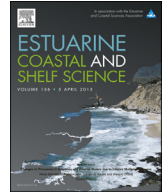




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The exergy of a phase shift: Ecosystem functioning loss in seagrass meadows of the Mediterranean Sea



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ABSTRACT

Sustained functioning of ecosystems is predicted to depend upon the maintenance of their biodiversity, structure and integrity. The large consensus achieved in this regard, however, faces to the objective difficulty of finding appropriate metrics to measure ecosystem functioning. Here, we aim at evaluating functional consequence of the phase shift occurring in meadows of the Mediterranean seagrass *Posidonia oceanica*, a priority habitat that is undergoing regression in many coastal areas due to multiple human pressures. Structural degradation of the *P. oceanica* ecosystem, consequent to increasing coastal exploitation and climate change, may result in the progressive replacement of this seagrass by opportunistic macrophytes, either native or alien. Reviewing published information and our personal records, we measured changes in biological habitat provisioning, species richness and biomass associated to each of the alternative states characterizing the phase shift. Then, ecosystem functioning was assessed by computing the exergy associated to each state, exergy being a state variable that measures the ecosystem capacity to produce work. Phase shift was consistently shown to imply loss in habitat provision, species richness, and biomass; structural and compositional loss was paralleled by a reduction of exergy content, thus providing for the first time an objective and integrative measure of the loss of ecosystem functioning following the degradation of healthy seagrass meadows.

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1. Introduction

The biodiversity-ecosystem function hypothesis holds on the positive relationship between ecosystem functioning and biodiversity (Schwartz et al., 2000; Hector et al., 2001; Cardinale et al., 2009; Connolly et al., 2013), where a reduction in biological diversity will cause a reduction in ecosystem-level processes and services (Costanza et al., 1997; Balvanera et al., 2006) and will lead to impoverished functioning of the ecosystem (Duarte, 2000). The maintenance of biodiversity, structure and integrity of an ecosystem is important for sustaining its functioning and services (Daily, 1997) and preventing ecosystem from tipping into undesired states (Folke et al., 2004). Local and global stressors caused by human activities in the marine environment triggered the necessity to reach the best available scientific knowledge on both the ecosystem status and functioning (Brown et al., 2013). To

understand the consequences of ecological change, research requires measurements that are not traditionally used to assess ecosystem condition, and needs to move beyond simple experimental studies towards a combined approach using macroecology and modelling (Russell et al., 2012; Personnic et al., 2014).

Although there are contradictory examples on the complex relationships among the range of biodiversity components (e.g. taxonomic, architectural and structural) and ecosystem functioning (Grime, 1997; Srivastava and Vellend, 2005), a large consensus on the role of biodiversity in maintaining the functioning of ecosystems has been achieved (Hector et al., 2001; Naeem and Wright, 2003; Balvanera et al., 2006; Mensens et al., 2014). This general consensus has motivated the use of biodiversity patterns as surrogates of ecosystem function when making conservation decisions (Mayfield et al., 2010 and references therein), but a quantification of ecosystem functioning remains one of the “grand challenges” to be faced by marine ecology in the 21st century (Borja, 2014). One of the main objective difficulties is finding appropriate metrics to assess ecosystem functioning.

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Perhaps there is no univocal definition of ecosystem functioning. Many papers measure it as primary production, biomass or, less frequently, respiration, decomposition and nutrient cycling (Pacala and Kinzig, 2002; Naeem and Wright, 2003; terHorst and Munguia, 2008; Raffaelli and Friedlander, 2012). Recent studies have stressed the need for new descriptors of ecosystem functioning (Pusceddu and Danovaro, 2009) that could be used to consider the actual transfer of energy through food webs, including the potential transfer/loss of genetic information (Jørgensen, 2000). In this regard, systemic indices, which try to embrace rather than reduce ecosystem complexity, might represent an adequate model of ecosystem functioning (Bendoricchio and Jørgensen, 1997 and references therein).

The statistical thermodynamic approach seems to be appropriate to capture the global properties of an ecosystem. Exergy (Mejer and Jørgensen, 1979, 1981) can be seen as a measure of the maximum amount of work that the system can perform when it is brought into thermodynamic equilibrium with its environment. In ecological terms, exergy has been expressed as the sum of energy and information contained in a given system due to living organisms (Bendoricchio and Jørgensen, 1997), and different organisms can have different strategies to obtain a certain level of exergy. Exergy express the quality factor of the energy stored in an ecosystem and, since it may be affected both by changes in the total biomass and in the species composition of the system, the measurement of exergy is frequently perfected by that of specific exergy, i.e. the ratio between (total) exergy and the total biomass of the system (Vassallo et al., 2012; Molozzi et al., 2013). Exergy and specific exergy are thus a couple of environmental indicators able to account for the quantity and quality of the system's biomass and an increase in their values is generally considered a measure of ecosystem efficiency, quality and functioning (Bendoricchio and Jørgensen, 1997; Pusceddu and Danovaro, 2009; Silow and Mokry, 2010; Vassallo et al., 2013a).

Seagrasses are recognized as key ecosystems in shallow coastal waters: they create keystone habitats with high structural complexity (Short and Wyllie-Echeverria, 1996) and enhance biodiversity (Mouquet et al., 2013), biomass and primary and secondary production (Duarte and Chiscano, 1999). Loss of seagrass-vegetated areas is now a world-wide issue that involves a shift in the dominance of different primary producers in the coastal ecosystem, which can only partially compensate for the loss of primary production (Duarte, 2002). Dramatic phase shifts are now documented for a range of marine ecosystems, including seagrasses, due to direct anthropogenic stress and climate change, which are often long lasting and difficult to reverse (Montefalcone et al., 2011).

Posidonia oceanica (L.) Delile is an endemic seagrass characterizing the ultimate succession stage ("climax") on infralittoral bottoms of the Mediterranean Sea (Molinier and Picard, 1952), where it forms extensive and monospecific meadows between the surface and about 40 m depth. These meadows represent one of the most important and productive Mediterranean ecosystem (Pergent et al., 2012) and are usually recognized as a biodiversity hot spot, hosting more than 400 species of algae and thousands of animals, and playing as base level of key trophic networks (Boudouresque and Meinesz, 1982; Personnic et al., 2014).

Posidonia oceanica meadows are listed as a priority habitat on Annex I of the EC Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Fauna and Flora (EEC, 1992). Among seagrasses, *P. oceanica* has the highest biomass values in the belowground root and rhizome system (Duarte and Chiscano, 1999). The monumental construction resulting from the horizontal and vertical growth of its rhizomes, which implies the accretion

of the intertwined rhizomes, roots and entangled sediment, is the so-called "matte" (Molinier and Picard, 1952). Thanks to this peculiar capacity among seagrasses to build the matte, *P. oceanica* can be viewed as a major ecosystem engineer (Koch, 2001) and its meadows have been compared to coral reefs for providing a keystone habitat for other organisms (Boudouresque et al., 1985).

Meadows of *Posidonia oceanica* are showing alarming signs of degradation and regression, especially in the northern parts of the Mediterranean (Boudouresque et al., 2009). In the Ligurian Sea, one of the coldest areas of the Mediterranean Sea (Morri and Bianchi, 2001), regression of the meadows has been particularly intense since the 1960s (Montefalcone et al., 2007a, 2007b, 2013). Degradation may be explained as the effects of multiple human pressures along the coastline, either local such as coastal development or global such as climate change (Brown et al., 2013), resulting in greater water turbidity and hence diminished plant vitality, as well as by the natural decline of the plant, which is believed to have had its climatic optimum around 6000 ± 2750 years Before Present (Pérès, 1984). The wide and strong regression of *P. oceanica* meadows in the Mediterranean has been often followed by its replacement by other macrophytes (Montefalcone et al., 2010). Substitutes for *P. oceanica* may be either native, such as the other common seagrass in the Mediterranean *Cymodocea nodosa* (Ucria) Ascherson and the green alga *Caulerpa prolifera* (Forsskål) Lamouroux, or alien invaders such as *Caulerpa taxifolia* (Vahl) C. Agardh and *Caulerpa cylindracea* Sonder (= *C. racemosa* var. *cylindracea*), both exhibiting among the fastest spread rates of marine bioinvasions (Meinesz et al., 2001; Ruitton et al., 2005). Although healthy and dense *P. oceanica* meadows can resist invasion, under regressive conditions *C. taxifolia* has been seen to outcompete *P. oceanica* (Jaubert et al., 1999, 2003). *C. cylindracea* has the highest colonization potential among the three species of *Caulerpa* occurring in the Mediterranean Sea, being also capable of outcompeting both *C. prolifera* and *C. taxifolia* (Montefalcone et al., 2010, and reference therein).

Cymodocea nodosa and the three species of *Caulerpa* do not form structures comparable to the matte, and thus have lower engineering capacity than *Posidonia oceanica*. Replacement of the habitat-forming species (*sensu* Bruno et al., 2003) in seagrass ecosystems has been considered a change as profound as to lead to a phase shift (Montefalcone et al., 2011), and such a change would be even more significant when the substitute is an alga instead of a seagrass (Orfanidis et al., 2003). A phase shift begins with the appearance of dead matte areas within a meadow. Dead matte, if not eroded by currents nor buried by sediment, may be recolonized by any of the potential substitutes, driving the system to shift into alternative states, thus advancing the level of phase shift (Fig. 1). Replacement of the key native seagrass species by opportunistic macrophytes (either another seagrass or algae) results in the structural degradation of the meadow ecosystem (Montefalcone, 2009). As *P. oceanica* degrades, its processes and services are compromised and ecological, economic, and social values declines (Mace et al., 2012; Vassallo et al., 2013b).

The goal of this paper is to use exergy as a synthetic measure of the expected change in ecosystem functioning following the structural degradation through the phase shift in *Posidonia oceanica* meadows. Changes in the ecosystem structure and composition with the phase shift are here evaluated by means of different descriptors, namely biological habitat provisioning, specific richness and biomass associated to each alternative state along the phase shift path, while changes in the functioning of the ecosystem have been assessed, in each state, by computing exergy (and specific exergy) as an expression of the ecosystem capacity to produce work (Jørgensen, 2000).

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