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RESEARCH ARTICLE

Metacommunity modelling, a fundamental approach for marine biodiversity studies

C. Moritz[1, *], J.M. Guarini[2], J. Coston-Guarini[2]

[1]Institut des Sciences de la Mer de Rimouski, Université du Québec à Rimouski
310, allée des Ursulines G5L 3A1 Rimouski, Québec, Canada
[2]UPMC University of Paris 06, Oceanography and Marine Environment, 4 Place Jussieu, 75252 Paris Cedex 05, France

*Corresponding author: E-mail address: c-m.moritz@laposte.net

Abstract

1 - Comprehensive understanding of biological diversity patterns requires quantifying spatial dynamic processes. Mathematical modelling offers an array of techniques to investigate ecosystem processes that cannot be observed directly or tested experimentally.

2 - In the 1990’s, a new paradigm for biodiversity studies appeared - called metacommunities - combining ecological and biogeographical concepts of species assemblages. A metacommunity is defined as a set of local communities linked by the exchanges of individuals at the regional scale. This relatively simple definition led to the development of theoretical frameworks (e.g. emphasizing neutrality, patch dynamics, species sorting and mass effects) that generated some controversy about the relative importance of the local ecological niche-based processes and regional dispersal processes. Recent studies have demonstrated that several of these proposed theories can lead to similar results when simulating the dynamics of metacommunity systems.

3 - Thus, it does not seem possible to adequately prove whether or not local processes predominate over regional ones from available datasets, even if several evaluation criteria are combined. This is why metacommunity modelling is an important step toward quantifying changes in marine biodiversity. Models can be improved by unifying population dynamics processes and by establishing accurate typologies of parameter estimates. Validation should be performed by carrying out *ad hoc* experiments, testing dynamic properties; however, the design and implementation of these experiments remain difficult because of the lack of large-scale experimental facilities under controlled conditions.

4 - Metacommunity modelling seems however to be promising for a broad range of applications in the domain of conservation of marine biodiversity, and particularly in that it can provide objective criteria to define Marine Protected Areas as a function of regional biodiversity conservation goals.

Keywords: marine biodiversity, metacommunity, mathematical modelling, conservation.

Introduction

The term “biodiversity” was introduced in the 1980’s to describe biological diversity at all possible levels of organisation and scales of observation (*e.g.* Wilson, 1988). Biodiversity is recognised as both a fundamental property of ecosystems and as a natural resource to protect and conserve. Although the characteristics of marine and terrestrial ecosystems are different and their hosted organisms have different adaptive strategies, it is possible to apply to both domains general definitions and theories about biodiversity (Mokany *et al.*, 2010). In both types of ecosystems, biodiversity has been assessed primarily at the levels of the molecules (genes, genomes), individuals (phenotypes, species) and ecosystems (communities, functions), but we focus in this study on species richness and species commonness (or rarity) as explicit characteristics of ecological diversity.

Many publications deal with ecological biodiversity (*e.g.* Schulze and Mooney, 1994; Levinton, 2008), but important ecological aspects of biodiversity remain poorly understood. Particularly, the dynamics of the basic processes governing community assembly in a given habitat remain unresolved and constitute a major challenge for ecology (Mc Gill, 2010). If studies of biodiversity should require identifying both spatial and temporal community patterns (Holyoak *et al.*, 2005), only few datasets exist to accommodate this need. The latter has led researchers to infer dynamics from a resulting information pattern assumed to be at steady-state (Hubbell, 2001).

Ecologists conceptualise how community structure and functions emerge from the interplay of abiotic (*e.g.* physical and chemical environment) and biotic variables (*e.g.* interactions between individuals, populations or species), and the respective research approaches should thus be based on a combination of techniques involving observations, experiments and modelling (Walters, 1993; Emmerson and Raffaelli, 2000). Despite the use of some simulated scenarios, standardised surveys of fauna, flora and habitats, and calculations of diversity indices or bioindicators are preferred if not required for most applications in ecology, including environmental impact assessments and natural resource management practices. However, information on underlying spatio-temporal processes is not taken into account for the calculation of these types of indices, even if they appear specifically designed to characterize both time and space diversity changes. Even if species richness and abundance declines can be observed in local or global marine biodiversity patterns (*e.g.* decreasing population viability, increasing habitat fragmentation, degradation of habitat quality, invading species overcoming resident ones, modified local community structure, reduced endemism), their causes may not be explained or predicted based explicitly on observations and primary analysis of the available datasets.

New data analysis methods were recently developed, which attempted to infer causes of community changes over time (Lynam *et al.*, 2010; Garrabou *et al.*, 2002), even though gaps remain when predictions have to be tested. To complement these methods, modelling has extensively developed over the last decade, which includes data assimilation techniques (*sensu lato*) for predictability power enhancement (Kooistra *et al.*, 2008). Substantial progress has also been made concerning the assessment of climate change impacts on species distributions (Hijmans and Graham, 2006) and on the optimal design of Marine Protected Areas (MPAs) (Gaines *et al.*, 2003).

In the frame work of community ecology mathematical models are conceptual probes, used to quantify the dynamics of complex systems and explore processes of species communities, which can be neither directly observed, nor tested experimentally. They can test hypotheses predicting biodiversity changes (Baselga and Araujo, 2009; Kaplan *et al.*, 2009). More specifically, community ecology extensively uses modelling in order to quantify the interactions between species, habitats and ecosystems.

Our objective here is to show how modelling can renew our views on the results of existing studies in spatially-structured community ecology, and to what extent mathematical community ecology has the potential to create new perspectives in marine biodiversity research.

Introducing metacommunity modelling into biodiversity research

Marine biodiversity is generally characterised by a large number of taxa with relatively high dispersal properties and adapted to take their resources from various environments. The ocean has a fundamental role in the evolution of species, acting as a distribution barrier for the terrestrial species and as a factor favouring the dispersal of marine ones. Many taxa, even entire phyla, such as Brachipoda, Ctenophora, Echinodermata or Placozoa, are exclusivey marine (May, 1994). Marine ecosystems are usually characterised by a strong coupling between biogeochemical cycles and the structure and dynamics of the communities (Sellanes and Neira, 2006; Schratzberger *et al.*, 2008) but few studies, mainly devoted to primary producers (Litchman *et al.*, 2006; Follows *et al.*, 2007) or decomposers (Yokokawa and Nagata, 2010), explore the relationships between causes and effects. This is partly due to the fact that movements of the water masses favour exchanges of benthic and pelagic populations between distant habitats, mathematical modelling often fails to represent the observed dynamics of marine ecosystems. The usual criticism is that models are based on over-simplifications which do not allow accurate simulations of the complexity of nature (Pahlow *et al.*, 2008; Gregg *et al.*, 2009). However, by taking into account the characteristics of ecosystem complexity and by designing appropriate models to represent them (Fulton *et al.*, 2003; Werner *et al.*, 2007), much progress can be achieved to improve accuracy. Many original methods have been developed to simulate population dynamics, individual-based behaviour, dynamic energy budget and size-distribution dynamics, which helped understand underlying processes of species coexistence and community dynamics. The diversity of individual and population life cycles is now represented by a large variety of mathematical models.

Over the last decade, community ecology has attempted to unify two fundamental fields of research on biodiversity: population ecology (the dynamics of a population interacting with its biotic and abiotic environment) and biogeography (originally, the spatio-temporal distribution of species in the biosphere). Renshaw (1991) stated that "the geographic distribution of a species over its range of habitats, and the associated dynamics of population growth, are inseparably related, a fact which no complete study of population development can afford to ignore". The overall objective of community ecology studies is to go a step further by combining sets of populations geographically distributed over several areas, in order to study properties of ecosystem dynamics (*e.g.* population coexistence, productivity, resilience, ecological drift). Species diversity and community structure have been considered as depending on biological interactions between individuals (intra- or inter-specific) and on the balance between exclusion and colonisation of species in a defined area (Holyoak *et al.*, 2005). Community ecology modelling in marine ecosystems must take into account the local dynamics of interacting populations and the exchanges of individuals between habitats, to better describe the processes occurring at larger regional scales. This challenge calls for a new approach to study the dynamics of marine communities, which scales up ecological processes in order to represent regional patterns of biodiversity. The concept of metacommunity was proposed for the purpose of representing explicitly spatial exchanges at regional scales between locally and dynamically interacting populations. It was initially introduced for terrestrial communities (Hanski, 1999), for which many developments and theoretical frameworks were built (Holyoak *et al.*, 2005), but it brought less attention for marine ecosystems (Guichard *et al.*, 2004;

Baskett *et al.*, 2007; Moritz *et al.*, 2009). This concept can be seen as an extension of the metapopulation introduced by Levins in 1969, and revised by Hanski (1989, 1991), with some specific developments for marine systems (Gaines and Roughgarden, 1985; Roughgarden *et al.*, 1985). A metacommunity, therefore, is defined as a set of local communities (composed of different species colonising local habitats) linked by exchanges of individuals at the regional scale. Metacommunity models take explicitly these two spatial scales into account, hence providing quantitative dimensions for them. This framework was often used to confront two different kinds of theories: the niche theory (promoted by ecology) and the neutral theory (used in biogeography).

The niche theory assumes that species have different characteristics (i.e. traits) to cope with their environment. Their coexistence is possible when a minimum of differences between their respective niches is ensured, a condition of the competitive exclusion principle (Gause, 1934). Niche differences determine not only which species are able to coexist in a given community, but also determine the structure of the community in terms of relative abundance. Although species interactions are very difficult to quantify, many experiments and observations demonstrate their importance for the spatial assembly of species and the functioning of ecosystems (Douglass *et al.*, 2008; Johnson *et al.*, 2009).

In contrast, the neutral theory assumes that communities are assembled randomly as favoured by dispersal processes. Individuals at the same trophic level are considered to be ecologically equivalent, irrespective of their species identity. Preston (1962) and MacArthur and Wilson (1963) developed the basis of the ecological neutral theory through their dynamic equilibrium concept, showing that the species richness remains constant (at steady-state) for a given area, and over time, even if the species composition changes (because immigration rate equals the extinction one). They also demonstrated experimentally (Simberloff and Wilson, 1969) that community composition (in term of species richness) reaches equilibrium at the ecological time scale, which is much shorter than the evolutionary time scale. However, the neutrality concept remains controversial. Hubbell (2001) attempted to unify neutral theories of biodiversity based on a simple neutral demographic stochastic model, which resulted in the conclusion that the overall species abundance distribution in a metacommunity follows a zero-sum multinomial (ZSM) distribution. He has demonstrated that many observed metacommunity datasets fit this ZSM, but subsequent studies (*e.g.* McGill, 2003) have shown that many datasets fit the basic lognormal distribution better than the ZSM one, suggesting that neutrality does not account for the full range of processes that structure the global species abundance distributions (Walker, 2007). Many of the studies that followed Hubbell's ones have shown how difficult it is to establish a general theory to explain community assembly (Chase, 2005; Etienne and Alonso, 2005; Wootton, 2005; Scheffer and van Nes, 2006; McGill, 2010). The statistical test to validate theories by using existing datasets is itself the cause of the absence of consensus: on the one hand, the interpolation and generalisation of a global property from a particular example is difficult, if not impossible, to perform; on the other hand, the dynamics itself is not accessible, and hence, one of the major difficulties is to infer a process from a single state, or from an observed snapshot of the ecosystem, which is only assumed to be at equilibrium. In the framework of this controversial debate, it appeared that ancillary statistical tests should be considered to infer distribution models from biodiversity patterns (McGill, 2010), but many basic ecological questions remain unsolved. For instance, how to explain the presence of few abundant species among a large number of rare species? How is endemism maintained? These questions require identifying and quantifying explicitly the dynamic processes that represent population interactions in their environment (McGill, 2003; Sizling *et al.*, 2009).

In this perspective, we developed a metacommunity model which simulates the dynamics of a set of structured marine metapopulations competing with each other (Moritz *et al.*, 2009). Basic demographic processes of maturation, mortality and reproduction were commonly defined for all species through a unified model of benthic marine invertebrate population dynamics. The structure of the populations was described by two stages (juveniles and adults), taking implicitly into account the third stage of larval development that precedes the juvenile stage. Dispersal takes place during this implicit larval stage, and is associated with a pelagic phase. Quantifying dispersal requires simulating accurately hydrodynamic properties of the considered region to calculate a connectivity matrix between local sites. Despite unification of the population dynamics, the number of parameters is several times the number of populations, multiplied by the number of sites when environmental conditions are heterogeneous. This underpins one of the fundamental problems of metacommunity models: the parameterisation, which needs to be solved.

An interesting way to address this challenge is to build a typology of the parameters. Basically, a main characteristic is identified (*e.g.* a trait such as the body size or food ratio), and all the required parameters are calculated from this characteristic. Rules of calculation were proposed such as the energetic equivalence rules (Damuth, 1981; Peters, 1983; Brown *et al.*, 2004), which stipulate that the quantity of energy taken and used by a population is independent from the size of the organisms (hence, growth and mortality are allometric functions of body size). Although these kinds of rules need to be evaluated (Loeuille and Loreau, 2006), and even if the calculation of interaction intensity between organisms needs to be improved (Berlow *et al.*, 2004), they represent one of the major research approaches to understanding the ecological processes behind the observed biodiversity patterns.

Comparisons between simulations and biodiversity patterns are not sufficient to infer the processes behind species assembly. In particular, designing experiments for biodiversity studies will help testing the general properties of the community dynamics as they were inferred from mathematical model analyses. Community experiments are usually performed in terrestrial ecosystems, with simplified communities composed of only few species or few habitats and in restricted sets of environmental conditions (Mouquet *et al.*, 2004; Douglass *et al.*, 2008). Similar experiments are very rare for marine communities, because the control of complex experimental conditions, even partial, is more difficult to perform in marine than in terrestrial ecosystems. Experiments performed in plant or bacterial metacommunities provided conclusive evidence on certain theoretical properties (Mouquet *et al.*, 2004; Venail *et al.*, 2008), but large scale facilities, allowing to rebuild and manipulate the marine seascape in controlled conditions, do not exist yet. Even if these experimental facilities are necessary to validate models, they still need to be conceived and developed. This represents a major challenge in the experimental marine biodiversity discipline.

Moreover, it clearly appears that future directions in biodiversity research should take into account an evolutionary component, making explicit the two processes that shape biodiversity: diversification (due to genetic mutation or other causes) and selection (which retains only the most adapted species). It seems impossible to represent the entire evolution of life from an assumed last common ancestor, because our knowledge about evolutionary processes and their drivers is far too incomplete and uncertain. Nonetheless, selection processes operate at short time scales, and are fundamental in adaptive dynamics. The canonical equation of adaptive dynamics links the evolutionary rate of the traits, the state of the populations and the selective value of the trait in a given environment (Loeuille and Leibold, 2008). The adaptive landscape is an extension of the concepts promoted by community ecology. Evolutionary ecology is mostly concerned with populations, incorporating most of the time only the invasion characteristics of a new mutant competing a resident population. Many problems (modalities of speciation, estimation of rates of speciation) remain to be solved in order to develop an evolutionary metacommunity approach (Loeuille and Leibold, 2008). This is a new challenge for ecology and biodiversity conservation in which marine ecology may well contribute. Particularly, the macro-evolutionary patterns of marine species diversification and extinction are very different from their terrestrial counterparts (Benton, 1995), suggesting that the processes governing the formulation of the species assemblages and their coexistence have fundamental differences.

Metacommunity modelling opens up a field of applications for conservation of marine biodiversity. By making explicit the connections between sites as well as the local colonisation success in a community, it can help designing MPAs and evaluate the effects of species re-introductions and their expected success. In this perspective, Guichard *et al.* (2004) have suggested that the observed species distribution may not be the best criterion to determine reserve placement, but dynamic criteria (like source and sink identification) should be taken into account. Baskett *et al.* (2007) have highlighted the fact that the effect of species interactions may vary with the size, spacing and location of MPAs. Additional studies are needed to have a better understanding of the mechanisms allowing marine conservation success.

Conclusion

Even if the study of marine biodiversity patterns is based on generally accepted concepts and methods, exploring fundamental differences in the processes that lead to the observed patterns of the diversification of marine life should be the focus of future research. Behind the complexity of an ecosystem, unified concepts and methods designed to represent the dynamics of the populations must be developed, in order to establish a typology of demographic parameters at the community level. By quantifying processes of dispersal through connectivity matrices from the local demographic processes of the populations, a metacommunity model is one way to address this issue. However, to validate these models, it is also necessary to conduct manipulation experiments to compare model simulations with observations. This has not been accomplished yet because no experimental facilities of this type exist for the investigation of marine systems.

The word “biodiversity” is now common in environmental policy, but it does not rely on the concepts promoted by community ecology. Models used to simulate the dynamics of interacting populations should be included in a global biodiversity evaluation framework, in order to help decision makers and policy makers define and implement appropriate life conservation measures. Facing an ever increasing number of threats to marine life, scientists must develop models that contribute to broadening our knowledge of complex adaptive systems, and methods that help defining appropriate actions to protect the marine environment and its resources. The latter can be incorporated into community ecology, where metacommunity models can be used to define protected areas or to evaluate the effect of the re-introduction of species in seascapes. However, more integrative studies at the level of interconnected marine meta-ecosystems are urgently required if we want to develop an accurate and reliable knowledge base on the conservation of our natural marine resources.

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