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Title: ECOSYSTEM FUNCTIONS AND ECONOMIC WEALTH: TRAJECTORIES OF CHANGE IN SEAGRASS MEADOWS

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Abstract: Increasing anthropogenic pressure on coastal regions, coupled with a conflicting relationship between ecosystem health and economic growth, has resulted in a worldwide deterioration of marine ecosystems and loss of ecosystem services. The seagrass Posidonia oceanica is an emblematic example, constituting extensive and highly valuable meadows whose extent largely declined in the last decades. In this paper, more than one century of history of P. oceanica meadows has been reconstructed in a NW Mediterranean region combining models and historical information. The equivalent economic value of P. oceanica ecosystem functions was evaluated according to a donor-side approach and compared with the main economic sector of the region. A loss of more than 50% of the original surface of P. oceanica meadow extent has been documented between 1850 and around 1980, followed by stabilization in the last decades. Decline of P. oceanica has often been coupled with its replacement by the more tolerant seagrass species Cymodocea nodosa, only partially compensating for the loss of P. oceanica. The loss of the value of ecosystem functions between 1861 and 2009 was computed in 1,106.8 billion emergy-euros (em€), a figure greater than the value added in the same period by tourism-related activities. Protection measures undertaken in the last decades slowed down the decline of P. oceanica meadows, while no concomitant decrease of the regional economic growth occurred. This study illustrates the tradeoffs between ecosystem conservation and economy growth, underlining the importance of long-term monitoring for environmental management and preservation of the natural capital.

Cover Letter

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Genoa, 4 September 2017

Dear Prof. Almeida,

please find attached the file of our manuscript, titled "ECOSYSTEM FUNCTIONS AND ECONOMIC WEALTH: TRAJECTORIES OF CHANGE IN SEAGRASS MEADOWS" (Ms. Ref. No.: JCLEPRO-D-17-02796R1), that we further revised following all the referee's suggestions.

We hope that with the present revised version we fulfill all the requirements. Let me know about any other need.

Many thanks in advance, hoping to read you soon.

Your sincerely

Monica (on behalf of all the co-authors)

Monica Montefalcone

Here are listed the main changes we did at our manuscript “**Ecosystem functions and economic wealth: trajectories of change in seagrass meadows” (JCLEPRO-D-17-02796R1).**
We took full consideration of all the further comments provided by the external referee to improve the paper content and we accepted all of them. All changes done within the text have been written in blue color.

Reviewer #1:

1) *Are the monetary values for P. oceanica, Cymodocea, or both?*
Answer: The paper by “Tuya et al. (2014)" we quoted is referred only to *C. nodosa*. Then we rephrase the sentence to make it clearer (page 4, 1st paragraph).

2) *I wouldn't say these approaches disregard the role of nature, but they do value from the anthropocentric perspective.*
Answer: We changed the sentence as suggested to “valuing from the anthropocentric perspective” (page 4, 1st paragraph).

3) *You need to be clear this is not a monetary value, it is a monetary equivalence emergy value (i.e. EmEuro).*
Answer: We changed the text accordingly to: "resulting in a monetary equivalent emergy value of 1.7E+6 em€$\cdot$ha$^{-1}\cdot$a^{-1}" (page 4, last rows and page 5, 1st paragraph).

4) *In m^2?*
Answer: We added the units: “8.8E+13 seJ$\cdot$m$^{-2}\cdot$a^{-1}” (page 11, paragraph 2.5).

5) *Unreliable?*
Answer: We changed the sentence to avoid misunderstandings (we do not want readers to understand that the maps we used are not reliable to our purpose): “Old maps can be little reliable to certain purposes and must be considered carefully” (page 16, 1st paragraph).

6) *The reference "*Campbell, D.E., 2000" *is incorrect*.
Answer: we changed with " Campbell, D.E., 2000. A revised solar transformity for tidal energy received by the earth and dissipated globally: implications for emergy analysis. In: Brown M.T. (Ed), Emergy Synthesis: Theory and Applications of Emergy Analysis. Proceedings of the First Biennial Emergy Analysis Research Conference, University of Florida, Gainesville, FL, 255-264" and with "Campbell, D.E., 2016. Emergy baseline for the Earth: A historical review of the science and a new calculation. Ecological Modelling, 339, 96-125" (page 21, Reference list).

Highlights (for review)

- History of seagrass meadows in NW Mediterranean was traced between 1850 and 2009
- Models and historical information are combined to draw trajectories of change
- Meadows experienced a huge regression followed by a stabilization in the last decades
- Loss of related ecosystem functions was greater than the regional economic growth
- Investment in nature protection is not in conflict with economic wealth increase

ECOSYSTEM FUNCTIONS AND ECONOMIC WEALTH: TRAJECTORIES OF CHANGE IN SEAGRASS MEADOWS.

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Abstract

Increasing anthropogenic pressure on coastal regions, coupled with a conflicting relationship between ecosystem health and economic growth, has resulted in a worldwide deterioration of marine ecosystems and loss of ecosystem services. The seagrass *Posidonia oceanica* is an emblematic example, constituting extensive and highly valuable meadows whose extent largely declined in the last decades. In this paper, more than one century of history of *P. oceanica* meadows has been reconstructed in a NW Mediterranean region combining models and historical information. The equivalent economic value of *P. oceanica* ecosystem functions was evaluated according to a donor-side approach and compared with the main economic sector of the region. A loss of more than 50% of the original surface of *P. oceanica* meadow extent has been documented between 1850 and around 1980, followed by stabilization in the last decades. Decline of *P. oceanica* has often been coupled with its replacement by the more tolerant seagrass species *Cymodocea nodosa*, only partially compensating for the loss of *P. oceanica*. The loss of the value of ecosystem functions between 1861 and 2009 was computed in 1,106.8 billion emergy-euros (em€), a figure greater than the value added in the same period by tourism-related activities. Protection measures undertaken in the last decades slowed down the decline of *P. oceanica* meadows, while no concomitant decrease of the regional economic growth occurred. This study illustrates the tradeoffs between ecosystem conservation and economy growth, underlining the importance of long-term monitoring for environmental management and preservation of the natural capital.

Keywords: *Posidonia oceanica*, reference condition, historical information, modelling, ecosystem functions, Mediterranean Sea.

1. INTRODUCTION

Human development and activities along coastal regions, coupled with the conflicting relationship among ecosystem conservation, economic growth and human well-being, have resulted in a worldwide decline of marine ecosystems and the detriment of their biodiversity (Boesch et al., 2001; Lotze et al., 2006; Montefalcone et al., 2011). Marine ecosystems provide many benefits to humans, which are not considered as marketed products or services in spite of being significant contributors to the human economy (Costanza et al., 1997, 2014). Therefore, the value of natural capital provided by ecosystems is often neglected in environmental management decisions. A broader consideration of environmental issues, taking into account tradeoffs between ecosystem status and economic wealth, is thus mandatory. This requires to identify and evaluate ecosystem services, which are the benefits that people derive from ecosystems (MEA, 2005), and ecosystem functions, the biological processes of functioning and maintaining ecosystems (Bouvron, 2009). Even if these functions are not completely perceived by society and economy, the providing of services depends on them since unhealthy ecosystem conditions compromise its ability to generate benefits, even economic, for coastal areas (e.g. fishery, tourism).

The seagrass *Posidonia oceanica* (Linnaeus) Delile is an emblematic species forming extensive meadows from the surface down to 40 m depth, and represent one of the most diverse and productive ecosystems in the Mediterranean Sea (Pergent et al., 1994, 2010). *P. oceanica* meadows provide many valuable functions and services, such as nursery areas for fish and invertebrates, high production, oxygenation of coastal waters, production of food for many species, sediments trapping and shoreline defence (Gacia et al., 2002; MEA, 2005; Hein et al., 2006; Mangos et al., 2010). The carbon sink role of *P. oceanica* meadows, due to slow decomposition rate of lignified rhizomes and roots within the so-called ‘matte’, a typical terraced structure consisting of interlaced remnants of roots, rhizomes, and sediment filling interstices (Giovannetti et al., 2008; Vacchi et al., 2017), has also been highlighted (Gacia et al., 2002; Boudouresque et al., 2006; Díaz-Almela and Duarte, 2008; UNEP MAP, 2010; Pergent et al., 2012). The beached deposits of dead leaves of *P. oceanica* are used as biomass source for anaerobic digestion to produce biogas (Balata and Tola, 2017) and as reinforcement for building materials (Saval et al., 2014; Herraiz et al., 2016).

Several authors calculated the value of services provided by seagrass with traditional anthropocentric (user-side) approaches. Terrados and Borum (2004) cautiously estimated the overall value of services provided by seagrass to be 1.6E+4 €·ha^{-1}·a^{-1} - possibly an underestimation, according to the authors themselves. Blasi (2009) estimated the monetary value of *P. oceanica* to be 1.4E+5 €·ha^{-1} for oxygen production, 3.1E+6 €·ha^{-1} for coastal protection, 1.7E+4 €·ha^{-1} for refuge for commercial fish, and 1.7E+4 €·ha^{-1} for primary production. More recently, the ecosystem services provided to humans by *P. oceanica* alone has been evaluated at 2.8-5.1E+2 €·ha^{-1}·a^{-1} (Campagne et al., 2015). Tuya et al. (2014) assessed the monetary value of *Cymodocea nodosa* (Ucria) Ascherson, another common seagrass in the Mediterranean Sea, as ‘fishery’ grounds equal to 8.6E+2 €·ha^{-1} and the value as ‘nursery’ grounds equal to 9.6E+1 €·ha^{-1}·a^{-1} using fish market values. These studies highlighted the importance of natural resources to support human economy (Vassallo et al., 2017), but they are based on the calculation of the amount of money that people are, or would be, willing to pay or save given the presence of seagrass, valuing from the anthropocentric perspective. Other authors recognized the existence of non-anthropocentric measures of value and proposed biophysical evaluation methods, providing a complementary approach to the economic assessment of natural resources (Odum, 1988, 1996; Wackernagel et al., 1999; Muller, 2005; Jørgensen, 2010; Muller and Burkhard, 2012; Paoli et al., 2017). In particular, Odum (1996) introduced a measure of natural value named “emergy” that has been widely applied to explore the interplay of natural ecosystems and human activities (Vassallo et al., 2009; Brown and Ulgiati, 2011; Franzese et al., 2013, 2014; Buonocore et al., 2014; Turcato et al., 2015; Nikodinoska et al., 2017). The emergy method consists in a donor-side approach where the evaluation of the ecosystem functions or services depends on the amount of resources invested by nature to generate and maintain them, independently of users ascribing a value to a function or service (Pulselli et al., 2011; Paoli et al., 2013; Vassallo et al., 2017). According to the emergy accounting method, the more work of biosphere is embodied in generating a function, the greater is its value (Odum, 1988, 1996). This amount, expressed in emergy or money equivalent terms (i.e. emergy-euros, em€), is the basis to assure to future generation the same provision of services currently enjoyed. Vassallo et al. (2013) performed an evaluation of *P. oceanica* functions based on the account of resources employed by nature through emergy analysis, in term of biophysical flows used to support their generation (Ulgiati et al., 2011), resulting in a monetary equivalent emergy value of 1.7E+6 em€·ha^{-1}·a^{-1}.

P. oceanica meadows have declined all along the Mediterranean coasts (Boudouresque et al., 2006, 2009) due to environmental alterations and physical damages resulting from human activities (Duarte, 2002; Montefalcone et al., 2008), climate warming (Jordà et al., 2012), and reduction of water quality (Waycott et al., 2009; Marbà et al., 2014). Structural degradation of *P. oceanica* ecosystem has resulted in its replacement by opportunistic species with lower ecosystem engineering potential, such as alien algae of the genus *Caulerpa* or the native seagrass *C. nodosa* (Montefalcone et al., 2007a, 2010). The loss of *P. oceanica* and the shift to alternative states dominated by different species compromise the functioning of the ecosystem in terms of exergy (maximum amount of work that the system can perform when it is brought into thermodynamic equilibrium with its environment, according to Mejer and Jørgensen, 1979), species richness and biomass (Montefalcone et al., 2015), thus leading to both ecological and economic decline (Vassallo et al., 2013).

In order to understand the effects of anthropogenic pressures on ecosystems, it is necessary to assess the long-term changes they have undergone (Leriche et al., 2004; Gatti et al., 2017). To this purpose, the present condition of an ecosystem must be compared to past scenarios and, when possible, to its reference condition (i.e. the condition of the ecosystem before heavy human impact). Identifying the reference condition of ecosystems in highly exploited coastal regions is challenging because these ecosystems have progressively changed through time. Such a ‘sliding baseline syndrome’ (Gatti et al., 2015, and references therein) can complicate the identification of the impacts that lead to the current status of ecosystems and, then, to the underestimation of their potential to provide resources and services. Reference conditions can be defined using three potential sources of information (Borja et al., 2012): 1) areas still recognized as pristine; 2) historical data; and 3) predictive modelling. Two major constrains limit the possibility of using the former two approaches: pristine areas are not expected anymore (Stachowitsch, 2003; Montefalcone et al., 2009), whilst historical information is often sparse and rarely reliable (Leriche et al., 2004; Ardizzone et al., 2006). Predictive models seem to have a great potential to surrogate or integrate past information (Vacchi et al., 2012), notwithstanding conceptual obstacles and problematic descriptor choice.

In this paper, change through time in the extent of the seagrass species *P. oceanica* and *C. nodosa* has been assessed and the functions played by *P. oceanica* meadows at each time have been evaluated according to Vassallo et al. (2013), who adopted a donor-side approach to appraise the processes that maintain and improve the ecosystem health conditions more than those having a direct benefit for humans. These approaches allowed estimating an equivalent economic loss due to ecosystem degradation, which was compared with the economic growth in a coastal touristic region. The following steps have thus been taken (Fig.1): i) the reference extent of *P. oceanica* meadows at a regional scale has been defined through the application of predictive models; ii) historical and recent cartographies have been combined in chronological series to highlight long-term (160 years) change in the extent of seagrass meadows (considering both *P. oceanica* and *C. nodosa*); iii) the amount of *P. oceanica* meadow and the value of the related ecosystem functions have been quantified; iv) the relationship between natural capital loss and regional economic increase has been investigated, comparing ecosystem functions value and value added of the tertiary sector.

2. MATERIALS AND METHODS

2.1 Study area

Liguria is an administrative region of NW Italy (Fig. 2) with a coastline of approximately 330 km. Liguria can be divided in two parts, the Western Riviera, from the French border to the chief-town Genoa, and the Eastern Riviera, from Genoa to the Tuscany border. The Western Riviera is characterized by rocky headlands alternating with beaches of sand and gravel (Rovere et al., 2015), and usually exhibits gentle slopes where *Posidonia oceanica* meadows form large and continuous fringes along the coastline (Bianchi and Peirano, 1995). The Eastern Riviera is characterized by rocky coasts with steep slopes, with alternating cliffs and pocket beaches (Vacchi et al., 2012), and where *P. oceanica* meadows are comparatively smaller and more patchy (Bianchi and Peirano, 1995). The Ligurian coast is mainly exposed to southern winds, with minor differences between the two Rivieras (Vacchi et al., 2012). Thus, the predominant wave direction is SW, followed by SE and S.

Burgos-Juan et al. (2016) illustrated an alarming regressive trend of the *P. oceanica* meadows in Liguria through the XX century. Since 1992, all the Ligurian *P. oceanica* meadows have been listed as priority natural habitats to be included in sites of European community interest (Relini, 2000) and starting 1997 four marine protected areas have been established, all of them hosting *P. oceanica* meadows (www.regione.liguria.it).

2.2 Predictive models

2.2.1 Meadow upper limit

A predictive model (Vacchi et al., 2014) has been used to locate the region of the seafloor where the upper limit of *Posidonia oceanica* meadows should lie under natural conditions (i.e. the reference condition), which depends on the depth where waves break (i.e. the breaking depth). The breaking depth depends, in turn, on the morphodynamic domain of the coast. The latter is defined by the interaction between seafloor morphology and hydrodynamic processes (Vacchi et al., 2010) and is measured through the surf scaling index (Dean and Dalrymple, 2004). The model was applied to 156 transects, located perpendicular to the coast and spaced by about 2 km from each other all along the Ligurian coast. Two steps were performed in order to define the morphodynamic domain and the reference conditions for the meadow upper limit at each transect:

(i) Calculation of the breaking depth (d_b) and of the surf scaling index (ε), which is a hydrodynamic index that combines the wave regime and the coast slope, by applying the equations 1 (Smith, 2003) and 2 (Guza and Inman, 1975), respectively:

$$d_b = H_b/\gamma b \qquad \text{(equation 1)}$$

$$\varepsilon = 0.5H_b\ \omega^2/g\ \tan\beta^2 \qquad \text{(equation 2)}$$

where $H_b = H_0K_{sh}\ \sqrt{\varphi_o/\varphi_b}$ is the breaking wave height, H_0 = offshore wave height in meters, K_{sh} = shoaling coefficient (change of the waves height in shallower waters), φ_o and φ_b = offshore and nearshore waves approach angle, respectively; $\gamma b = (b\text{-}a)\ (H_b/gT_0^2)$ is the breaking index, a and b being empirical coefficients depending on the slope of the coast from the coastline to 5 m depth, g is the gravity acceleration, T_0 is the wave period in seconds; $\omega = 2\pi/T_0$. The wave parameters (H_0 and T_0) were the annual values (with a return time of 1 year) of the predominant wave direction at each sector of the coast. The wave directions and the corresponding wave parameters were taken from previous studies carried out during beach nourishment activities (www.regione.liguria.it) and from the available meteomarine data (www.idromare.it).

(ii) Application of the equations 3 and 4 that correlate the theoretical *P. oceanica* upper limit position with the surf scaling index (Vacchi et al., 2014):

$$k_{min} = 5.94 + 0.29\varepsilon \qquad \text{(equation 3)}$$

$$k_{max} = 17.83 + 0.41\varepsilon \qquad \text{(equation 4)}$$

where k_{min} and k_{max} represent the position of the meadow upper limit as predicted using 2.5% and 97.5% of the model parameter estimates, respectively. k_{min} and k_{max} provide the range of distances from the breaking depth, within which the upper limit is expected to be located in absence of any source of anthropogenic disturbance.

2.2.2 Meadow lower limit

The lower limit of seagrass meadows is controlled by both light availability and water movement. Two different models were applied to discriminate which was the limiting factor in correspondence of each transect: the model by Duarte (1991) predicts the position of the lower limit depending on water transparency, while the model by Vacchi et al. (2012) considers the interaction of the offshore wave and the seafloor as the limiting factor. In this study, the shallower value obtained at each transect was considered as the theoretical lower limit position.

The lower limit of *P. oceanica* meadow as governed by water movement was calculated by applying equation 5 (Vacchi et al., 2012):

$$Z_c = 0.32\ L_0 + 5.62 \qquad \text{(equation 5)}$$

where Z_c is the depth of the meadow lower limit (meters) and L_0 is the offshore wave length (meters). To apply this model, the coastline was divided in sectors according to the predominant wave direction. The annual L_0 value (with a return time of 1 year) of the predominant direction (www.regione.liguria.it; www.idromare.it) was used to calculate the theoretical lower limit at each sector.

The lower limit of *P. oceanica* as governed by light availability was calculated by applying equation 6 (Duarte, 1991):

$$\ln Z_c = 0.26 - 1.07\ \ln k \qquad \text{(equation 6)}$$

where Z_c is the depth (in meters) of the meadow lower limit and k is the coefficient of light attenuation underwater (m^{-1}). This model showed no prediction bias under 5 m depth and light attenuation of 0.27 m^{-1} (which does not affect the prediction of the *P. oceanica* lower limit in Liguria) and a prediction error of less than 10% when compared to an updated *P. oceanica* dataset (Duarte et al., 2007).

Considering the increase of water turbidity in Liguria during the last decades (Attolini and Coppo, 2005), the oldest information available about light penetration came from the Secchi Disc depths (SD, in meters) measured during the 1970s (Della Croce, 1980). Water transparency in the 1970s was likely to be already altered with respect to the situation in mid XIX century, which might bias the positioning of the reference lower limit. Della Croce (1980) divided the Ligurian coastline in 10 sectors and gave the average SD value for each sector. The coefficient of light attenuation underwater (k) was calculated from SD using equation 7:

$$k = 1.7 \cdot SD^{-1} \qquad \text{(equation 7)}$$

2.2.3 Assessment of the reference extent of Posidonia oceanica *meadows*

Once the breaking depth and the k_{max} and k_{min} values were obtained for each transect, the breaking depth was located using a digital terrain model on a GIS platform, and k_{min} and k_{max} distances were measured from the position of the breaking depth on map. Both theoretical lower limits were represented on the digital terrain model and only the shallower one at each sector was used to calculate the reference meadow extent.

The predicted limits were used to draw polygons, defined by k_{min} and the lower limit (maximum extent) and by k_{max} and the lower limit (minimum extent), whose total area led to assess a range for the reference extent of *P. oceanica* in Liguria. The areas known to be under the influence of the main stream discharges, and thus expected to be ‘naturally’ not suitable for the development of *P. oceanica*, were subtracted from the polygons to compute the final reference extent.

The present bathymetries in front of the main cities of Liguria, i.e. Imperia, Savona, Genoa and La Spezia, do not correspond with the original topography of these areas prior to the construction of their commercial harbours. Due to the need of accurate bathymetric data to obtain reliable predictions, the models were not applied in correspondence of these cities. Considering that these commercial harbours already existed before the construction of the coastal railway, started in the late 1850s (Betti Carboncini, 1992a, 1992b), the reference extent of *P. oceanica* meadows resulting from the application of the predictive models was referred to the 1850, assumed as the date when human impacts on the coast were still minimal.

2.3 Historical and recent information on seagrass meadows extent

In Liguria, the oldest qualitative information on the distribution of *Posidonia oceanica* meadows dates back to the beginning of the XX century, around 1910 (Issel, 1912, 1918). Mancini (1934) added little detail. Combining these old descriptions with the analysis of nautical charts produced by the Italian Navy, Bianchi (1998) provided a first estimation of *P. oceanica* meadow extent at the epoch. No further information existed until the 1960s, when the first historical cartographies became available (Table 1; see also Fig. 3 for selected examples). These first cartographies consisted in fishing maps that typically depicted bottoms covered by 'algae' (Santi, 1962; Fusco, 1968, 1972). In ancient non-scientific publications, the term 'algae' was normally used to define any large marine macrophyte. Fishermen used to call 'alga' especially *P. oceanica*, and what these old maps called 'algal bottoms' corresponded essentially to seagrass meadows (Bianchi and Peirano, 1995). From the information available in the first half of the XX century it was not possible to discriminate with certainty between *P. oceanica* and *Cymodocea nodosa*. Earliest studies only reported *P. oceanica* (Issel, 1912, 1918; Tortonese and Faraggiana, 1937; Tortonese, 1962; Fierro and Piacentino, 1969) but it is unclear whether *C. nodosa* was absent or simply not recognized (Bianchi and Peirano, 1995). Many marine botanical studies conducted in Liguria at the turn of the XX century (see Barberis et al., 1979 for references) never mentioned *C. nodosa*, and it is difficult to believe that so many experienced marine naturalists failed to recognise this distinctive species. It is therefore likely that once *C. nodosa* was at least very scarce in Liguria.

The relative importance of *P. oceanica* and *C. nodosa* in the 1960-70s was roughly estimated from an unpublished map prepared by C.N. Bianchi and R. Cattaneo-Vietti for the Italian Society of Marine Biology based on grey literature and personal experience (Bianchi and Peirano, 1995). Ligurian seagrass meadows extent in the 1980s was obtained by the maps of Cattaneo et al. (1980), while those of Tunesi et al. (1985) and Seaway (1986, 1988) allowed calculating the relative importance of the two seagrass species in those years. The atlas of the seagrasses of Liguria by Bianchi and Peirano (1995) was the first to provide detailed quantitative information about *P. oceanica* and *C. nodosa* meadow extents, mostly derived from acoustic surveys in the early 1990s; in addition, it offered an overview and critical analysis of past data. Finally, a more complete atlas of the marine habitats of Liguria, seagrass meadows included, was produced by Regione Liguria in 2006 (Diviacco and Coppo, 2006), subsequently updated to 2009 (Diviacco and Coppo, 2009). These latter cartographies also display areas with living *P. oceanica* mixed with dead matte (called ‘mosaic’), as well as areas with only dead matte. To the purpose of the present study, half the surface of the mosaic was considered as living *P. oceanica*, while the dead matte was not considered in the calculation of the total *P. oceanica* extent.

Only the most recent cartography (Diviacco and Coppo, 2009) was available in digital format (www.regioneliguria.it/cartografia), whereas all the others were available only as printed maps and were therefore scanned at a resolution of 600 dpi. Once digitalized, all maps were georeferenced using the Universal Transverse Mercator (UTM) metric coordinate system and processed in ArcMap®. The limits of the meadows were traced manually and the total extent of the meadows at each time was calculated on the basis of the area of the polygons obtained. Temporal trend of *P. oceanica* meadows extent has been drawn combining both modelling, as previously described, and cartographic information.

2.4 Artificialization of the coastline

Changes in seagrass meadow extent and composition were compared to the trend in the artificialization of the Ligurian coastline to explore the possible causes of seagrass meadow degradation at regional scale. Historical series about coastline typology (i.e., beach, rock/high coast, artificial coast) were obtained from the Liguria Region cartographic database (http://www.cartografia.regione.liguria.it/) and the linear distance corresponding to each category at each time was calculated on the GIS platform.

2.5 Monetary equivalents account through emergy evaluation

The value of the ecosystem functions provided by *Posidonia oceanica* meadows in Liguria was calculated according to Vassallo et al. (2013), who reported an emergy value of 8.8E+13 seJ$\cdot m^{-2} \cdot a^{-1}$. It is possible to calculate the corresponding monetary equivalent through a conversion factor called "Emergy-to-money ratio" (EMR). Monetary equivalents of biophysical values are expressed in emergy-euros. An alternative to the employment of EMR has been suggested by Pulselli et al. (2011): dividing the value of world ecosystem services (Costanza et al., 1997) by the emergy flow to the biosphere (Campbell, 2000; Campbell, 2016, and references therein), the amount of money that is, on average, produced by one seJ of solar emergy is obtained. Pulselli et al. (2011) proposed a seJ to em€ ratio equal to 5.1E+11: applying this ratio, the emergy value calculated for *P. oceanica* by Vassallo et al. (2013) becomes 1.7E+6 $\text{em€}\cdot\text{ha}^{-1}\cdot\text{a}^{-1}$. This calculation can be considered as an estimate of the ability of *P. oceanica* ecosystem to provide economic wealth for humans. Currently, a debate on merging biophysical and economic values has arisen (Campbell and Tilley, 2014). Here the em€ value is simply employed as a conversion to allow an easier understanding of the ecological value of ecosystem functions in decision-making processes and to permit the comparison between emergy and economy metrics (Bastianoni et al., 2007). However, even if the applied ratio partially depends on market dynamics, its adoption does not affect the biophysical and donor-side nature of emergy analysis (Franzese et al., 2015; Vassallo et al., 2017), while it represents an additional step to facilitate the communication of the importance of natural capital in socio-economic and policy contexts (Vassallo et al., 2017).

The monetary value of the functions provided by the *P. oceanica* meadows in each year (i.e. from 1850 to 2009) was then calculated by multiplying the meadow surface area by the *P. oceanica* monetary value per unit area (Vassallo et al., 2013). The estimation of the total monetary loss associated to the gradual reduction of *P. oceanica* natural capital was made according to the modelled temporal trend of reduction in the extent of the meadows (Fig. 4) and by applying equation 8:

$$\text{total monetary loss} = \sum_{i=1850}^{2009} \Delta_i \text{ value per unit area} \qquad \text{(equation 8)}$$

where Δ_i = *Posidonia oceanica* extent_i – *Posidonia oceanica* extent_{1850} is the quantity of *P. oceanica* being lost in the i^{th} year with respect to the reference year (i.e. 1850), while the total monetary loss is accounted for as the sum of ecological functions that, every year, were not provided due to the decrease of *P. oceanica* since the reference year.

Total monetary loss associated with ecosystem functions drop due to *P. oceanica* natural capital decrease was then compared with the increase of the value added of the tertiary sector in the same time frame. Gross value added is a measure of the contribution to Gross Domestic Product (GDP) made by an individual producer, industry or sector (http://stats.oecd.org/glossary/). The tertiary sector in Liguria is strongly dependent on tourism and related activities and then can be considered as a proxy of local economy. The Italian Bank (http://www.bancaditalia.it) provided data of the value added of the tertiary sector in Italy between 1861 and 2009, while the National Institute of Statistics (ISTAT) (http://www.istat.it) provided the same data for Liguria and Italy between 1995 and 2015. All the values were converted to the Euro value in 2009. Italy and Liguria recent data were correlated to estimate the value added of the tertiary sector in Liguria from 1861 (the oldest data available), and the total gain in terms of added value was calculated from 1861 to 2009 using equation 9:

$$\text{total gain} = \sum_{i=1861}^{2009} (\text{Value added}_i - \text{Value added}_{1861}) \qquad \text{(equation 9)}$$

where total gain represents the total wealth stocked as accounted by the economy. The adoption of monetary equivalents within the context of natural capital and ecosystem functions evaluation performed with emergy does not aim at assigning a market value to nature but at making them visible and more comprehensible to users, policy makers and the general public.

3. RESULTS

3.1 Application of the predictive models

Mapping the contours of the upper and lower limits of *Posidonia oceanica* meadows expected under natural conditions allowed visualizing the present alterations in their extent (see Fig. 5 for three selected examples). Present *P. oceanica* meadows lie within their predicted natural limits only in those sectors far from tourist harbours or other major anthropogenic modifications of the coastline. In front of harbours (e.g., Loano, Sanremo), coastal reclamations and frequently nourished beaches (e.g., Monterosso al Mare), both the upper and the lower limit appear regressed, therefore implying shrinkage of the meadow. On the contrary, meadows can extend beyond the predicted upper limit in front of rocky (either natural or artificial) coastlines (e.g., Sanremo, east of the harbour). Present lower limits deeper than those predicted by light extinction (e.g., Sanremo) are probably indicative of unreliable historical Secchi disk measurements. Areas where *P. oceanica* has apparently disappeared are today occupied by dead matte or by stands of *Cymodocea nodosa* (e.g., Loano, Sanremo, Monterosso al Mare).

3.2 Temporal trend of *Posidonia oceanica* meadows extent

Models predicted that the extent of *Posidonia oceanica* in Liguria in 1850 (i.e., before the coastal railway construction and therefore before major generalized human impacts on the coastline) ranged between 11,665 and 12,216 ha (Fig. 4). By the beginning of the XX century, the estimated extent was only 6000-8000 ha and continued to drop until recent decades. It stabilized around 4300 ha (nearly one third of the predicted original extent) since the early 1990s. This temporal trend was better described by a second order polynomial (Fig. 4).

3.3 Temporal trend of seagrass meadows extent and composition

Notwithstanding large variations in the estimates, the total extent of seagrass meadows (either *Posidonia oceanica* or *Cymodocea nodosa*) in Liguria remained roughly stable around 6700-7600 ha, or even slightly increased of approximately 900 ha (provided that such an apparent increase is significant), between the 1960s and 2009 (Fig. 6a). This stability or slight increase was due to the expansion of *C. nodosa*, which compensated or over compensated for the loss of *P. oceanica* extent. The above described trend in seagrass meadows extent exhibits intriguing parallelisms with changes in the naturalness of the Ligurian coastline during the XX century (Fig. 6b): the proportion of beaches and rocky coasts decreased, and so did (with a similar pace) *P. oceanica* meadows; the proportion of artificial coast increased, and so did *C. nodosa* meadows. The situation, for both the coastline and meadows, has apparently stabilized in the last two decades.

3.4 Temporal trend of ecosystem functions provided by *Posidonia oceanica*

Ecosystem functions provided by *P. oceanica* meadows in Liguria declined from 1.04E+22 seJ·a^{-1} (equivalent to 20.4 em€ billion per year) in 1850 to 3.77E+21 seJ·a^{-1} (equivalent to 7.4 em€ billion per year) in 2009 (Fig. 7). The value added of the tertiary sector showed a very slow increase from 1861 to the Second World War, when it fell abruptly. After the war the value increased enormously, to reach 32.1 € billion in 2009 (Fig. 7). The total economic gain between 1861 and 2009, due to the value added accumulated each year, was 1001.1 billion €.

The total loss of ecosystem functions provided by *P. oceanica* accumulated annually between 1850 and 2009 was 6.96E+23 seJ, equivalent to 1368.3 billion em€. The loss of ecosystem functions calculated between 1861 and 2009 summed up to 6.91E+23 seJ, equivalent to 1106.8 billion em€.

4. DISCUSSION

4.1 Combining predictive models and historical information to draw trajectories of change

The Ligurian coastal zone has undergone intense alterations starting with the construction of the main roads and railways in the 1850s. Expansion of urban centres and construction of many infrastructures for tourism through the XX century caused further major changes (Ferrari et al., 2005). Progressively, the tertiary sector on the coastal strip, mainly represented by tourism, became fundamental for the economy of the region (Ugolini, 1996; Callegari, 2003; Ferrari et al., 2005; Vassallo et al., 2009). Building activities reached a peak in the 1960s, and the heavy coastal development was recognized as the main cause of the massive decline experienced by *Posidonia oceanica* meadows (Bianchi and Peirano, 1995).

In the absence of any quantitative information on the original extent, the application of predictive models (Duarte, 1991; Vacchi et al., 2012, 2014) was the only possible approach for defining the reference condition for *P. oceanica* meadows in Liguria. These models have a relatively easy formulation and may be also applied where the coastline has been largely modified, provided that the assessment of the original terrain morphology remains possible. Reconstructing the upper and lower limits of *P. oceanica* meadows of Liguria allowed calculating for the first time their dramatic regression under the synergic effects of both local and global impacts (Montefalcone et al., 2007b). The upper limits presently found shallower than predicted could be due to the protection against waves by artificial structures and to the ability of *P. oceanica* to grow on hard substrates (Giovannetti et al., 2008; Vacchi et al., 2017), where stronger anchoring of the roots make the plant more resistant to wave action (Montefalcone et al., 2016).

Historical information and cartographies allowed drawing the trajectories of change of *P. oceanica* meadows in the last century. Old maps can be little reliable to certain purposes and must be considered carefully (Leriche et al., 2004; Montefalcone et al., 2013) but yet contain precious information. Scientific mapping of marine habitats is relatively recent (Bianchi et al., 2012) and the existence of fishery maps can compensate, after a critical evaluation, for the lack of more rigorous historical data (Canessa et al., 2017). By the time of the first available cartographies, in the 1960s, the *P. oceanica* meadows of Liguria had already lost nearly half their original extent, when compared to model predictions. The chronological series of quantitative data indicated a continuous, although comparatively slower, decline in the meadow extent between the 1960s and 1990s. Enforcement of conservation policies in the last decades apparently stopped further degradation between the 1990s and 2009. Recent signs of recovery have ever been observed in a meadow presently included in a marine protected area (Oprandi et al., 2014a); however, invasion by alien species increases the risk of hysteresis and only continued monitoring will help understanding the on-going evolution of the meadow under improved environmental conditions (Oprandi et al., 2014b).

The magnitude of *P. oceanica* regression in Liguria was comparable to those reported for other regions of the Mediterranean Sea (Marbà et al., 2014; Holon et al., 2015; Telesca et al., 2015). In Liguria, the regression of *P. oceanica* was often accompanied by its replacement by the comparatively ruderal species *Cymodocea nodosa* (Montefalcone et al., 2006), which has tripled its extent since the 1960s. *C. nodosa* is favoured by higher amounts of nutrients (Barsanti et al., 2007): its further expansion may therefore be expected with growing coastal urbanization. In 2009, the proportion of *C. nodosa* with respect to *P. oceanica* in Liguria reached 44%, a figure higher than in other regions of the NW Mediterranean (Boudouresque et al., 2009).

4.2 Loss of natural capital and associated functions

The decline of *Posidonia oceanica* meadows implies the loss of natural capital and the functions it generates. *Cymodocea nodosa* has often replaced *P. oceanica* after its decline. Even if it has not been possible to evaluate the functions provided by *C. nodosa* in emergy terms, other indices indicative of the ecological properties of the two ecosystems suggest that *C. nodosa* has a lower value than *P. oceanica* (Table 2). Higher figures of rhizome and leaf length, above- and below-ground biomass, exergy, specific exergy, and species richness in *P. oceanica* illustrate its greater capacity to store natural capital (Montefalcone et al., 2015). *P. oceanica* meadows are more complex, in both structural and functional terms, than *C. nodosa* ones (Paoli et al., 2016). Thus, the capacity of *C. nodosa* to compensate for the loss of *P. oceanica* functions is supposedly limited. In particular, the most valuable function provided by *P. oceanica* meadows is sediment retention, which contributes up to the 99% of the total ecosystem functions (Vassallo et al., 2013). The capacity of attenuating water movement and retaining sediment by *C. nodosa* (Rull et al., 1996; Delbono et al., 2003; Holmer et al., 2004) is not comparable to that by *P. oceanica*, due to the latter's unique ability among seagrass to construct the matte (Giovannetti et al., 2008; Vacchi et al., 2017).

Contrasting ecosystem function loss (evaluated with a biophysical approach) with economic gain (measured as value added of the tertiary sector) evidenced that the greatest loss of *P. oceanica* occurred in the period when the value added exhibited a very slight increase (1850-1950) while, on the contrary, the greatest economic growth occurred when *P. oceanica* extent stabilized thanks to protection measures undertaken in the last decades. This result evidences a decoupling between nature and economy trends. On the whole, gains were lower than losses, as the economic gain derived from the tertiary sector did not compensate for the economic loss in terms of *P. oceanica* ecosystem functions.

5. CONCLUSIONS AND PERSPECTIVES

This study represents a first approach to trace the history of the extent and composition of seagrass meadows over a time period longer than one century: for the first time, all the available historical and recent information has been combined with modelling to set the reference and to draw trajectories of change. The innovative comparison between the equivalent economic value of ecosystem functions provided at each time and the evolution of the tertiary economic sector, allowed exploring the tradeoffs between economic development and conservation of natural capital in a touristic coastal region. The main findings of our study may be summarized as follows:

- A huge regression of *Posidonia oceanica* meadows took place in Liguria since 1850, followed by a slowing of regression and then a stabilization of their extent entering the XXI century;

- This trend was consistent with the increased artificialization experienced by the Ligurian coastline, which started in the XIX century, was very intense during the XX century and then stabilized since the 1990s;
- On the contrary, *Cymodocea nodosa* increased its extent within the meadows during the same period;
- The loss of *P. oceanica* cannot be compensated by the increase of *C. nodosa*, implying a great loss of ecosystem functions provision;
- The accumulated equivalent economic loss due to the decline of *P. oceanica* meadows was greater than the economic gain in the same time frame expressed as value added of tertiary sector, which in Liguria is mostly linked to tourism-related activities;
- The stabilization of *P. oceanica* meadow extent in the last decades apparently did not affect the gain in the value added, suggesting that investment in nature protection is not in conflict with economic wealth increase.

Our results highlight the need of robust policies to preserve the quality of coastal waters and the physical integrity of the surviving meadows and to maintain, or possibly recover, the ecosystem functions of *P. oceanica* meadows. Further studies should consider the estimation of the economic value of *C. nodosa* meadow functions and also of the investments required to protect and restore *P. oceanica* meadows. The great potential of ecosystems to provide benefits to humans should foster the engagement in more large-scale and long-term measures to preserve ecosystems, considering carefully the tradeoffs between their degradation by wrong-planned actions and short term benefits.

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Figure captions and Table headings

Figure 1. Flow chart synthesizing the methodologies employed and the aims of this paper.

Figure 2. Geographical setting of Liguria. The localities mentioned in the text are indicated, from west to east: Bordighera (BO), Sanremo (SA), Imperia (IM), Loano (LO), Capo Noli (CN), Savona (SV), Genoa (GE), Portofino (PO), Sestri Levante (SL), Monterosso al Mare (MM), Riomaggiore (RI), and La Spezia (SP).

Figure 3. Selected examples of historical and recent cartographies displaying information about seagrass meadows in Liguria. The area represented corresponds to Portofino (PO in Figure 2). The years correspond to publication year of the cartography (see Table 1). '*P. oceanica* on rock' indicates *P. oceanica* growing on a rocky substrate, '*P. oceanica* and dead matte' indicates the mosaic of living *P. oceanica* and dead matte, and 'dead matte' corresponds to the regressed and dead areas of the meadow.

Figure 4. Temporal trend of *Posidonia oceanica* meadow extent in Liguria, combining modelling, estimations, and quantitative cartographic measurements. The second-grade polynomial represents the best fit of the data.

Figure 5. Examples of the application of the predictive models in the localities of Loano, Sanremo and Monterosso al Mare (see Figure 2 for their geographical position). Extents of *Posidonia oceanica* and *Cymodocea nodosa* meadows are taken from Diviacco and Coppo (2009). On maps are represented k_{min} and k_{max}, which encompass the seafloor region where the predicted upper limit is located, and the two predicted lower limits controlled by water movement and by light, respectively.

Figure 6. Temporal trend of the seagrass meadow extent (total, *Posidonia oceanica* and *Cymodocea nodosa*) in Liguria (a) and of the percentage of artificial structures, rocky

coasts and beaches characterizing the Ligurian coastline (b). In panel a, open symbols indicate estimations, solid symbols measurements from maps.

Figure 7. Temporal trend of the value added of tertiary sector in Liguria and of the ecosystem services provided by *Posidonia oceanica* meadows.

Table 1. A synopsis of the historical and recent cartographies containing information about seagrass meadows in Liguria. The column ‘decade’ indicates the year to which data are referred into the text and graphs; the cartographies published before 1990 were combined to complete the available information for each decade. Relevant localities are indicated in Figure 2.

Table 2. Comparison of *Posidonia oceanica* and *Cymodocea nodosa* ecosystem performances.

Table 1.

Decade	Area represented	% coastline	Type	Scale	Acquisition method	Positioning	Rendering	Source
1960	Bordighera to Riomaggiore	81	Fishing map	1:100,000	Ecosounder, dredging	Land marks	Manual	Santi (1962)
1960	Capo Noli to Sestri Levante	42	Fishing map	1:120,000	Ecosounder, dredging	Land marks	Manual	Fusco (1968)
1960	French border to Capo Noli	29	Fishing map	1:120,000	Ecosounder, dredging	Land marks	Manual	Fusco (1972)
1980	Liguria	100	Atlas of marine habitats	1:100,000	Ecosounder, diving	Triangulation, land marks	Manual	Cattaneo et al. (1980)
1980	Imperia to Sestri Levante	57	Fishing map	1:150,000	Ecosounder, diving	Triangulation, land marks	Manual	Tunesi et al. (1985)
1980	Imperia to Portofino + Portofino to Tuscany	39	Fishing map	1:100,000	Ecosounder	Triangulation, land marks	Manual	Seaway (1986, 1988)
1990	Liguria	100	Atlas of seagrasses	1:25,000	Side Scan Sonar, ROV, bathyscope	GPS	Manual	Bianchi and Peirano (1995)
2006	Liguria	100	Atlas of marine habitats	1:10,000	Side Scan Sonar, ROV, aerial and satellite imagery	dGPS	GIS	Diviacco and Coppo (2006)
2009	Liguria	100	Atlas of marine habitats	1:10,000	Multibeam, Side Scan Sonar, ROV, aerial and satellite imagery	dGPS	GIS	Diviacco and Coppo (2009)

Table 2.

	Cymodocea nodosa	*Posidonia oceanica*	Unit	Reference
Biomass	9.83E+02	7.01E+03	$g_{AFDW} \cdot m^{-2}$	Montefalcone et al. (2015)
above-ground	4.95E+02	1.93E+03		
below-ground	5.87E+02	5.08E+03		
Exergy	8.50E+05	2.46E+07	$kJ \cdot m^{-2}$	Montefalcone et al. (2015)
above-ground	3.56E+05	5.90E+06		
below-ground	4.94E+05	1.87E+07		
Specific exergy	8.64E+02	3.51E+03	-	Montefalcone et al. (2015)
above-ground	8.98E+02	3.05E+03		
below-ground	8.41E+02	3.68E+03		
Species richness	2.32E+02	4.01E+02	N	Montefalcone et al. (2015)
above-ground	1.79E+02	3.14E+02		
below-ground	5.30E+01	8.70E+01		
Leaf height	2.00E+01	8.00E+01	cm	Montefalcone et al. (2015)
Rhizome-root length	5.00E+00	2.50E+01		Montefalcone et al. (2015)
Overall Complexity Index (OCI)	2.09E+00	3.04E+00	$kJ \cdot m^{-2}$	Paoli et al. (2016)
Sedimentation rate	6.36E+00	2.00E+01	$g_{DW} \cdot m^{-2} \cdot d^{-1}$	Holmer et al. (2004)

Figure 1

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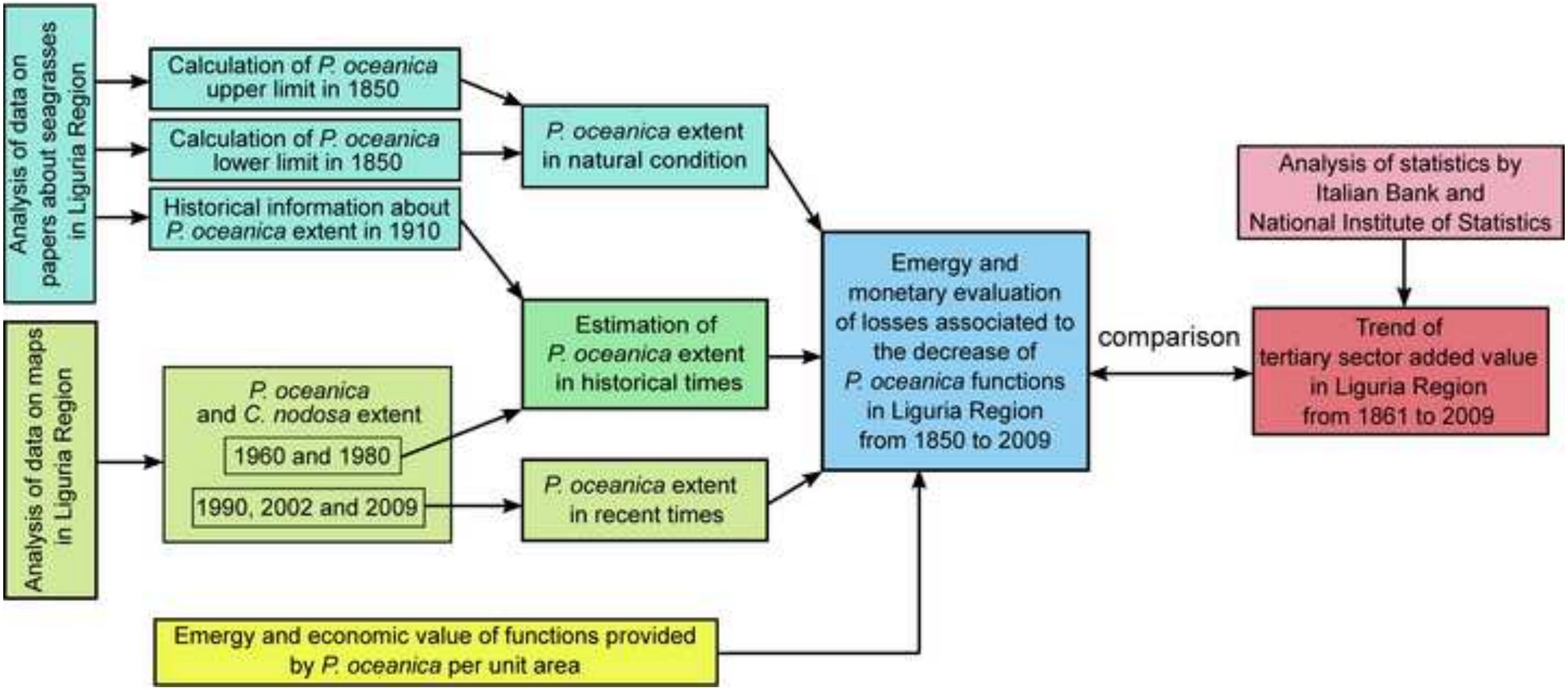

Figure 2

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Figure 3

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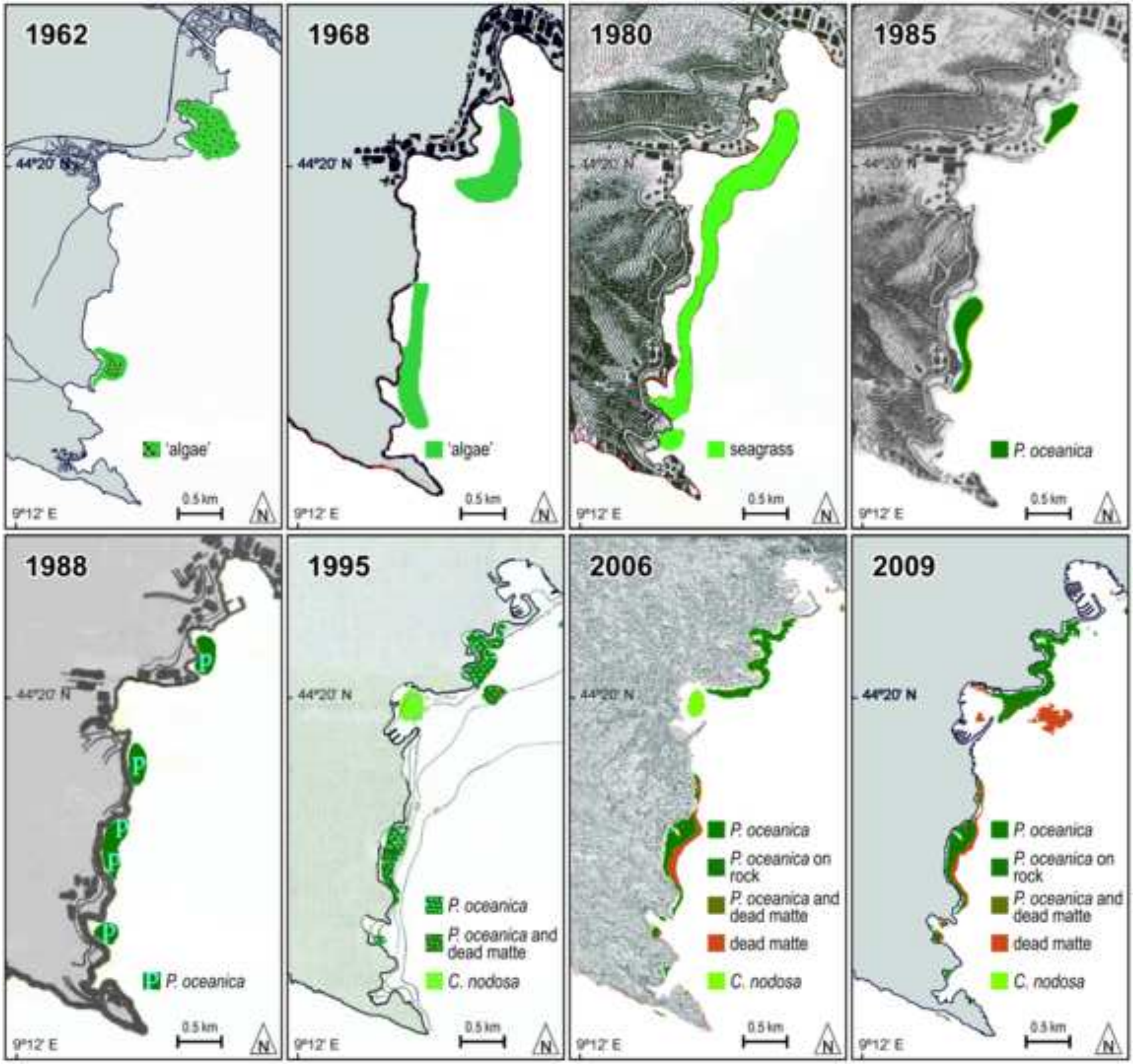
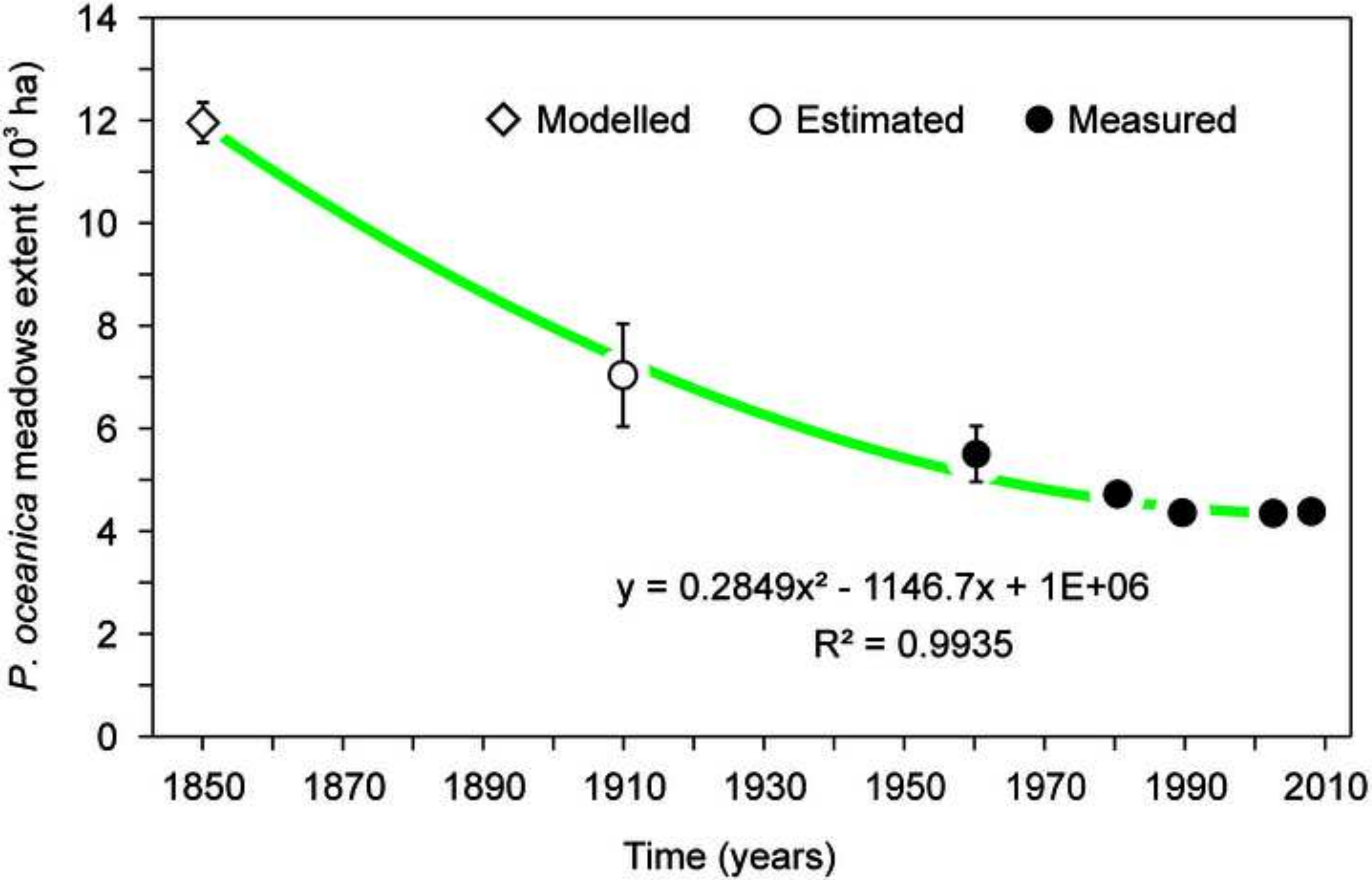


Figure 4



◇ Modelled
○ Estimated
● Measured
y = 0.2849x² - 1146.7x + 1E+06
R² = 0.9935
P. oceanica meadows extent (10³ ha)
14
12
10
8
6
4
2
0
1850
1870
1890
1910
1930
1950
1970
1990
2010
Time (years)

Figure 5

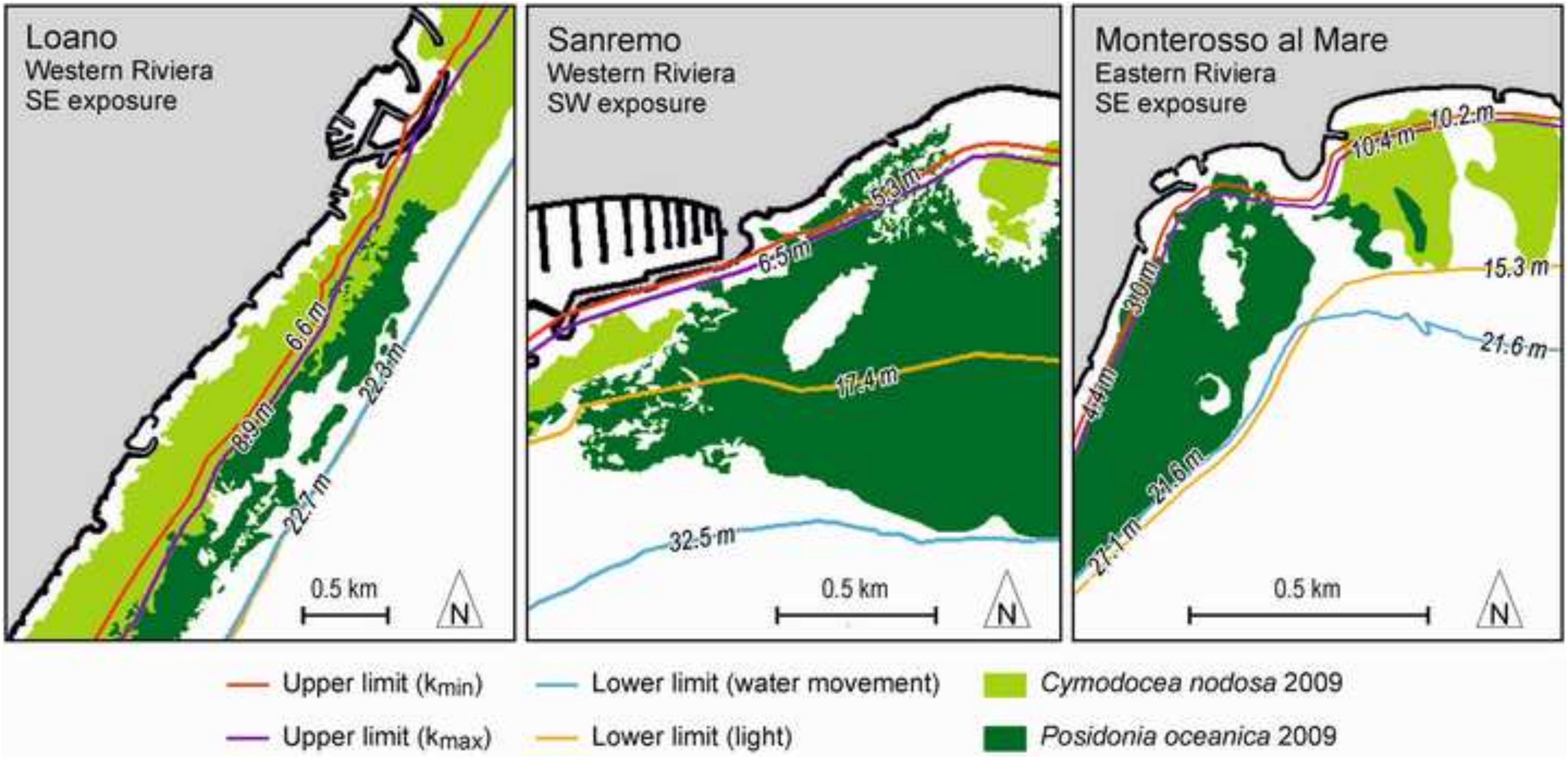

Loano
Western Riviera
SE exposure
6.6 m
8.9 m
22.3 m
22.7 m
0.5 km
N
Sanremo
Western Riviera
SW exposure
5.3 m
6.5 m
17.4 m
32.5 m
0.5 km
N
Monterosso al Mare
Eastern Riviera
SE exposure
10.4 m
10.2 m
15.3 m
21.6 m
3.0 m
4.4 m
21.6 m
27.1 m
0.5 km
N
Upper limit (k_{min})
Upper limit (k_{max})
Lower limit (water movement)
Lower limit (light)
Cymodocea nodosa 2009
Posidonia oceanica 2009

Figure 6

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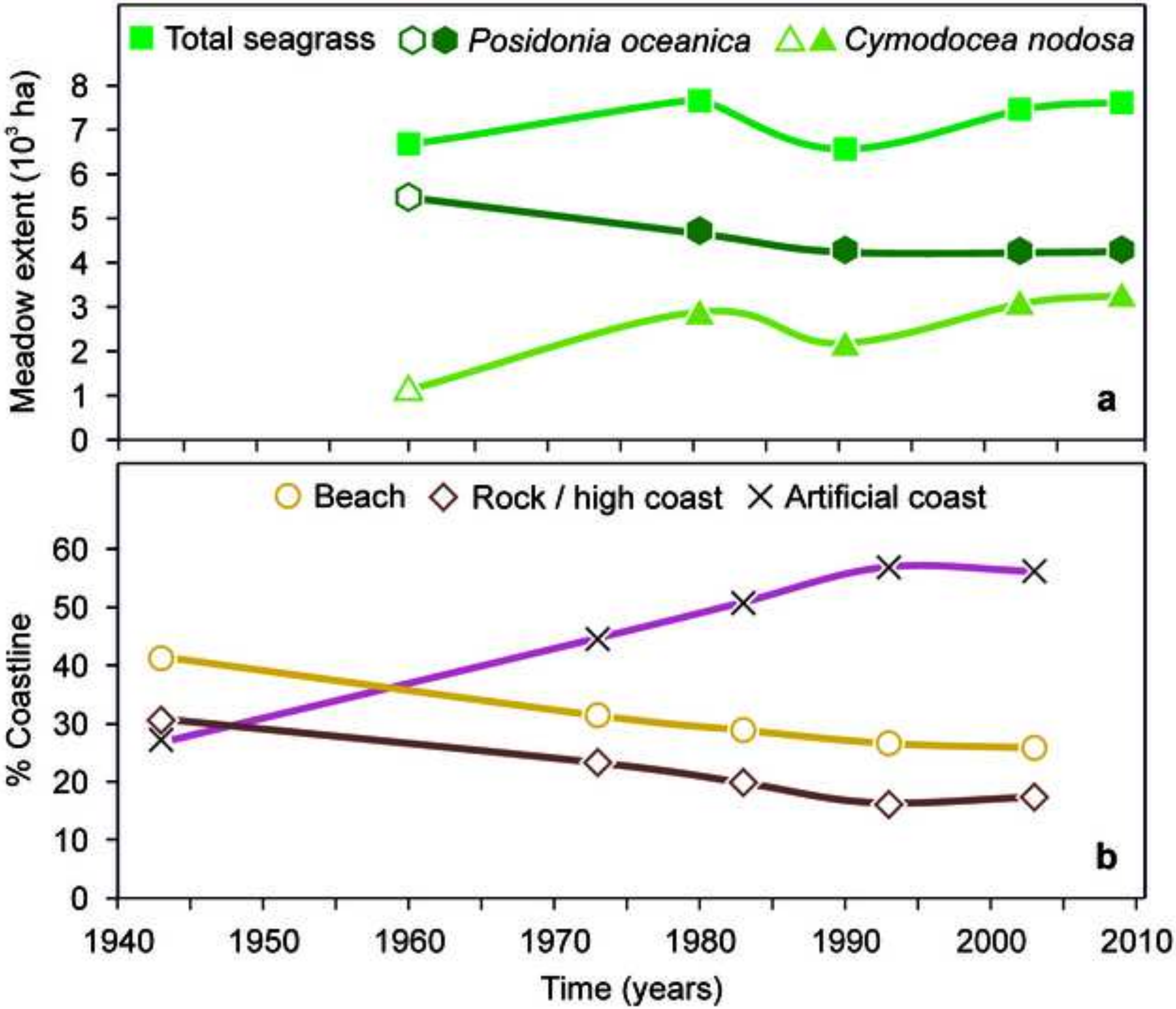

Figure 7

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