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

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Running head: Stability-diversity relationships in marine ecosystems

Abstract

The relationship between biodiversity and stability of marine benthic assemblages was investigated using existing data sets (n = 28) covering various spatial (m-km) and temporal (1973-2006) scales in different benthic habitats (emergent rock, rock pools and sedimentary habitats) through meta-analyses. Assemblage stability was estimated by measuring temporal variances of species richness, total abundance (density or % cover) and community species composition and abundance structure (using multivariate analyses). Positive relationships between temporal variability in species number and richness were generally observed at both quadrat (<1 m^2) and site (~100 m^2) scales, while no relationships were observed by multivariate analyses. Positive relationships were also observed at the scale of site between temporal variability in species number 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, suggesting that biodiversity *per se* is important for the stability of ecosystems. Changes within community assemblages in terms of structure are, however, generally independent of biodiversity, suggesting no effect of diversity, but the potential impact of individual species, and/or environmental factors. Except for sedimentary and rock pool habitats, no relationship was observed between temporal variation of the aggregated variable of total abundances and diversity at either scale. Overall our results emphasise that relationships depend on scale of measurements, type of habitats and the marine systems (North Atlantic and Mediterranean) considered.

Keywords: Biodiversity ecosystem functioning, temporal variability; diversity–stability relationships; community variability; benthic marine coastal habitats.

Highlights

- Generally, diversity estimates increase temporal variations in richness.
- Changes in community structure are independent of richness stability.
- Diversity-stability relationships depend on the scale at which diversity is measured.
- Diversity-stability relationships vary among habitats (e.g. rocky shore, sediment).
- Meta-analytic tools are useful with data sets with different sampling strategies.

1. Introduction

There is an accumulation of evidence that high number of species within communities is desirable to maintain key ecosystem function. The maintaining of ecosystem function in high species number or phenotypic trait within community is thought to be realized with the mechanisms of complementary association that enhance collective performance and/or with the inclusion of an extreme trait by selection effect (Huston, 1997; Tilman et al., 1997; Loreau, 2000). Natural fluctuations in species richness within communities may generate spatial or temporal variability in the functional properties of ecosystems and make them less predictable. Understanding the mechanisms underlying the variability in species richness is therefore a key issue to understand the stability of ecosystems properties. Investigations into the mechanisms behind the relationship between stability and diversity have been revived due to the increasing awareness that biodiversity is being lost at an unprecedented rate in all systems and future scenarios are merely pessimistic (Sala et al., 2000; Worm et al., 2006; Butchart et al., 2010). The causes of biodiversity loss and the consequences for the functioning and stability of ecosystems are the current focus of intense research activity (Schmid et al., 2009; Hooper et al., 2012; MacDougall et al., 2013).

For a long time, ecologists (e.g. MacArthur, 1955; Elton, 1958) have suggested that more diverse communities are more stable and diversity-stability relationships have been explored using various theoretical models (e.g. May, 1974; Raffaelli, 2004; Solan et al., 2004; Loreau and de Mazancourt, 2013) laboratory and field studies (e.g. Tilman and Downing, 1994; McGrady-Steed and Morin, 2000; Petchey et al., 2002). Many of the theoretical and experimental studies have produced idiosyncratic results (Cottingham et al., 2001; Balvanera et al., 2006). Empirical support about causal 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, increasing diversity may reduce (Li and Charnov, 2001; Ives and Hughes, 2002; Loreau and de Mazancourt, 2013), increase (e.g. Tilman, 1996; McCann, 2000; Isbell et al., 2009), 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. Loreau et al., 2001; Hector et al., 2007), calculation method and bias in estimating temporal variability (McArdle et al., 1990; Cottingham et al., 2001) 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. 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. Several studies have shown that rich assemblages are 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).

Studies into general biodiversity-ecosystem functioning relationships have been strongly focussed on terrestrial systems (Loreau et al., 2001; Hooper et al., 2005). Even if the number of studies on marine biodiversity and ecosystem functioning has recently increased (Stachowicz et al., 2007), it is doubtful that results from terrestrial systems can be extended directly to marine systems and specific understanding of the relationship between diversity and the stability of marine ecosystems is essential. Since empirical studies have shown diverse outcomes, it is unlikely that a significant increase in understanding diversity-stability relationships will originate from the accumulation of isolated case studies. Alternative approaches exist with the analyses of data from diverse studies using meta-analyses (e.g. Balvanera et al., 2006; Worm 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 other mechanism at another scale. 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 regions, habitats, and across 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 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; ~ 0.10 m^2); (ii) at the scale of shores (~ 100s of m^2); and (iii) relationships between temporal variability and biodiversity at either scale varies according to the type of habitats and regions (marine systems) within Europe. We are aware that the above hypotheses tested with observational data sets remain strictly correlative, not causal. However, rather than examining and comparing the results of different experiments separately, this study represents one of the first attempts to address the relationship between biodiversity and stability using extensive data sets in order to generate robust quantitative synthesis that may also be valuable in deciding the most urgent research needs, and for guiding future empirical research.

2. Methods

2.1 Data bases description

Existing data sets of macrobenthic communities (n = 28) have been compiled (see list in Table 1). Each data set consists of multi-sites 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).

-Table 1-

-Figure 1-

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 randomised spatial samples at each sampling date, temporal variability (σ_t^2) in targeted variables were 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 quadrats 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 structure, all abundances were square-root transformed while for variation in community composition, they were absence-presence transformed.

2.3 Diversity estimates

In each region, identification was done to the lowest taxonomic level possible in the field or in the lab (usually species). 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: the quadrat/grab scale (~ 0.10 m^2) and at the site scale (~ 100s m^2). Estimates at the quadrat scale refer to the average values of variables within quadrats (i.e. all dates pooled) while estimates at site scale (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*n) in order to address the comparability of richness by standardizing abundances (see Appendice 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*n) was also used as a predictor of temporal variation in average species richness, community structure and composition (see supplementary results in Appendice 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. 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 (Hedges and Olkin, 1985; Gurevitch et al., 2001). Fisher *Z*-transformed correlation coefficients $r_z = 0.5 \times \ln(1+r)/(1-r)$ were used, with sampling variance $v_z = 1 /(N\text{-}3)$, 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_β 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 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 (~ 100s 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 Mediterranean (ME) region at both scales. At the site scale, 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 were 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 $E(S\text{n})$ (or rarefaction index) at site scale as an independent variable depicted some differences with observed species richness (see Fig. A1 in supplement materials).

-Figure2-

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 at the site scale only (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 site scale, 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 site scale (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 multivariates 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 same trends (Fig. 3c-f) with an exception for SD habitats at the quadrat scale (Fig 3c), where r_z was positive but β not.

-Figure 3-

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 was however observed for SD habitat (both scales) and NA region (site scale 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.

-Figure 4-

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 (results not shown). The sampling effort, as composite variable of number of date and sample per date, negatively affected the size effect of strength r_z from analyses of temporal changes in community structure (quadrat: p-value = 0.0255) and composition (quadrat: $p = 0.0114$; site: $p = 0.0049$) within assemblages with species richness as an independent variable. Sampling effort did not affect effect sizes for analyses with temporal variation in richness with evenness as an independent variable and all analyses of temporal variation in total abundances. Slope β-values were not affected by sampling effort in any of the analyses (results not shown).

Diversity indices measured at the scale of quadrat versus indices measured at the site scales 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 together at the quadrat (r = 0.36 ±0.08) and at the site scale (r = 0.11 ±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 European marine benthic assemblages. These results suggest that greater diversity leads to less stability. Species structure (abundance or composition) variations within communities and temporal variation in total community abundance were, however, generally not linked to species richness and evenness. It was also observed that 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.

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, constancies in positive relationships with other diversity indices (evenness and rarefaction index) and with richness assessed at the shore scale were observed. This strengthens the hypothesis that fluctuations within assemblages are closely controlled by their constituent species, their dominance structure and also perhaps with those from immediate neighbouring communities. Empirical and theoretical studies have generally showed that diversity levels affect population variation abundances and patterns of colonization and extinction rates (e.g. Inchausti and Halley, 2003; Solan et al., 2004) which determine species richness variability. The cycle of colonization and extinction of species, variation in species richness or diversity *per se*, 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 (Shaffer, 1981; Pimm et al., 1988; Inchausti and Halley, 2003; Melbourne and Hastings, 2008).

The identity of species within communities undoubtedly plays an important role since more diverse communities are more likely to include influential species (i.e. sampling effect, Huston, 1997; Tilman et al., 1997) or functional groups (McCann, 2000) that can affect the function or properties of the whole community. Such species-rich communities may include facilitators or strong competitors that lead to different susceptibilities to invasion of new species and are more generally affecting temporal fluctuation in richness. 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 sandflats sites (Thrush et al., 2008). These results were explained by strong connections between functional groups in 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, while using different measure of stability and data sets 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. Petchey et al., 2002; de Mazancourt et al., 2013). In particular, main concomitant 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 covariance 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 of diversity and stability of above-ground biomass (Grman et al., 2010) or total abundances in marine hard bottom benthos (Benedetti-Cecchi, 2009; Bulleri et al., 2012) and production in grassland plants (Isbell et al., 2009; de Mazancourt et al., 2013). Increasing the number of taxa present in a community would reduce mean and variance in the total community abundance and, then statistically reduce the community variance (see Cottingham et al., 2001). On the contrary, rich communities may also increase average strength among species favouring 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 the more diverse sites. 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 (Polley et al., 2007; Grman et al., 2010; Sasaki and Lauenroth, 2011; Valdivia et al., 2013). Yet, the identity effects, or the effect of a single species, rule the relationships seen in marine experiments (Cardinale et al., 2006; Stachowicz et al., 2007), however long term studies reveal that diversity remains a stronger factor effect (Stachowicz et al., 2008).

The results of the present study also suggest that communities from different habitats exhibit different patterns. 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 partly may explain this, inherent differences exist in forces that structure communities among habitats. Strong interactions among species in soft sediments are limited largely 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 unimportant in sediment habitats compared to hard-bottom substrates (Peterson, 1979; Black and Peterson, 1988). Following the work of Danovaro et al. (2008) in the deep sea sediment, Loreau (2008) suggested that infaunal species by the reworking of sediment could generate a prevalence of positive species interactions in soft sediments (in contrast to hard-bottoms, cf Noël, 2007; Benedetti-Cecchi, 2009) leading to complementarity effects (Loreau, 2000), where variation in trait or species number enhances the collective performance of aggregated variables. Positive covariance, that is observed when species fluctuation depicted similar responses to the environment, overcomes in most communities (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 term of stress (i.e. desiccation Noël, 2007), they can be much more heavily grazed. 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 of community abundances were observed in speciose rock pools mesocosms (Romanuk and Kolasa, 2002), the effect of evenness still remains unclear.

4.3 Temporal change within communities

Using multivariate analyses, it has been shown in the present study that stability of assemblages in structure and in composition are generally not correlated with diversity indices. Such absence of linear relationship might reflect an unpredictable (i.e. idiosyncratic) or different relations. Our results also suggest that relationships between diversity and community stability may be ruled by species identity and dominance structure (evenness) within assemblage rather than the number of species. Also, contrasting results among habitats exist, with sediment communities with high evenness being less stable, perhaps from prevalence of positive species interactions in this habitat that has been evocated in the previous section. 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 alone that alter patterns of dominance and total abundance among species (Stevens et al., 2003).

Among other results, Stevens et al (2003) reported that community variation in composition, given that total abundance stay equal, would show positive correlation with evenness. Our empirical observations would give only little support to these predictions. 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). Empirical results from grassland studies have also contradictory outcomes showing that various measures of 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.

4.4 Scale of observation

Consistent results were often observed between scaled diversity measures in our study as patch (quadrat) and shore diversity indices were positively correlated. Many rich benthic communities are actually composed by rare species (Gray, 2000; Gray et al., 2005; Ellingsen et al., 2007) which are more prone to local extinction. 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 and patterns occur at various scales on the shore and shallow marine habitats (e.g. Chapman et al., 2010; Kraufvelin et al., 2011). Indeed, variation in number of taxa may be influenced by a combination of random spatial and temporal sampling errors that cause species, particularly those species that are either sparse or rare, to be included or not in a patch (McArdle et al., 1990). This can interact with real local pattern of colonization and extinction. 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. Ricklefs, 1987; Witman et al., 2004; Kotta and Witman, 2009). Indeed, taxa number observed on a site may act as a supply to patch diversity through source-sink dynamics and contribute to sustain local species richness number (Hillebrand et al., 2008). Even if systematic sampling effects on size effects were not detected, temporal variation in taxa number in this study reflect both spatial and temporal processes.

When all data sets were analysed 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 relationship results from 5 data sets out of 28 have significant results (p value < 0.05) and 6 show correlation coefficients over 0.5. 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 lead to erroneous comparisons across sites unless abiotic conditions are very tightly controlled (Loreau, 1998, 2008). While this study remains correlative, the use of weighted local effect sizes may reduce, but not control totally, this methodological problem.

5. Concluding remarks

This study provides the first comprehensive assessment of large spatial scale variation in the stability of marine systems. The analyses presented here include a large number of locations each with many sites, and with some data sets including long time series. Our study indicates that biodiversity (either in number of taxa or in evenness) is important for the stability of marine community in various habitats. Our results suggest that diverse assemblages enhance variability in species richness without affecting a large amount of variability in community species structure or composition. The use of complementary diversity indices (e.g. richness and evenness) over various marine 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 the observation need to be considered in diversity-stability studies and outcomes may also depend on the habitats and the systems considered (e.g. North-Atlantic or Mediterranean). Conversely, there are needs to extend the analyses showed here to more sites in order to generate better pictures for sandy shores and rock pool habitats. Long-term series of community data 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 alternative to generate further hypotheses on diversity-stability relationships. For this reason, it will have a great impact of research on marine biodiversity, providing information about generalities of patterns which is critical for sound management of marine habitats.

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Figures Legends

Figure 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).

Figure 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.

Figure 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 Figure 2 for abbreviations.

Figure 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 Figure 2 for abbreviations.

Figure A1. 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 expected richness $E(S\mathrm{n})$ at the scale of site. Effect sizes are displayed by type of analysis (species richness variability: A; community assemblage variability in: structure: B; and composition: C). See Figure 2 for abbreviations.

Table 1. List of data sets included in the meta-analysis. Region category: NA: North Atlantic; Med: Mediterranean.

Dataset #	Country	Location	Number of time serie	Number of date	Temporal range	Samples per date	Range of taxa number		Habitat	Region	Organisation
							quadrat scale	site scale			
1	Estonia	Gulf of Finland, Gulf of Riga, Tallin Bay	8	7 to 18	1993-2001	2 to 3	3.9-8.5	13-38	Sediment	Baltic	EMI
2	France	Baie de Seine, Vimereux, 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	41	2	2003	4	.8-12.6	2-36	Rock Pool	NA	CIMAR
24	Portugal	Porto region	12	2	2003	20	3.9-10.9	20-63	Emergent Rock	NA	CIMAR
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: dataset #27
Intertidal zone : #2, 4-6, 17-27

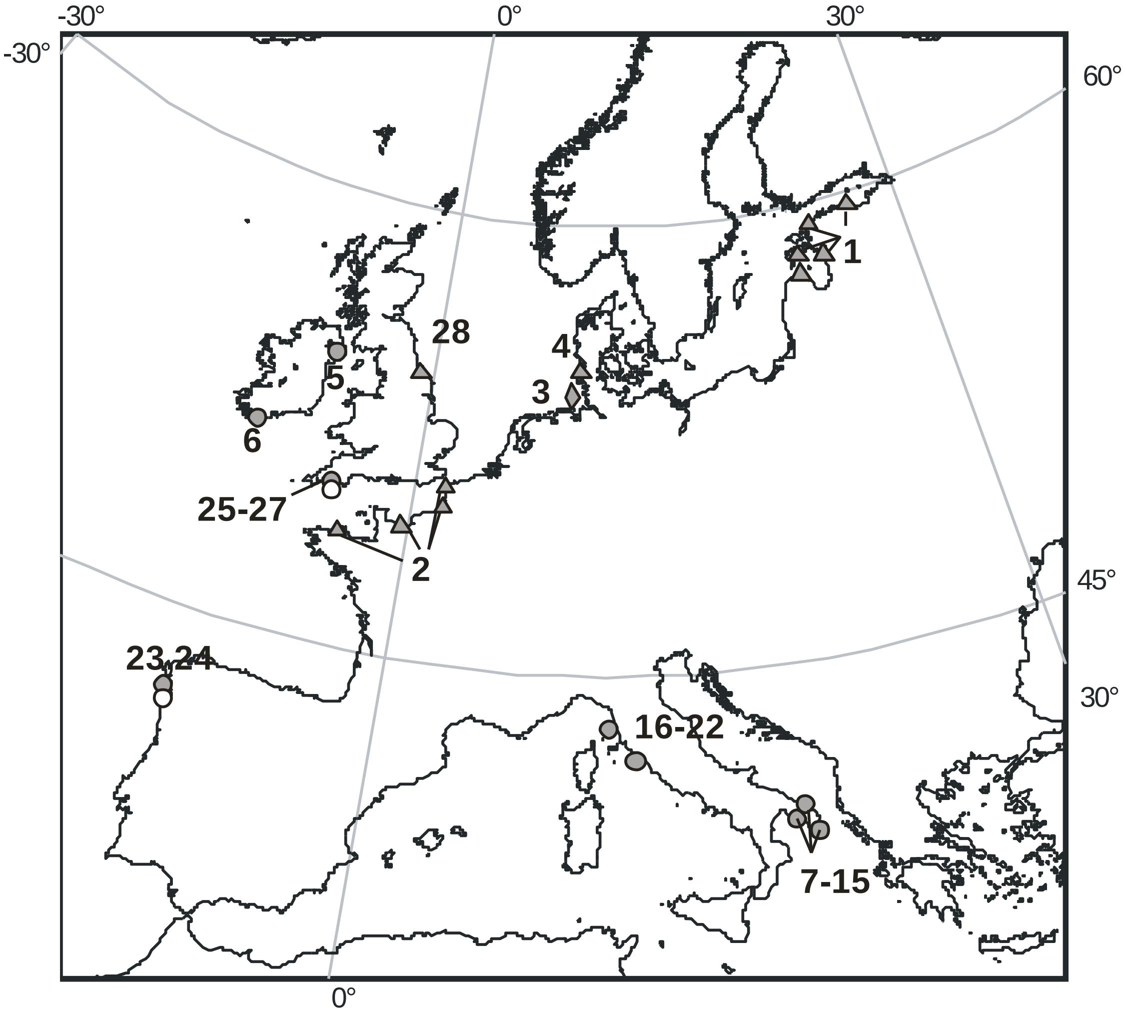


Figure 1. Approximate location of sampling areas (with data set number, see Table 1) included in this study. Multiple sites were sampled in each area. Full circle: emergent 810 rock habitat; open circle: rock pool; triangle: soft sediment; diamond: artificial substrata (PVC-panels).

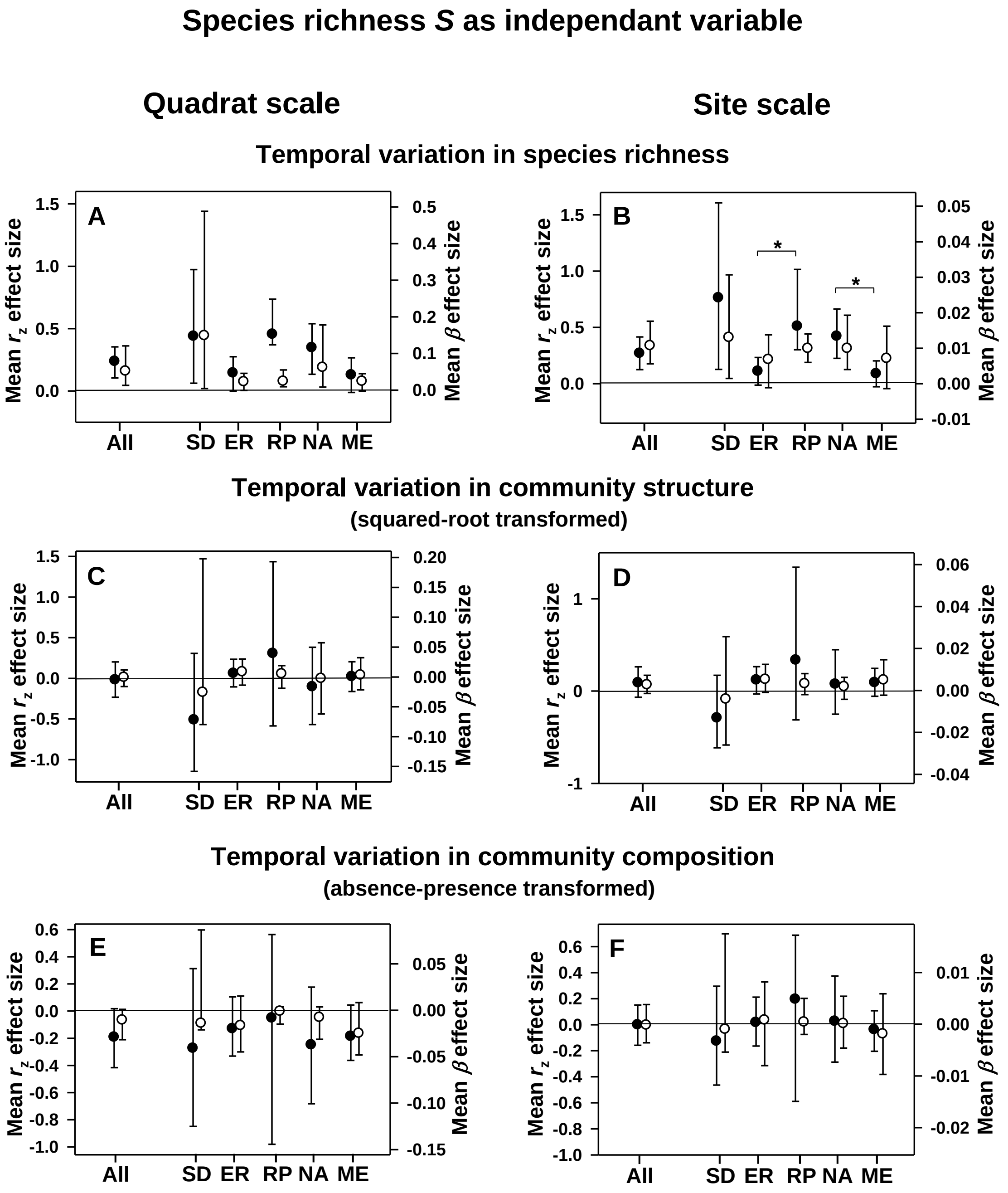


Figure 2. Mean effect size (±95% CI) for overall effect (All data: All), by habitat (Sediment: SD; Emergent rock: ER; Rock pool: RP), and by region (North Atlantic: NA; Mediterranean: ME) of the relationship strength r_z (black circle) and slope β (open circle) between temporal variability and species 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). Horizontal 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.

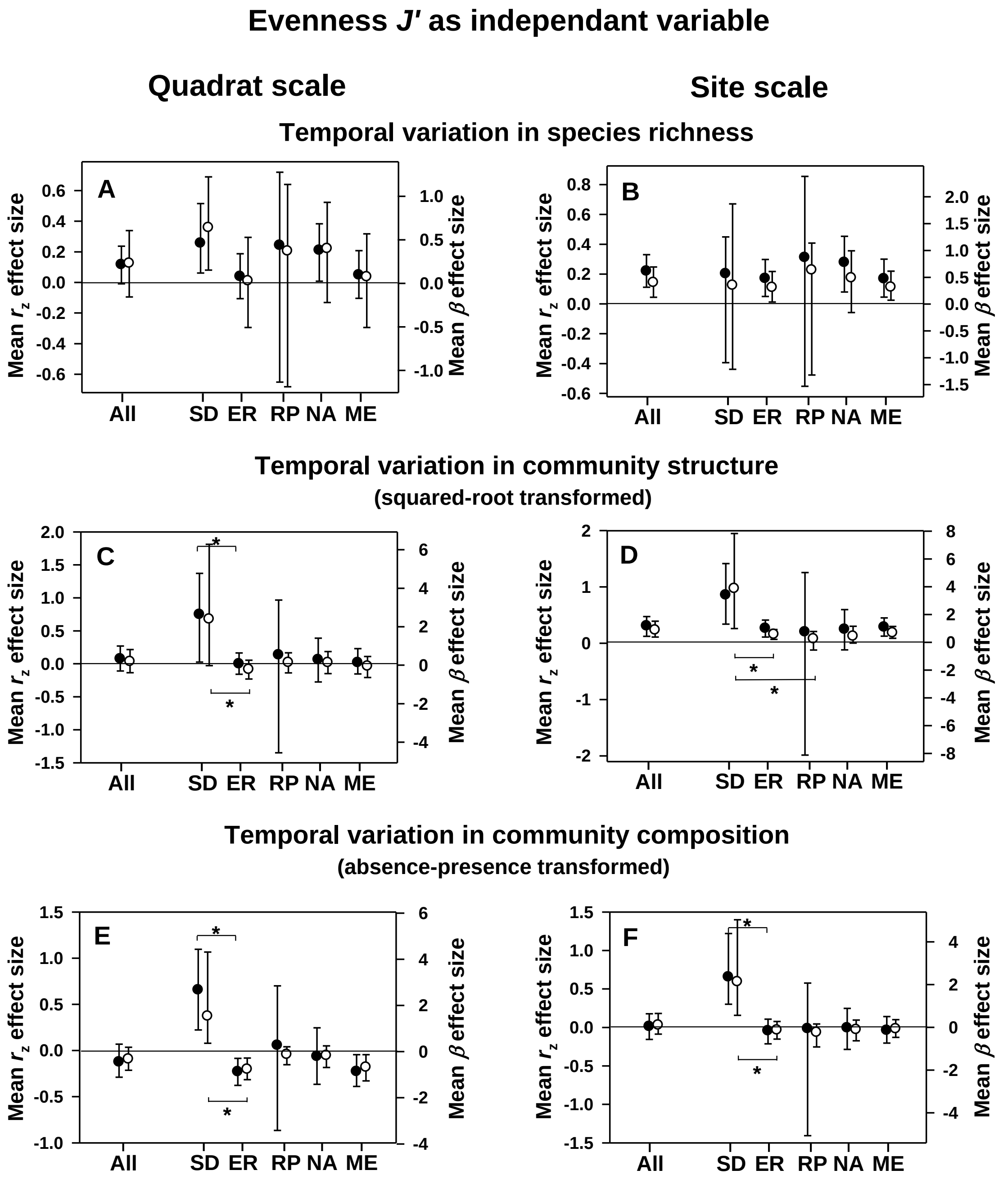


Figure 3. Mean effect size (±95% CI) for overall effect, by habitat and by region of the relationship strength r_z (black circle) and slope β (open circle) between temporal variability and evenness *J*'. Effect sizes are displayed by type of analyses (species richness variability: A, B; community assemblage 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 Figure 2 for abbreviations.

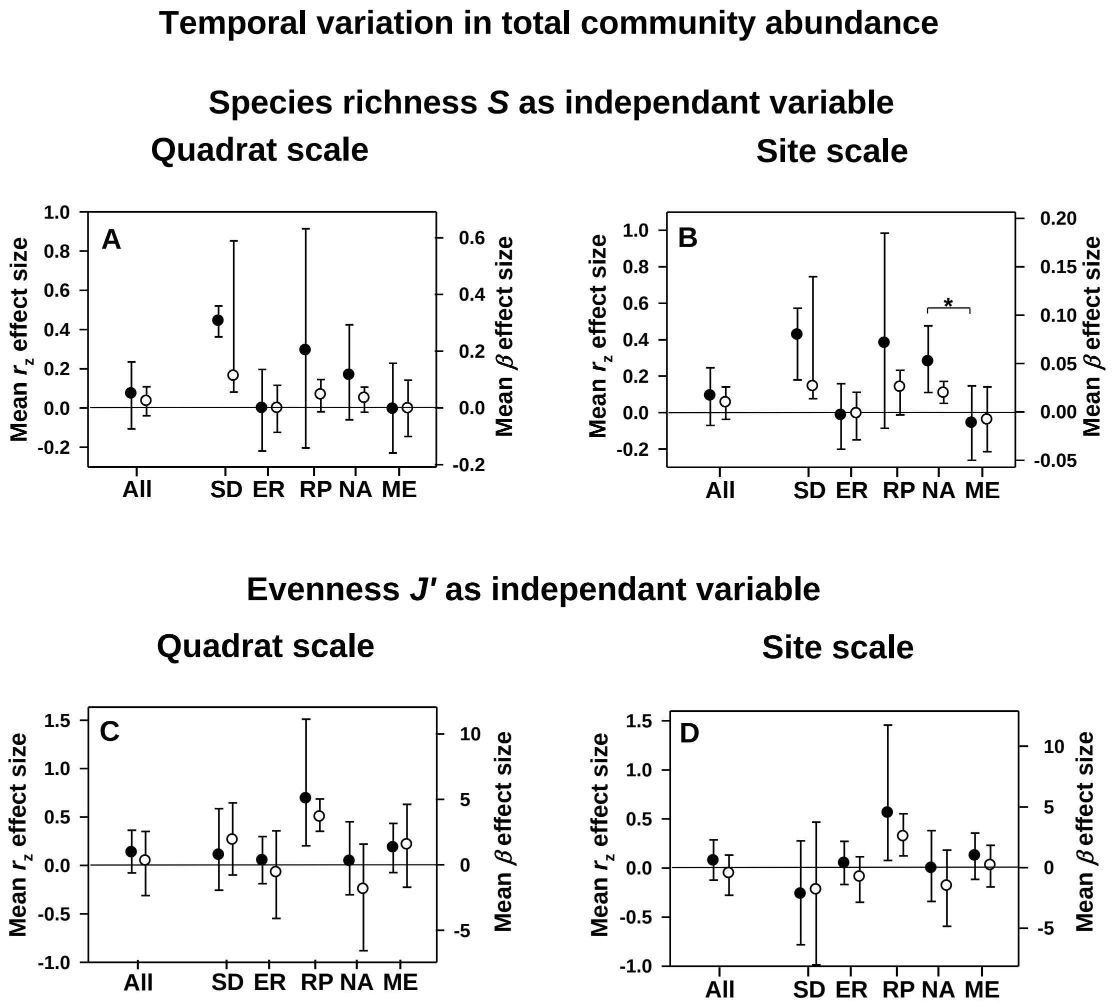


Figure 4. Mean effect size (±95% CI) for overall effect, by habitat, and by region of the relationship strength r_z (black circle) and slope β (open circle) between temporal variability in total abundance (density or % cover) and: species richness (A, B), and evenness *J*’ (C, D). Effect sizes are displayed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

Electronic Supplemental Material (see methods section).

Appendice 1.

Analyses with expected number of taxa as independent variable

Methods

We used the normalised expected number of taxa rarefaction method (Sanders 1968, as modified by Hurlbert, 1971) as an independent variable in order to address the comparability of richness by standardizing abundances (see Gotelli and Colwell, 2001). This method calculates the expected number of taxa, *E*(*S*n), in a reduced standardised sample of *n* individuals selected from the given sample. For this rarefaction approach a reduced number of individuals (*n*) were chosen which took into account the lowest abundances at the scale of site (i.e. all quadrats and dates pooled) for each data set. Abundances (in density or % cover) within quadrat were not consistent or sufficient to perform quadrat scale analyses. The average of *n* used was 125 and a minimum was set at $n = 40$ to ensure satisfactory assessment. In a very few cases (7 out of 336 sites) the total abundances at the site scale show numbers slightly below the minimum of 40.

Results

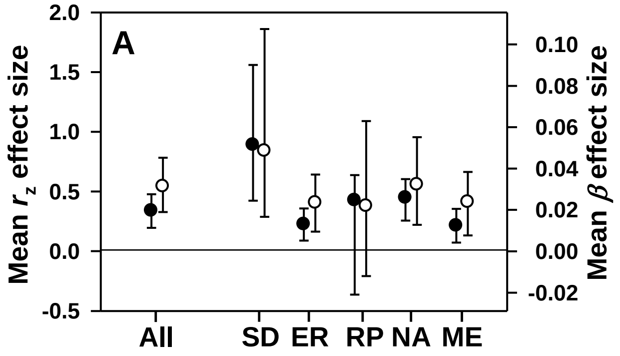
We observed positive overall relationships between temporal variations in observed species richness and expected number of taxa *E*(*S*n) (Fig. A1a). All categories, except for rock pool (RP) habitats, showed positive strength r_z and slope β. Changes in community structure also showed positive trends, while only the effect size for emergent rock habitat was positively significant (Fig. A1b). We did not observed significant general trend with compositional community analysis, except for sediment habitat (Fig. A1c).

Difference when using observed species richness and E(Sn)

The most notable difference we observed between results using observed species richness and *E*(*S*n) as independent variables was that temporal changes in species abundance within the assemblage become positively correlated with *E*(*S*n) values (cf. Figs. 2d and A1b). Minors differences were also observed using *E*(*S*n): Temporal variation in species richness: emergent rock (ER) habitat and Mediterranean (ME) region became positive while RP habitat become non-significant (Fig A1a). Temporal variation in community: ER habitat (community structure) and sediment habitat (community composition) became positive (Fig. A1b,c).

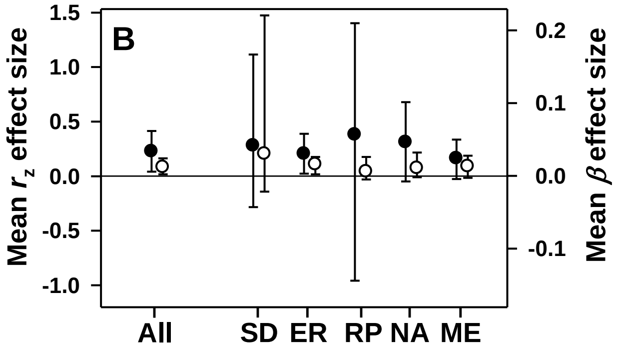
E(*S*n) as independant variable - Site scale

Temporal variation in species richness



Temporal variation in community structure

(squared-root transformed)



Temporal variation in community composition

(absence-presence transformed)

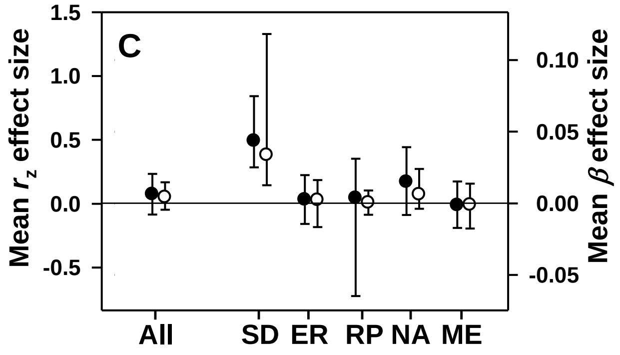


Figure A1. Mean effect size (±95% CI) for overall effect, by habitat, and by region of the relationship strength r_z (black circle) and slope β (open circle) between temporal variability and expected richness *E*(*S*n) at the scale of site. Effect sizes are displayed by type of analysis (species richness variability: A; community assemblage variability in: structure: B; and composition: C). See Figure 2 for abbreviations.