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Predictability of marine nematode biodiversity

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ABSTRACT

In this paper, we investigated: (1) the predictability of different aspects of biodiversity, (2) the effect of spatial autocorrelation on the predictability and (3) the environmental variables affecting the biodiversity of free-living marine nematodes on the Belgian Continental Shelf. An extensive historical database of free-living marine nematodes was employed to model different aspects of biodiversity: species richness, evenness, and taxonomic diversity. Artificial neural networks (ANNs), often considered as "black boxes", were applied as a modeling tool. Three methods were used to reveal these "black boxes" and to identify the contributions of each environmental variable to the diversity indices. Since spatial autocorrelation is known to introduce bias in spatial analyses, Moran's *I* was used to test the spatial dependency of the diversity indices and the residuals of the model. The best predictions were made for evenness. Although species richness was quite accurately predicted as well, the residuals indicated a lack of performance of the model. Pure taxonomic diversity shows high spatial variability and is difficult to model. The biodiversity indices show a strong spatial dependency, opposed to the residuals of the models, indicating that the environmental variables explain the spatial variability of the diversity indices adequately. The most important environmental variables structuring evenness are clay and sand fraction, and the minimum annual total suspended matter. Species richness is also affected by the intensity of sand extraction and the amount of gravel of the sea bed.

1. Introduction

As a consequence of the ever increasing anthropogenic pressure on the sea floor, there is a growing need for sustainable management of this vulnerable environment. These management decisions have to be based on sound scientific data concerning the functioning of the environment and the diversity of the benthic organisms. Biodiversity indices are often used to describe areas of high biological interest. Biodiversity, however, is a broad concept covering different aspects of a community, e.g. evenness, taxonomic diversity, and species richness. Species richness is the most commonly used indicator, but it is highly dependent on sampling effort. This is not an issue in datasets collected by a single investigator. However, in large datasets originating from different sources, sampling strategy and effort can vary considerably. Therefore, we focused on indices which are assumed to be independent of sampling effort: estimators for total species richness (Chao, 1984, 1987) and evenness (Chao and Shen, 2003), the expected species richness (Sanders, 1968; Hurlbert, 1971; Simberloff, 1972), and taxonomic diversity indices (Clarke and Warwick, 1998). These diversity indices can exhibit spatial autocorrelation (SA), meaning that nearby observations are more similar than observations farther away (Odland, 1988; Legendre, 1993). Although, spatial autocorrelation can be an important source of bias in spatial analyses (Segurado et al., 2006), it is often ignored in ecological studies (Dormann, 2007). If SA remains in the residuals of the model, it may even invert the observed pattern of an environmental variable (Kühn, 2007). Although SA should always be investigated, it does not necessarily generate bias, and should be considered a tool to investigate the factors influencing richness on different spatial scales (Diniz-Filho et al., 2003).

Studies of the freshwater environment employed artificial neural networks (ANNs) to predict the occurrence of macrobenthic invertebrates (Dedecker et al., 2004) and diversity measures (Park et al., 2003). ANNs are a data driven modeling technique which received increased attention in ecological sciences as a powerful, flexible tool for uncovering complex patterns in data (Park et al., 2005). These models can simulate any continuous mathematical function and are therefore more appropriate to describe complex ecological functions than linear models. In spite of their appealing characteristics, their exploratory value is often criticised, being coined a "black box" approach (Lek et al., 1996a) since the contribution of the input variables to the output is difficult to disentangle

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from the network. Several methods have been proposed to eliminate this problem, three have been applied herein: the Perturb (Yao et al., 1998; Scardi and Harding, 1999; Gevrey et al., 2003), the Profile (Lek et al., 1995, 1996a,b; Gevrey et al., 2003) and a Modified Profile algorithm.

To our knowledge, similar modeling efforts on marine free-living nematodes (part of the meiobenthos) have not been attempted yet. This is surprising since free-living nematodes represent the highest metazoan diversity in many benthic environments in terms of species numbers (Heip et al., 1985): more than 50 species are commonly found in a single 10 cm^2 core. Owing to their interstitial life style, biogeochemical properties of the sediment have a strong influence on the diversity and the composition of nematode assemblages (Heip et al., 1985; Steyaert et al., 1999). Therefore, nematode-biodiversity studies are appropriate to assess environmental impact in the marine benthic environment (Heip et al., 1985; Kennedy and Jacoby, 1999; Schratzberger et al., 2000; Boyd et al., 2000). Moreover, nematode communities seem to be resilient and their restoration occurs easily after temporal, low impact disturbances (Kennedy and Jacoby, 1999; Schratzberger et al., 2002), making them a pertinent community to model based on long term environmental data.

In this paper, nematode biodiversity on the Belgian Continental Shelf (BCS) was modeled with a wide range of environmental variables, and the following issues were addressed: (1) the predictability of different aspects of biodiversity, (2) the effect of spatial autocorrelation on the predictability and (3) the environmental variables affecting these biodiversity indices for free-living marine nematodes.

2. Methods

2.1. Study area

The Belgian Continental Shelf (BCS) is situated in the southern part of the North Sea (Fig. 1). The total surface area is 3600 km^2 (approximately 0.5% of the total area of the North Sea), and reaches 42 m depth. The seabed is a heterogeneous environment characterised by shallow sandbanks and a broad spectrum of sediments, ranging from clay to coarse sands (Van Hoey et al., 2004).

2.2. Biological data

Within the EU Network of Excellence MarBEF, MANUELA is a Responsive Mode Project focusing on the meiobenthos (metazoans passing a sieve of 1 mm and retained on a 38 μm sieve). A central MANUELA database was compiled comprising the available data on meiobenthos on a broad European scale (Vandepitte et al., 2009). We restricted the analyses to the BCS, since extensive environmental data were available for this region. The final dataset consisted of 209 samples belonging to 75 different stations on the BCS (Fig. 1), collated from nine different datasets. This data includes information on 29783 nematodes identified to species level and collected in the period 1972–2004.

2.3. Environmental predictors

Some of the environmental variables were measured during sampling and could be retrieved from the MANUELA database. However, for most of the environmental predictors no data was readily available and these values were retrieved from area covering maps of the Belgian Continental Shelf (Table 1).

A map of the intensity of sand extraction, representing the number of extractions per year at a certain raster cell, was constructed with data collected by the Fund for Sand Extraction during the years 1996–2005 (data courtesy of the Federal Institute of Economics). The construction of one single map for the whole period is acceptable, since comparison of the recent data with older publications (Rzonzef, 1993) showed that the regions where sand extraction occurred remained unchanged.

Biochemical data and current properties data were supplied by the Management Unit of the North Sea Mathematical Models and

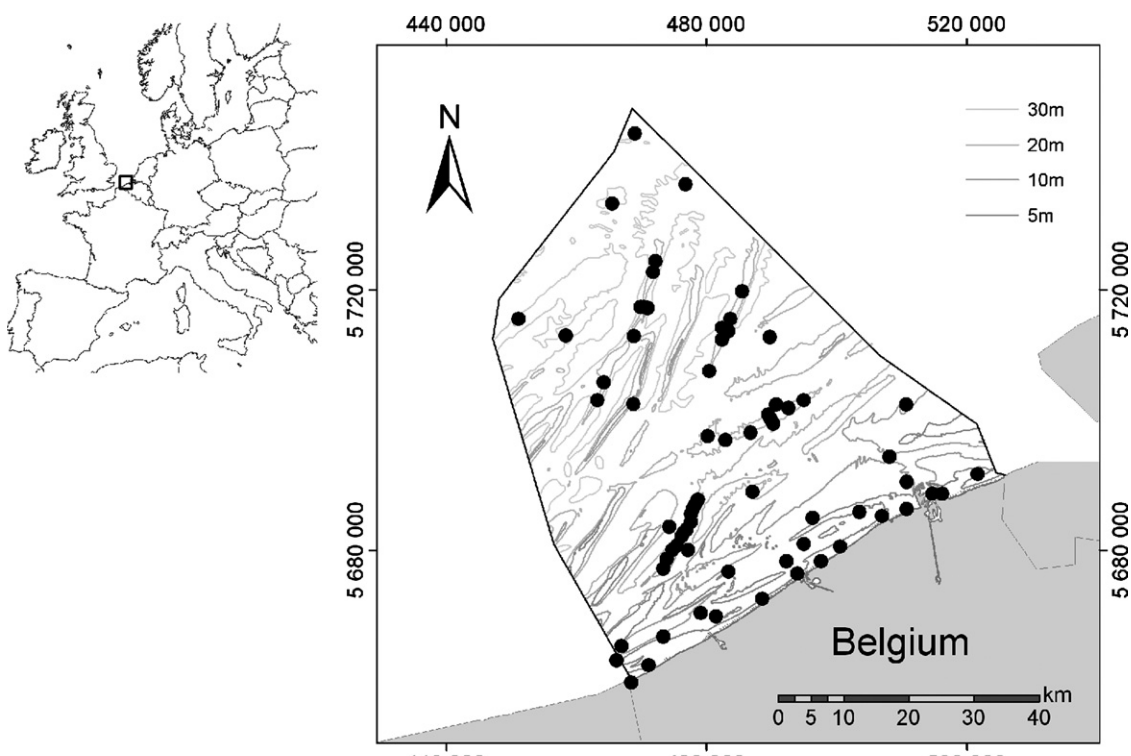

Fig. 1. Sampling stations on the Belgian Continental Shelf.