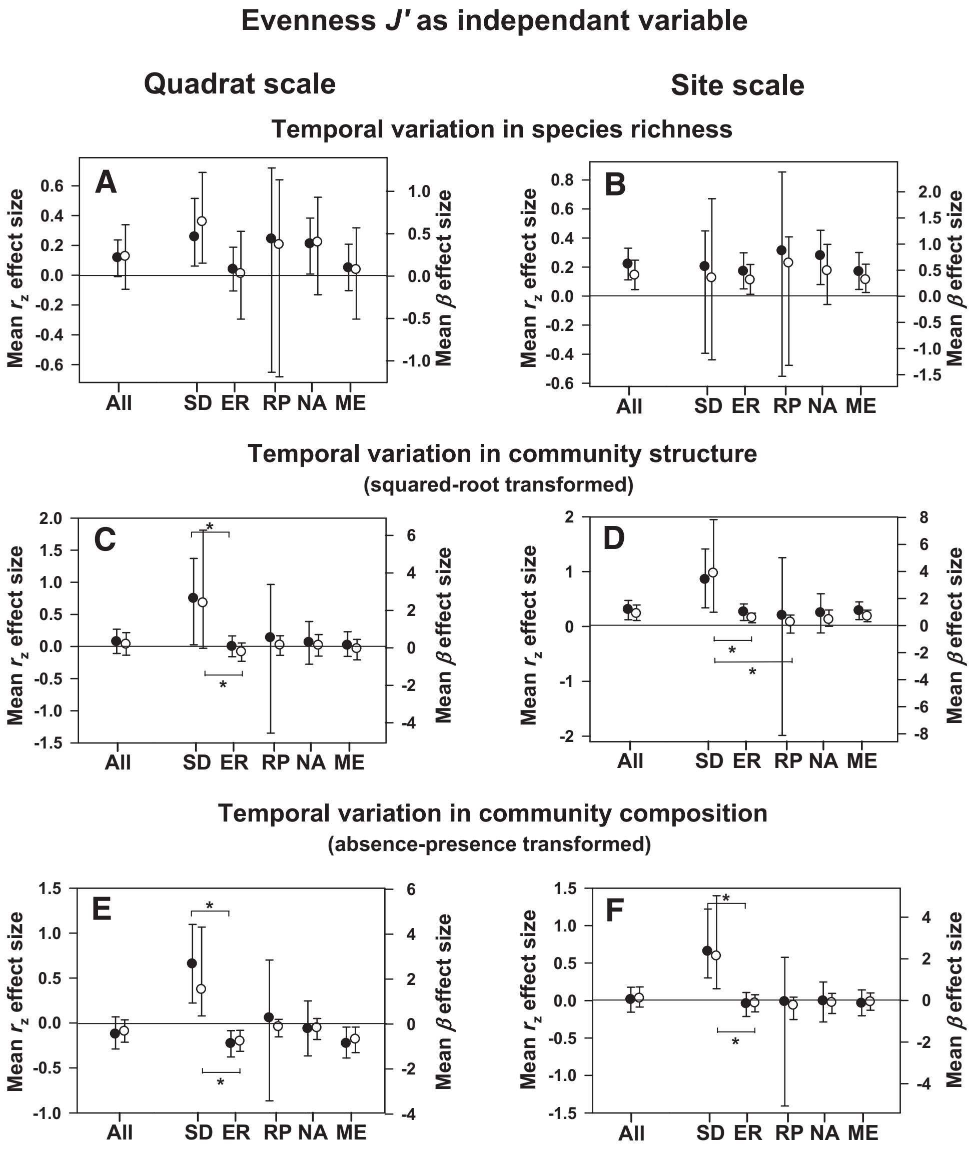

Fig. 3. Mean effect size (±95% CI) for overall effect, by habitat and by region of the relationship strength r_z (black circle) and slope β (open circle) between temporal variability and evenness J'. Effect sizes are displayed by type of analyses (species richness variability: A, B; community assemblage variability in: structure C, D and composition E, F) and scale of evenness measure (average by patch scale as quadrat: A, C, E; reassessed by shore as Site: B, D, F). See Fig. 2 for abbreviations.

4.1. Temporal variation in species richness

Our results suggest that the overall stability in species richness is negatively related to diversity estimates (species richness, evenness and rarefaction index). To some extent, the observed negative relationship between species richness and stability in species richness may be explained by simple mean–variance scaling effect. However, positive relationships between other diversity indices (evenness and rarefaction index) and richness assessed at the scale of the site were consistent in our analysis. This strengthens the hypothesis that fluctuations within assemblages are closely controlled by their constituent species and their dominance structure. Empirical and theoretical studies have generally shown that diversity levels affect variations in relative abundances, patterns of colonization and extinction rates (e.g. Inchausti and Halley, 2003; Solan et al., 2004), which, in turn, determine species richness variability. The cycle of colonization and local extinction of species, variation in species richness, are affected by processes that influence average population sizes and their temporal stability. Indeed, small or highly variable populations are more likely to become locally extinct (Inchausti and Halley, 2003; Melbourne and Hastings, 2008; Pimm et al., 1988; Shaffer, 1981).

The identity of species within communities undoubtedly plays an important role since more diverse communities are more likely to include species or functional groups (McCann, 2000) that can affect the function or properties of the whole community (i.e. sampling effect, Huston, 1997; Tilman et al., 1997). Outcomes from various studies of temporal variation in species richness have led to different results. Simulation studies have demonstrated that species variation (turnover) is reduced with increasing richness when high number of taxa may either facilitate colonization or reduce extinction of present species, or when environmental conditions are variable (Shurin, 2007). In contrast, higher temporal stability (assessed as low values of the coefficient of variation) in species richness was associated with low richness and evenness values in New Zealand sandflat sites (Thrush et al., 2008).

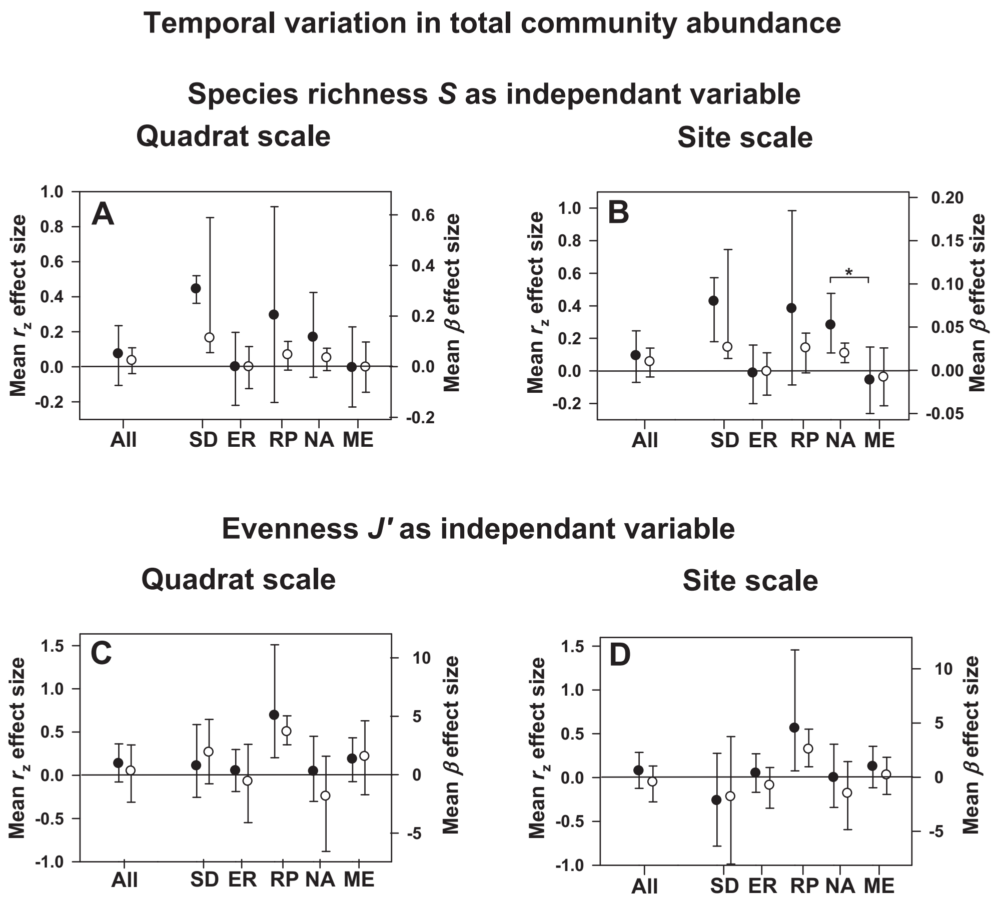

Fig. 4. Mean effect size (±95% CI) for overall effect, by habitat, and by region of the relationship strength r_z (black circle) and slope β (open circle) between temporal variability in total abundance (density or % cover) and: species richness (A, B), and evenness J' (C, D). Effect sizes are displayed by scale of diversity measure (average by patch scale as quadrat: A, C; reassessed at site scale: B, D). See Fig. 2 for abbreviations.

These results were explained by strong connections between functional groups in species-poor communities.

4.2. Temporal variation in abundance

Stability in total abundance of community was generally not linearly linked to species richness nor evenness indices. Balvanera et al. (2006) also failed to observe significant relationships between stability (as natural variation) and diversity, although using different measures of stability and data sets that study did not exclusively represent marine habitat. Temporal variability of aggregated community (total abundance, total biomass, etc.) or population (density, biomass) properties are preferred response variables used in studies of diversity–stability relationships and most of the relationships were negative (Stachowicz et al., 2007; Valdivia and Molis, 2009). Many mechanistic approaches were identified to interpret theoretical and empirical outcomes from relationships between variability of such aggregated variable and diversity measures (e.g. de Mazancourt et al., 2013; Petchey et al., 2002). In particular, different non-exclusive mechanisms were reported to regulate the link between diversity and stability: the statistical averaging (Doak et al., 1998; "portfolio effect" Tilman et al., 1998); negative covariances among populations (Tilman et al., 1998); asynchrony in response to environmental fluctuation (Ives and Hughes, 2002) and overyielding (Tilman, 1999). These mechanisms have been considered important to shape the relationship between diversity and stability of above-ground biomass (Grman et al., 2010), total abundances in marine hard bottom communities (Benedetti-Cecchi, 2009; Bulleri et al., 2012) and production in grassland plants (de Mazancourt et al., 2013; Isbell et al., 2009). Increasing the number of taxa present in a community would reduce mean and variance in the total community abundance and, then statistically reduce community variance (see Cottingham et al., 2001). On the contrary, rich communities may also increase average strength among species favoring competitive exclusion and enhancing abundance fluctuations. Even if mean–variance scaling effects were present, intrinsic community properties such as negative covariance in species occurrence could lead to lower temporal variation at sites with higher species richness. Several empirical studies have highlighted the role of dominant species traits for the function of the whole community. For example, lower variability of dominant species than subordinate species may affect the whole community stability (Grman et al., 2010; Polley et al., 2007; Sasaki and Lauenroth, 2011; Valdivia et al., 2013).

The results of the present study also suggest that communities from different habitats exhibit different diversity–stability relationships. While data from emergent rocky habitats exhibited no relationship, richness decreased stability of sandy community abundances while evenness decreased stability in rock pool community abundances (see Fig. 4). If poor correlation between richness and evenness measures at each scale may partly explain this, inherent differences exist in forces that structure communities among habitats. Strong interactions, mainly competition, among species in soft sediments are largely limited to the provision of biogenic habitat communities that are commonly maintained in early successional stages by frequent physical and biological disturbances. Competitive displacement and exclusion are generally less frequent in sediment habitats compared to hard-bottom ones (Black and Peterson, 1988; Peterson, 1979). Following the work of Danovaro et al. (2008) in deep sea sediments, Loreau (2008) suggested that infaunal species, through the reworking of sediments could generate a prevalence of positive species interactions in soft sediments (in contrast to hard-bottoms, cf Benedetti-Cecchi, 2009; Noël, 2007) leading to complementarity effects (Loreau, 2000). Positive covariance, which is observed when species fluctuate synchronously in response to environmental change, is widespread (Houlahan et al., 2007; Valone and Barber, 2008) and contributes to increase variability in total abundance. However when present, the compensatory dynamics among intertidal species that contribute to stability has a lower effect in high latitude where environmental forcing may prevail on biological interactions (Bulleri et al., 2012). While rock pools are benign environments compared to emergent rock in terms of physical stress (i.e. desiccation, see Noël, 2007), they can be much more heavily grazed (e.g. Benedetti-Cecchi et al., 2005). This high grazing pressure observed in rock pools may change the nature of interactions between species from competition to facilitation (Bertness and Callaway, 1994) and increase the number of grazer resistant-species (Noël et al., 2009). If stabilizing effects of species richness on community abundances were observed in rock pool mesocosms (Romanuk and Kolasa, 2002), the effect of evenness still remains unclear.

4.3. Temporal variation within communities

Using multivariate analyses, we found that stability (measured with Bray–Curtis dissimilarities) of species abundance and composition within communities are generally not correlated with diversity indices. Our results suggest that relationships between diversity and community stability may be governed by evenness rather than the number of species (cf. Figs. 2 and 3). Moreover, contrasting results among habitats exist, with sediment communities with high evenness being less stable, perhaps from prevalence of positive species interactions in this habitat previously discussed. Theoretical studies have revealed that relationships between community variability in composition and number of taxa may increase, decrease or remain unchanged mainly due to the type of calculation of variability used but also stochastic processes that alter patterns of dominance and total abundance among species (Stevens et al., 2003). Among other results, Stevens et al. (2003) reported that simulated community variation in composition, given that total abundance stays equal, would show positive correlation with evenness. Our empirical observations would give only little support to these predictions (see Fig. 3E). At high dominance (or low evenness), it was observed that stability in species composition within a community may be either enhanced on emergent rocky shores or become reduced on sediment shores (see Fig. 3E). Results from empirical studies have also contradictory outcomes showing that various measures of grassland diversity (including species richness and evenness) can enhance (Frank and McNaughton, 1991) or decrease stability (Rodriguez and Gomez, 1994, while no effect was recorded for J') measured by temporal variance in compositional richness. Moreover, in contrast to our study, Mykrä et al. (2011) observed that stability within assemblage in streams is promoted by species richness, although this relationship disappeared when compositional stability was related to species richness estimated with a rarefaction index that standardized abundance.

4.4. Scale of observation

Many rich benthic communities are actually composed by rare species (Ellingsen et al., 2007; Gray, 2000; Gray et al., 2005). Uncommon species are theoretically important to maintain ecosystem functions in the context of the insurance hypothesis (Yachi and Loreau, 1999) and are important to ensure community persistence and resilience (Hillebrand et al., 2008). Spatial species distributions are highly heterogeneous at various scales (e.g. Chapman et al., 2010; Kraufvelin et al., 2011). Indeed, variations in the number of taxa may be influenced by a combination of random spatial and temporal sampling errors that cause species, particularly those that are either sparse or rare, to be included or not in a patch (de Juan and Hewitt, 2014; McArdle et al., 1990). The recent work of de Juan and Hewitt (2014) illustrated how seasonality and inter-annual sampling schemes may affect variability in species composition and species accumulation profiles. In our study, care was taken to select data sets with sampling dates spread among seasons or within years. There was no effect of the duration of the studies on effect sizes measured, but seasonal variations within studies may have influenced our overall results. Patterns of diversity in small patches have been identified as potential contributors to ecological stability (Frank and McNaughton, 1991), but the consistency seen in our results at both quadrat and site scales indicates that mechanisms not related to heterogeneity among patches may dominate and create the observed patterns. It has been generally accepted that regional species pools may regulate the species richness seen at smaller scales (e.g. Kotta and Witman, 2009; Ricklefs, 1987; Witman et al., 2004).

When data sets were analyzed separately, a large proportion of the observed relationships between stability and biodiversity were weak or not significant. For example, in the analyses shown in Fig. 2A, only 5 data sets out of 28 showed significant relationships and 6 show correlation coefficients over 0.5 (Table A1, appendix 2). The observed significant results with combined data sets illustrate the importance of using robust meta-analytical tools to investigate such hypotheses. Nonetheless, more data from soft sediments and rock pool habitats are needed to generate more conclusive results. The available data sets in this study were to some extent over-represented in the Mediterranean region and in the emergent rock habitat. Indeed, the Mediterranean region was solely represented by studies on emergent rock. On the other hand, consistent results between Mediterranean and North Atlantic results for emergent rock were seen. Large scale comparison of diversity effects on ecosystem processes may be masked systematically by the effects of variation in environmental variables on these processes and may lead to erroneous conclusions (Loreau, 1998, 2008).

5. Concluding remarks

This study provides one of the few comprehensive assessments of large spatial scale variation in the relationship between diversity and temporal stability across different marine systems. Our results suggest that diverse assemblages enhance variability in species richness without affecting variability in species abundance and composition within community. The use of complementary diversity indices (e.g. richness and evenness) over various time series warrants the generation of robust stability–diversity analyses. Despite the caveat resulting from incomplete and unevenly distributed data, it has been highlighted that the scale of observation needs to be considered in diversity–stability studies and outcomes may also depend on the habitats and the biogeographic systems considered (e.g. North-Atlantic or western Mediterranean). Conversely, there are needs to extend the analyses shown here to more sites (and time series) in order to generate better pictures across habitats. Targeted long-term observations and experiments are undoubtedly important to unravel effects of environmental variables, species interaction strength within assemblages and potential effect of climate changes on biodiversity and the functioning of ecosystems. Nevertheless, where sufficient data sets exist, a meta-analysis like the one presented here can provide a cost-effective approach to clarifying and generating further hypotheses about diversity–stability relationships.

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Appendix A. Supplementary data

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