



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 m²) and site (~100 m²) 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; $\sim 0.10 \text{ m}^2$); and (ii) at the scale of shores (site; $\sim 100 \text{ s of m}^2$); 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

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