2018

Millennial-scale trends and controls in *Posidonia oceanica* (L. Delile) ecosystem productivity

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[10.1016/j.gloplacha.2018.07.011](https://doi.org/10.1016/j.gloplacha.2018.07.011)

This is the Author's Accepted Manuscript of: Leiva-Dueñas, C., López-Merino, L., Serrano, O., Cortizas, A. M., & Mateo, M. A. (2018). Millennial-scale trends and controls in *Posidonia oceanica* (L. Delile) ecosystem productivity. *Global and Planetary Change*. 169(October), 92-104.

<https://doi.org/10.1016/j.gloplacha.2018.07.011>

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records obtained are compared with previous palaeoecological records obtained for the area, showing a common environmental history. First, a relative seagrass ecosystem stability at ~4000 and 2000 cal. yr BP. Then, after a productivity peak at ~1400-800 cal. yr BP, productivity shows an abrupt decline to unprecedented low values. The fluctuations in ecosystem productivity are likely explained by increases in nutrient inputs related to human activities – mostly in the bay watershed – concomitantly with changes in total solar radiation. Cumulative anthropogenic stressors after Roman times may have started to affect ecosystem resilience, dynamics and productivity, with more abrupt regime shifts during the last millennium. These results add into recent research showing the potential of seagrass archives in reconstructing environmental change and seagrass post-disturbance dynamics, hence providing unvaluable information for improving the efficiency in managing these key coastal ecosystems.

Keywords: Late Holocene; Western Mediterranean; environmental reconstruction; coastal setting; seagrass archive; palaeoproductivity; sedimentology; stable isotopes.

1. Introduction

Seagrass meadows provide unvaluable ecosystem services, as they constitute biodiversity hotspots, improve the quality of coastal waters, stabilize sediments and reduce shoreline erosion (Duarte, 2002). However, they are declining worldwide due to anthropogenic pressures, including global change (Short & Neckles, 1999; Orth *et al.*, 2006). In recent times, substantial efforts have been invested to preserve seagrass meadows, key in current European environmental policies. *Posidonia* meadows are protected as a priority habitat (Council Directives, 1992, 1997), as a species (Berne Convention, 1979; Barcelona Convention, 1976), under specific legal protection actions in individual countries (e.g., Albania, Croatia, France, Italy, Spain and Turkey), and included in marine protected areas along the Mediterranean Sea (UNEP-MAP-RAC/SPA, 2009). Monitoring programs are taken place since the end of the 20th century,

such as the Posidonia Monitoring Network in the Provence-Alpes-Côte d'Azur region (PACA) in France, or the POSIMED project along the Mediterranean coast of Spain.

However, monitoring programs present several handicaps, including the limited time-span they cover (i.e., short-term environmental records). Ecosystem dynamics occur at multiple spatiotemporal scales, and the discrimination of centennial and millennial patterns and processes needs an adequate time perspective (Seddon *et al.*, 2014). Therefore, long-term environmental records are a priority. In this sense, a palaeoecological approach provides long-term environmental records. The longer time span they cover enables the reconstruction of pre-anthropogenic scenarios, the discrimination between natural and human-induced perturbations, and the determination of regime shifts as well as the ecosystems' resilience to perturbations (e.g., Willard & Cronin, 2007; Benton & Harper, 2009; Davies & Bunting, 2010; López-Merino *et al.*, 2012). Regime shifts are abrupt changes on several trophic levels leading to fast ecosystem reconfiguration, usually after abrupt climatic changes or anthropogenic impacts (Andersen *et al.*, 2009). Knowing the relevant long-term processes resulting in abrupt ecological changes provides priceless information for guiding ecosystem conservation strategies (Willis *et al.*, 2005, 2007; Davies & Bunting, 2010; Birks, 2012).

P. oceanica shows seasonal dynamics in productivity with shoot growth peaking in late summer and declining in fall (Alcoverro *et al.*, 1995, 1997). This annual pattern is mainly regulated by changes in light and water temperature associated with solar insolation (Alcoverro *et al.*, 1995, 1997). Moreover, a feedback control on growth is caused due to seasonal variability in resources and local conditions generated by the seagrass growth. *P. oceanica* growth is controlled by light and temperature in winter, while in summer it is limited by nutrients (Alcoverro *et al.*, 1997). Considering this information, on a centennial to millennial scale it would be expected a productivity pattern regulated by solar irradiance if no other limiting resource or disturbance occurred. Local factors (e.g., nutrients, carbon, redox potential, physical processes) play a major role in growth as

limiting factors in meadows with high light availability (Perez & Romero, 1992; Alcoverro *et al.*, 1995, 1997), especially nutrient availability (Romero *et al.*, 2006). Disturbances may cause deviations from the observed seasonal pattern caused by solar irradiance (Short & Wyllie-Echeverria, 1996). On the one hand, natural disturbances are extreme climatic events, changes in wave exposure and tidal currents, diseases, grazing and bioturbation. On the other hand, human-induced disturbances are eutrophication, dredging, filling and certain fishing practices causing direct physical damage (Short & Wyllie-Echeverria, 1996).

Environmental archives are especially scarce in marine coastal areas owing to high hydrodynamic energy and bioturbation (Mateo *et al.*, 2010). However, *P. oceanica*, a slow-growing and climax seagrass species, amongst the most productive of all marine ecosystems (Duarte, 1991a; Mateo *et al.*, 2006), forms coherent sedimentary sequences with temporal resolution ranging from 2 to 17 yr cm⁻¹ (Serrano *et al.*, 2016a).

P. oceanica is composed by rhizomes, leaf shoots and roots. The leaves proximal end presents a cylindrical structure known as leaf sheath, attached to the rhizome. The high lignin and phenolic content of the seagrass debris confers them a remarkable decay-resistant nature (Kaal *et al.*, 2016). The annual accumulation of the refractory fraction of the *P. oceanica* organic debris, together with the accumulation of other organic and inorganic particles trapped in the meadow, results in a bioconstruction known as mat (or “matte”; Boudouresque & Meinesz, 1982), consisting in massive pools of organic matter (OM) sequestered over millennia and with a thickness reaching up to 6.5 m (Mateo *et al.*, 1997; Lo Iacono *et al.*, 2008; Pergent *et al.*, 2012). The anoxic conditions prevailing in the mat favour the preservation of abiotic and biotic proxies (Mateo *et al.*, 1997; 2006), thus enabling the application of a palaeoecological approach on the *P. oceanica* archive (e.g., López-Saéz *et al.*, 2009; Mateo *et al.*, 2010; Serrano *et al.*, 2011, 2013, 2016b, 2016c; López-Merino *et al.*, 2015, 2017; Kaal *et al.*, 2016).

Soils under *P. oceanica* meadows are usually mixed siliciclastic–carbonate, the carbonate fraction mainly derived from epiphytic carbonate production and the great diversity of calcifying organisms that require the seagrass as shelter, source of food and substrate (Mateu & Vicens, 2012; Gaglianone *et al.*, 2017). The main control on the relative abundance of calcareous epiphytes is seagrass biomass. Mature and longer leaves with higher surface area host more epiphytes than the young ones and meadows with higher shoot densities and canopies host more calcifying organisms (Mazarrasa *et al.*, 2015). Moreover, calcification within the meadow is enhanced with the increase of seawater pH due to the photosynthetic activity of the seagrass (e.g. Semesi *et al.*, 2009). Following these premises, the carbonate content in the mat under the meadow could be a proxy of the seagrass productivity. However, if the geological substrate of the bay watershed is dominated by limestone, the carbonate content would not allow the discrimination between the biogenic production and the terrestrial input (Gaglianone *et al.*, 2017).

Despite successful applications of stable isotope ratios in paleoceanography (Koch, 1998; Hayes *et al.*, 1999), their potential to reconstruct changes in seagrass ecosystems remains largely unexplored. The stable isotope composition of plant tissues changes in response to environmental variability (Amundson *et al.*, 2003; Mateo *et al.*, 2004; Cernusak *et al.*, 2013). Positive correlations between stable carbon isotopes ($\delta^{13}\text{C}$), solar irradiance and productivity have been reported for *P. oceanica*, opening the possibility of using $\delta^{13}\text{C}$ as a proxy for past changes in seagrass productivity, or even in solar irradiance if no other abrupt environmental disturbances occurred (Hemminga & Mateo, 1996; Mateo *et al.*, 2000, 2010).

Nitrogen stable isotopes ($\delta^{15}\text{N}$) are more difficult to interpret due to their inherent variability (Fogel & Tuross, 1999). Different processes may influence the N isotope composition in aquatic plants. First, the isotopic signature of available N sources is highly variable (Gaye-Haake *et al.*, 2005). Second, isotopic fractionation during nitrate and

ammonium assimilation leads to post-assimilation changes in $\delta^{15}\text{N}$ values (Fogel & Cifuentes, 1993; Teranes & Bernasconi, 2000). Finally, bacterial degradation can also lead to a depleted isotopic signal in the residual organic matter during early diagenesis under anoxic conditions (Lehman *et al.*, 2002). Despite of this variability, $\delta^{15}\text{N}$ in aquatic plants has been used to discriminate between external N sources, mainly related to human disturbance (Chappuis *et al.*, 2017).

In this study, we have applied a multi-proxy palaeoecological approach on a four-thousand-year-old *P. oceanica* mat located at the Portlligat Bay in NE Spain. We have analysed for the first time biological proxies such as the proportions of sheath-, root- and rhizome-derived debris as well as the C and N elemental and isotopic composition of *P. oceanica* sheaths with the overarching aim of reconstructing the meadow productivity dynamics in order to reveal possible ecological regime shifts and the environmental drivers behind them.

2. Study area

The Portlligat Bay (Cap de Creus Natural Park, NE Spain) is a small and shallow inlet (0.14 km² and < 10 m deep) connected to the sea by a 213 m opening to the NE. It is a sheltered bay, protected from winds and sea storms. A large part of the bay (41%) is covered by a meadow of *P. oceanica* with an average thickness of ~4.5 m alternating with sandy bioclastic patches (Lo Iacono *et al.*, 2008). The meadow shows a strong phosphorus deficiency (Alcoverro *et al.*, 1995, 1997). There is not a permanent stream providing volumetrically important terrestrial inputs. The latter are instead modulated by run-off and by eventual strong discharges of a torrent, a seasonally active creek flowing into the bay from its NW shore (Fig 1a).

The climate of the area is Mediterranean xerotheric (Franquesa i Codinach, 1995). The annual precipitation ranges between 200 and 1300 mm and mainly occurs from October to December (average range for 1950–2016, Servei Meteorològic de Catalunya). The

bedrock geology of the catchment is mostly composed of phyllites, slates, schists and some quartzites and marbles which date from the Paleozoic (Cartographic Institute of Catalonia, 1997). More than 50% of the watershed area has very steep slopes (>60%). Soils are poorly developed, very shallow, fast draining and coarse textured. They have a 0.3% of carbonate and 1.8-4.3% of organic matter contents (Cartographic Institute of Catalonia, 2006).

Mediterranean shrubland dominates the current landscape. It mainly comprises *Cistus monspeliensis* L., *Cistus albidus* L., *Lavandula stoechas* L., *Calicotome spinosa* (L.), *Ulex parviflorus* Pourr, *Pistacia lentiscus* L., *Juniperus oxycedrus* L., *Arbutus unedo* L., *Quercus coccifera* L. and *Erica arborea* L. Forest cover is sparse, with small areas covered by cork oak trees (*Quercus suber* L.) and pines (*Pinus halepensis* Miller, *Pinus pinea* L.), while *Quercus ilex* L. and *Quercus pubescens* Willd. occur in sheltered areas (Franquesa i Codinach 1995). The current landscape has been influenced by a long history of human activities, mostly related to farming (Franquesa i Codinach, 1995; López-Sáez *et al.*, 2009; López-Merino *et al.*, 2015, 2017). However, traditional dry-land farming and fisheries have recently been replaced by tourism, resulting in the abandonment of terraced vineyards (*Vitis vinifera* L.) and pasturelands.

3. Material and methods

3.1. Coring procedures and laboratory analyses

A 475-cm long core of *P. oceanica* mat was obtained in AD 2000 (Core 2000 from now on) from the Portlligat Bay at a depth of ~3 m (42° 17'32" N; 3° 17'28" E; Fig. 1a). It was recovered using a floating drilling platform with a self-powered drill, which combined percussion and rotation (see details in Serrano *et al.*, 2012). The stratigraphy showed a dense mat with abundant organic matter for the first forty centimeters, changing to sands (fine to coarse size) with rhizomes, roots and leaf sheaths embedded within the sediment matrix below this depth (Fig. 1b). The core was sliced into 1 cm-thick slices and 176 samples were selected for the analyses. The samples were dried at 70°C in order to

calculate dry bulk density. Soil organic matter <1 mm (SOM) was determined by loss-on-ignition (450°C for 5 h) after dry-sieving (1 mm) bulk subsamples. Total carbonate content (CaCO₃) was measured in bulk subsamples using a Scheibler calcimeter.

Subsamples were wet-sieved in seawater into two fractions, a coarse (>1 mm) and a fine (1mm ≥ fine >63 µm) fraction. The coarse fraction was sorted into organic (coarse organic matter, COM, >1 mm) and inorganic fractions. The organic fraction of COM was composed of rhizomes, leaf sheaths and roots, which were separated to account for their biomass. All fractions were dried at 70°C until constant weight.

Elemental and isotopic C and N composition of *P. oceanica* sheaths were obtained using a Finnigan Delta S isotope ratio mass spectrometer 196 (Conflo II interface). Carbon and nitrogen isotope ratios are expressed as δ values in parts per thousand (‰) relative to the Vienna PeeDee Belemnite and atmospheric N₂ (air) standards, respectively. Analytical precision based on the standard deviation of internal standards ranged from 0.11 to 0.06‰.

After wet digestion of the *P. oceanica* sheaths, phosphorus content was measured at the Serveis Científic-Técnic, Barcelona University, using a JobinYvon JI-38 (3600 grooves mm⁻¹) ICP-AES following Mateo & Sabaté (1993).

Grain size distribution was determined using a Retsch AS 200 analytical sieve shaker for 15 min after wet-sieving (1 mm and 0.063 mm mesh) with distilled water and removing the COM only. Grain sizes were classified as gravel (>2 mm), coarse sand (2-0.5 mm), medium sand (0.5-0.25 mm), fine sand (0.25-0.063 mm) and mud (silt and clay, <0.063 mm), according to Brown & McLachland (1990).

The carbon and nitrogen stable isotopes, nitrogen and phosphorus content of *P. oceanica* sheaths are original data for this paper, while the other data used were first published in Serrano *et al.* (2012).

3.2. Age-depth model

Serrano *et al.* (2012) presented an age-depth model for Core 2000 using a smooth-spline model. Here, we used Bacon.R software (Blaauw & Christen, 2011) and the same radiocarbon dates (Table 1). However, while Serrano *et al.* (2012) discarded two of the fourteen radiocarbon dates, we included them in the model so that the Bacon software could decide whether those radiocarbon dates should be considered outliers. They were finally not discarded. Moreover, we also included the age of the surface of the core, which is the year of recovery (AD 2000, Fig. 2). Radiocarbon dates are expressed as calibrated years before present. Dates were calibrated using the marine ^{13}C calibration curve (Reimer *et al.*, 2013) and a local marine reservoir correction was applied ($\Delta R = 23 \pm 71$ years, Siani *et al.*, 2000).

3.3. Numerical exploration

The dataset used for the numerical analyses comprises 176 samples and 16 variables. These variables include: SOM, COM, CaCO_3 , $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, carbon, nitrogen and phosphorus contents in sheath remains, sheath debris biomass percentages, root debris biomass percentages, rhizome debris biomass percentages and five sediment grain-size fractions (Fig. 3).

Bulk density, accretion rates, CaCO_3 , SOM and COM contents were used to estimate mass accumulation rates (MAR) of carbonates and organic matter, following Zachos *et al.* (2004). MAR are used rather than weight/weight percentages as they better express fluxes (e.g., delivery and preservation). Percentages are influenced by the closed nature of their calculation and, therefore, subjected to dilution/concentration effects (Meyers & Lallier-Vergès, 1999).

After data for each variable were transformed and standardized by subtracting its mean and dividing by its standard deviation, we applied a series of numerical analyses using

R software (R Development Core Team, 2011) and CPQtR1.0.3 (Gallagher *et al.*, 2011) in order to detect common trends, main changes, and evaluate the influence of selected factors on the palaeoenvironmental history of the seagrass meadow of the last 4000 years.

Compositional data (granulometric distribution, elemental composition of sheath and organs biomass percentages) were transformed by centered log-ratio (Aitchinson, 1986), while Box-cox transformation method (Box & Cox, 1964) was applied to SOM MAR, COM MAR ($\lambda=0$), and CaCO_3 MAR, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ in plant debris ($\lambda=1$).

Principal component analysis (PCA) was applied to the variables dataset using the correlation matrix with a varimax rotation, determining the number of significant principal components (PC) with Parallel Analysis (Horn, 1965).

Change-point modelling was applied to all records of PC scores together using a Bayesian transdimensional Markov chain Monte Carlo approach in order to identify common shifts in the trends obtained after the PCA. This approach infers probability distributions for the number and locations in time of changepoints and the mean values between changepoints on several trends (Gallagher *et al.*, 2011).

Using **partial redundancy analysis** (pRDA), the PC scores were used as 'composite' response variables on which the influence of climate and anthropogenic activity was tested. Five pRDA models were run, one per PC, so one of the PC was the response variable in each of them. All models had the same four explanatory variables. Two explanatory variables were chosen to assess the influence of global climate patterns: Total Solar Irradiance (TSI, Steinhilber *et al.*, 2012) and Northern Hemisphere temperature anomalies (NH temperature, Kobashi *et al.*, 2013). The other two explanatory variables were selected to assess the influence of local factors. They are two records of heavy metals obtained after the PCA of the geochemical composition in sheaths in Core 2000 by Serrano *et al.* (2011). One record is related to heavy metals

derived from anthropogenic activities (PC1m), likely linked to increased soil erosion in the catchment, while the other integrates metals with a more lithogenic and hence, natural geogenic origin (PC2m). All statistically significant pRDA models ($p < 0.05$) had sample ages partialled out as a covariable. It is important to partial out the statistical effects of age because of the strong temporal auto-correlation, a common feature of time series (Legendre *et al.*, 2002). Most inferential statistical tests assume that residuals are independently and identically distributed, assumption violated if residuals are autocorrelated. Ignoring autocorrelation can result in false inferences. Monte Carlo permutation tests were used to test the significance of the model and of each predictor variable (999 permutations), obtaining the partial explained variation and the significance for every explanatory variable.

Additionally, **Lomb-Scargle periodograms** – specifically for unevenly sampled times series – were performed to detect statistically relevant periodicities present in the records of PC scores. All data were detrended by linear regression prior to analysis.

4. Results

4.1. Age-depth model and accretion rates

According to the age-depth model (Fig. 2), the Core 2000 dated back to 4000 cal. yr BP with accretion rates ranging from 0.7 to 1.7 mm yr⁻¹ (mean = 1.2 ± 0.3 mm yr⁻¹) and an average resolution of 8.8 ± 2.4 yr cm⁻¹. The 1-295 cm section (~2000-0 cal. yr BP) showed higher accretion rates (mean = 1.4 ± 0.2 mm yr⁻¹) than the 295-475 cm section (~4000-2000 cal. yr BP) (mean = 0.9 ± 0.1 mm yr⁻¹, Mann-Whitney U, two-tailed $p < 0.001$)

4.2. Principal component analysis and change point modelling

Five principal components explain 73% of the variance (Fig. 4). The first principal component (PC1) accounts for 24% of the variance, showing positive loadings for SOM MAR, COM MAR, $\delta^{15}\text{N}$ and medium and fine sands. The second principal component (PC2) explains 14% of the variance, showing negative loadings for root and rhizome biomass and positive loadings for sheath biomass and nitrogen in sheath. The third principal component (PC3) explains 13% of the variance, showing positive loadings for coarse sands and N in sheath and a negative loading for mud. The fourth principal component (PC4) explains 11% of the variance, showing positive loadings for CaCO_3 MAR and $\delta^{13}\text{C}$ and a negative loading for root biomass. Finally, the fifth principal component (PC5) explains 11% of the variance, showing a positive loading for P in sheath and a negative loading for C in sheath.

The change-point modelling applied to the five records of PC scores suggests 12 statistically significant regime shifts (change-points CP-1 to CP-12; Fig. 5). Four of them (CP-3, CP-4, CP-7 and CP-8) at the scale of centuries, while the rest are more abrupt, occurring within decades. CP-6, CP-9, CP-11 and CP-12 are the most abrupt regime shifts.

4.3. Influence of explanatory variables

pRDA models for the records of PC scores were all statistically significant ($p=0.001$) except for PC2 (Fig. 6; Table 1 of Supplementary material), and they explained from 15 to 36% of the variance of the response variables.

On the one hand, the variance explained by the pRDA model for PC1 as a composite variable was the lowest (15.3%), PC1m composite variable being the main predictor followed by TSI and its interaction with NH temperature (Fig. 6; Table 1 of Supplementary material). On the other hand, the variance explained for PC3 as a composite variable was the largest (36%). Again, PC1m composite variable explained the largest proportion

of variance, followed by TSI. Other second-degree interactions between climatic variables and PC1m composite variable contributed to explain up to 11% of variance. For PC4-composite variable, climatic variables explained 6.5% (comprising TSI, NH temperature and their interaction), quite similar to the 6.9% explained by local factors (PC1m and PC2m composite variables). A contribution of 5.6% by the interactions between local and large-scale factors was also found. The predictor which explained a higher proportion of PC5-composite variable was the interaction between NH temperature and PC2m composite variable (7.1%) followed by the record of PC1m (4.9%).

4.4. Spectral analysis

PC3 and PC4 present comparable cycles with periodicities of ~1000 yr (1100 and 970 yr, respectively), while PC1 and PC5 show similar cycles with wavelengths centered at ~2000 yr (2060 and 1710 yr, respectively; Fig. 7). Moreover, PC4 presents a significant periodicity at 2500 yr, as well as one close to significance at 520 yr (Fig. 7). There was not any significant cycle observed for PC2.

5. Discussion

5.1. Trends in the *P. oceanica* long-term ecosystem dynamics

PC1 seems to indicate **changes in organic matter (OM) accumulation and diagenesis** (Fig. 4; COM MAR and SOM MAR positive loadings). PC1 positive scores reflect a higher accumulation and lower degree of degradation of OM in the upper section of the mat (Fig. 5; i.e., top ~250 cm, since ~1700 cal. yr BP). The decrease of the score values with depth would be partially related to OM decomposition. $\delta^{15}\text{N}$ of sheath debris also shows a positive loading (Fig. 4), most likely linked to a better preserved OM, generally enriched in the heavy isotope (Möbius *et al.*, 2010). In the case of *P. oceanica*, Fourqurean & Schrlau (2003) and unpublished data of project SUMAR (CTM2006-12492/MAR) reported that $\delta^{15}\text{N}$ values decreased substantially during decomposition.

The positive loadings that medium and fine sands also show (Fig. 4) are probably related to the fact that the OM <1mm was not digested prior the granulometric analysis and it may predominate in the fine fractions (<1mm), at least in the upper part of the core. Hence, these sands are mostly corresponding to that OM fraction. The changes observed in the OM accumulation indicated by PC1 scores seem to be mainly explained by anthropogenic activities (PC1m) and secondarily by TSI (Fig. 6; Table 1 in Supplementary material). The anthropogenic metal pollution record (PC1m) could be used as an indicator of general human impact, whose main consequence in coastal areas is catchment soil erosion (López-Merino *et al.*, 2017). Changes in catchment soil erosion rates can have a large effect in sediment inputs into the bay and, hence, in the availability of nutrients and oxygen in the seagrass soils, factors known to be key drivers for the decay rates of *P. oceanica* and other aquatic angiosperms remains (Godshalk & Wetzel 1978a, 1978b; Mateo & Romero, 1996). Climatic variables exert an inherent control on ecosystem productivity (e.g., effect of irradiance and temperature in photosynthesis), likely affecting the OM supply to the soil.

The positive loading of sheath biomass and negative loadings of root and rhizome (i.e., belowground) biomass in PC2 (Fig. 4) suggest a link with the **availability of nutrients in the column water for the plant**. PC2 positive scores indicate higher amounts of sheath biomass in comparison with the belowground biomass. The negative relationship between the sheath and the belowground biomass would indicate changes in the allocation of plant biomass, which in seagrasses is related with changes in nutrient concentration change (McGlathery, 2008). The shoot:root ratio increases with high-nutrient availability, while with low-nutrient conditions seagrasses allocate biomass to belowground tissues in order to increase the surface area for nutrient uptake (Powell *et al.*, 1989; Vogt *et al.*, 1993; Pérez *et al.*, 1991, 1994, 2001; Nixon *et al.*, 2001). Furthermore, N in sheath debris also shows a positive loading (Fig. 4), another indicator

of higher nutrient availability since N content in tissues increases with higher N availability (e.g., Pérez *et al.*, 2008).

PC3 scores record accounts for the opposite distribution of coarse sands (positive loading) and mud (negative loading) (Fig. 4), likely recording changes in **soil erosion**. Soil erosion affecting the granulometry of seagrass soils could have different drivers. One driver could be climate, as Mediterranean climate is characterised by sporadic torrential floods resulting in transport of coarser sediments (e.g., Walling *et al.*, 2000; Roca *et al.*, 2009). Land-use change in the catchment could also drive changes in the grain size distribution of the seagrass soils, as it could trigger soil erosion (López-Merino *et al.*, 2017). Coarser fractions in seagrass soils could also be explained by higher local hydrodynamism in the meadow. Higher hydrodynamism (e.g., due to riverflow or runoff waters) causes resuspension and removal of the mud fraction. In fact, PC3 is mostly influenced by anthropogenic activities triggering catchment soil erosion (PC1m) followed by TSI (Figs. 6 and 8; Table 1 in Supplementary material). TSI controls atmospheric and rainfall patterns that also affect catchment soil erosion.

PC4 relates key variables linked to the **productivity of the ecosystem**. CaCO₃ MAR and $\delta^{13}\text{C}$ show positive loadings versus the negative loading of root biomass. Carbonates content in seagrasses is consistent with bio-calcification in seagrass meadows and the meadow overall productivity (e.g., Gacia *et al.*, 2003; Semesi *et al.*, 2009). The continental origin of carbonates is less likely than the biogenic source since the phyllosilicate minerals dominate the catchment geology of the Portlligat Bay. The positive loading of $\delta^{13}\text{C}$ of sheath would agree with the known positive correlation between $\delta^{13}\text{C}$ and seagrass productivity (Hemminga & Mateo, 1996; Mateo *et al.*, 2000). The negative loading of root content fits in the overall picture, as the allocation of biomass to belowground tissue is reduced with high nutrient availability and, hence, productivity (Powell *et al.*, 1989; Pérez *et al.*, 1991, 1994, 2001). PC4 is influenced by anthropogenic

activities, as shown by the PC1m record (Fig. 6; Table 1 in Supplementary material). Human impact would be associated with enhanced soil erosion and, therefore, nutrient input. Higher inputs of nutrients and trace metals, such as iron, may stimulate seagrass productivity and sheath biomass production (Marba *et al.*, 2007; Udy & Denison, 1997; Lee & Dunton, 2000). NH temperature and TSI climatic variables also affect PC4 (Fig. 6; Table 1 in Supplementary material), consistent with the positive effect of temperature and irradiance on seagrass productivity (Duarte, 1991b; Pérez & Romero, 1992; Ruiz & Romero, 2001; Nejrup & Pedersen, 2008; Marbà & Duarte, 2009; Mateo *et al.*, 2010; Gacia *et al.*, 2012).

PC5 contrasts P and C contents in sheath, likely linked with the P:C ratio, a known proxy for **phosphorus availability in seagrasses** (e.g., Duarte, 1990). When the plant is strongly limited by P, its tissues are depleted in this nutrient relative to C content, so the P:C ratio would be lower. As nutrient availability increases plant tissues become enriched in P relative to the C content, resulting in increasing P:C ratios (Duarte, 1990). PC5 is mainly affected by local factors (PC1m and PC2m), as they influence soil erosion in the watershed which largely controls the delivery of nutrients into the bay (Fig. 6; Table 1 in Supplementary material).

The variance explained by pRDA models ranged from 15.3 to 36%, evidencing that a substantial part of the principal components variability is unexplained by the chosen global and local predictors (Fig. 6; Table 1 in Supplementary material). Other factors that could have played an important role controlling seagrass ecosystem dynamics for the last ~4000 years are local changes in water transparency or temperature – as they can enhance sulphide stress (García *et al.*, 2012) –, dissolved inorganic C availability (Invers *et al.*, 1999, 2001), competition with other primary producers and soil bacteria (e.g., López *et al.*, 1998; Dumay *et al.*, 2002; Alcoverro *et al.*, 2004), or herbivory (e.g., Tomas *et al.*, 2005).

The spectral analysis showed that soil erosion and productivity (PC3 and PC4) share a periodicity of ~1000 yr; while OM accumulation and P availability (PC1 and PC5) share a periodicity of ~2000 yr. Other periodicities, only linked to productivity (PC4), are 520 and 2500 yr (Fig. 7). Although periodicities may be affected by non-climatic factors (e.g., internal seagrass dynamics), analogous cycles do appear in power spectra of solar activity reconstructions: a ~500 yr cycle, the Eddy cycle (~1000 yr) and the Hallstatt cycle (~2000 yr) (Yin et al 2007; Dima & Lohman, 2008; Steinhilber *et al.*, 2012). The 2500 yr cycle could be a fingerprint of the Hallstatt cycle, as Yin *et al.* (2007) observed that its ranges from 2040 to 2400 yr. Therefore, the spectral analysis and the pRDA results provide evidence to support the effect of TSI in the seagrass ecosystem trends.

The productivity record (PC4) is the only one presenting the three cycles. TSI and productivity trends follow a similar pattern, with intervals of increased TSI associated with increased productivity at ~1000, 2000, 3000 and 4000 cal. yr BP (Fig. 9). Terrestrial ecosystems functioning and photosynthesis depend on downward solar radiation at the Earth's surface (Sinclair *et al.*, 1976; Medvigy *et al.*, 2010). An analogous pattern is followed by *P. oceanica* ecosystems, suggesting that the productivity of underwater vegetation is also sensitive to changes in TSI (Fig. 9). However, even if the detected periodicities are driven by solar cycles, they could also be affected by autogenic mechanisms, sub-sampling resolution, or a combination of the two factors (Turner *et al.*, 2016).

5.2. Limitations of using $\delta^{13}\text{C}$ measured in *P. oceanica* sheath debris as a proxy of productivity

A larger positive loading of $\delta^{13}\text{C}$ of plant tissues in the productivity component (PC4) was expected, coherent with the relationships between $\delta^{13}\text{C}$ of plant tissues, leaf net production and irradiance found by Mateo *et al.* (2000, 2010) in field observations and experiments. $\delta^{13}\text{C}$ in plant tissues (and derived detritus) responds to changes in the

trade-off between C availability and demand, related to light and temperature variations. The long-term ecological results obtained in our work suggest that other factors are superimposed to changes in $\delta^{13}\text{C}$ values.

One factor that could affect $\delta^{13}\text{C}$ of plant tissues is meadow depth, as the correlation with production and irradiance is weaker in shallow meadows, as in Portlligat, than in those growing closer to the compensation irradiance (Mateo *et al.*, 2000). Assuming no significant changes in sea level for the last four millennia in the area (Vacchi *et al.*, 2016), the depth at which the meadow was growing 4000 years ago would have been around 7 m (3 m water depth at present plus 4 m mat thickness; Lo Iacono *et al.*, 2008). A lower irradiance would have resulted in a lower photosynthetic demand and a higher discrimination against the heavy isotope. Following this rationale, the $\delta^{13}\text{C}$ of ancient seagrasses debris should have been more negative than more recent debris. However, no evident trend is found, indicating that this effect is not as important as other factors. Another factor that could affect $\delta^{13}\text{C}$ of plant tissues is that the shape of the transfer functions found for the reconstructions was that of a saturation curve (Mateo *et al.*, 2010). This means that resolution of changes in $\delta^{13}\text{C}$ at higher productivity levels is lower and consequently changes might not be properly paralleled by the proxy, making the values at the higher end less accurate. Hence, small changes in the $\delta^{13}\text{C}$ record would be more meaningful than they seem to be.

The preservation of $\delta^{13}\text{C}$ in plant tissues exposed to diagenetic processes is still a long-standing matter of controversy (Wu *et al.*, 2003; Wang *et al.*, 2008; Alewell *et al.*, 2011), questioning its potential as palaeoecological proxy. Microbial reworking of OM during early diagenesis can modify its bulk carbon isotopic content (Meyers & Lallier-Verges, 1999; Boström *et al.*, 2007). However, there is no clear trend in the literature. According to Meyers & Lallier-Verges (1999) the overall diagenetic isotope shift in OM isotopic composition in Lake Michigan is minimal, ~1-2 ‰ shifts towards less negative $\delta^{13}\text{C}$

values. Wang *et al.* (2008) observed differences in $\delta^{13}\text{C}$ of up to 2.8‰ between vegetation and bottom organic matter. Fourqurean & Schrlau (2003) observed a steady decline in $\delta^{13}\text{C}$ of the seagrass *Thalassia testudinum* leaves during decomposition over the course of a year, so that leaves detritus became depleted in ^{13}C by ~2‰. This could indicate that variations in underwater soil conditions (e.g., higher nutrient inputs that could increase soil anoxia) could vary the diagenetic effect on $\delta^{13}\text{C}$ of the detritus and, hence, blur the correlation between $\delta^{13}\text{C}$ in sheaths with TSI and plant production. Preliminary results from *in situ* degradation experiments of *P. oceanica* sheaths in anoxic conditions (buried at around 10 cm in the sediment), showed no significant changes in $\delta^{13}\text{C}$ over 277 days (Project SUMAR, CTM2006-12492/MAR, unpublished data). Although this is an important finding to support the adequacy of $\delta^{13}\text{C}$ for palaeoenvironmental reconstruction, the effect of diagenesis over much longer periods of time remains untested and, therefore, further work is required to validate $\delta^{13}\text{C}$ signatures of *P. oceanica* tissues as a proxy of productivity.

5.3. Chronology of the environmental and ecological changes

Four phases are distinguished according to the main regimen shifts identified by change point modelling (CP-12, CP-11, CP-9 and CP-6; Fig. 5).

Phase I: Two millennia of relative stability with a steady decline in productivity (~4000-2000 cal. yr BP)

The records of PC scores showed lower values and variability from ~4000 to 2000 cal. yr BP. The productivity record (PC4) presents high scores at ~4000 cal. yr BP, following a decreasing trend until ~2000 cal. yr BP. The lower scores of the OM accumulation record (PC1) and the record of nutrient availability (PC2) are in accordance with the decreasing trend in ecosystem productivity. This period is described as arid in the Portlligat Bay owing to the abundance of *Pinus* and evergreen *Quercus* as well as in other Iberian records by the expansion of *Pinus*, sclerophyllous and/or steppe taxa (López-Merino *et al.*

l., 2017 and references therein). The arid conditions occur in the context of a decline in TSI (Fig. 5; Steinhilber *et al.*, 2009).

The first half of Phase I (~4000-3400 cal. yr BP), shows low impact of anthropogenic activities in the area, as indicated by other studies (Fig. 5; Riera-Mora & Esteban-Amat, 1994; López-Merino *et al.* 2017), suggesting low nutrient supply to the marine environment from soil erosion. The onset of agriculture practices in the catchment is observed by palynological analysis at ~3400-2900 cal. yr BP (López-Merino *et al.*, 2017). Anthropogenic impact steadily increased after ~3400 cal. yr BP, peaking at ~2600-2400 cal. yr BP with an increase in metal pollution due to mining and a larger importance of agriculture (Fig. 5; Serrano *et al.*, 2011; López-Merino *et al.*, 2017).

Overall, Phase I shows a decreasing trend in TSI and an increasing trend in anthropogenic pressure, but still low human impact on the coastal environment. Light seems to have been the main limiting factor for productivity. The strong decline in TSI likely overrode the effect in production derived from higher nutrient availability.

Phase II: Higher productivity and variability (~2000-800 cal. yr BP)

Throughout this phase the records of most principal components show higher scores, although with higher variance. Phase II starts with two abrupt changes: CP-5 and CP-6, both taking place during Roman times. An important increase in the coarser sediment fraction, sheath:belowground ratio and productivity are recorded between CP-5 and CP-6. Coarser sediments, along with increased productivity and nutrient inputs, could be explained by the conjunction of more intense human activities (i.e., mining and agriculture) in the catchment during Roman times (Serrano *et al.*, 2011; López-Merino *et al.*, 2017) and to enhanced flooding in eastern Iberia between ~2450 and 2150 cal. yr BP (Benito *et al.*, 2015). Seagrass meadows in Portlligat Bay may have been nutrient-limited; hence anthropogenic- and climate-induced terrigenous inputs would have increased the concen

tration of nutrients resulting in a higher productivity and a lower allocation of resources to belowground tissues.

The record of scores of all principal components reach a minimum at ~1600 cal. yr BP, when crops decreased in the catchment (Fig. 5; López-Merino *et al.*, 2017). Cropping resumed at the onset of the Visigothic period at ~1500 cal. yr BP (Fig. 5; López-Merino *et al.*, 2017). Productivity, sheath:belowground ratio and P availability increased during the Visigothic period, the first two reaching some of the highest values recorded. Therefore, the seagrass productivity at the bay recovered previous levels of production. The end of the Visigothic period is synchronous with another major regime shift, CP-8 (~1400-1050 cal. yr BP). Phosphorus availability and sheath:belowground ratio decrease, while productivity remains constant. The reduction in nutrient supply following the decrease in the agricultural activity at the end of the Visigothic period (López-Sáez *et al.*, 2009; López-Merino *et al.*, 2015, 2017) had no impact on the productivity of the ecosystem. Higher values in TSI could be behind this trend (Fig. 5).

Phase II shows high, constant TSI values, as well as increased nutrient inputs, linked to higher human impact. Despite this, during this phase there is an abrupt change in productivity at ~1600 cal. yr BP coeval with lower evidence of human activities, the overall trend indicates that the seagrass growth over Phase II is regulated by nutrient availability.

Phase III: Abrupt decline in productivity: crossing an ecological threshold? (~800 -200 cal. yr BP)

An abrupt change in productivity took place at ~800 cal. yr BP (CP-9). The region experienced an increase in crops at ~800-600 cal. yr BP, that is reflected in the higher magnetic susceptibility (i.e., soil erosion) of the seagrass mat and in the abundance of foraminifera linings (i.e., eutrophication) as detected in the nearby Core 2006 (Fig. 5; López-Merino *et al.*, 2017). These changes are consistent with rapid deforestation in the area (Riera-Mora & Esteban-Amat, 1994; López-Sáez *et al.*, 2009; López-Merino *et al.*, 2015, 2

017). During this chronological interval, TSI exhibits several minima (Figs. 5 and 8), within the context of the Little Ice Age, a climatic anomaly driven by a decline in summer insolation (Mayewski *et al.*, 2004; Steinhilber *et al.*, 2012; Oliva *et al.*, 2018). The combination of low TSI with increasing human impact might have impacted the dynamics of *Posidonia* meadows through diverse and complex mechanisms. First, an excess of sediment and nutrient loadings entering the bay may derive in a poor light environment reinforced by the low TSI, as well as in an increased sediment anoxia (Rabalais & Turner, 2001). Second, decreased carbohydrates reserves which are crucial to survive during periods of low TSI (when C balance can be negative) could have compromised the seagrass growth. These decreases in carbohydrates reserves have been observed in the field following nutrient increases, since N assimilation requires energy and C skeletons, resources obtained from the carbohydrate reserves (Invers *et al.*, 2004; Alcoverro *et al.*, 2001). The overall ecosystem resilience seems to have crossed a threshold, causing the sudden regime shift by CP-9 and bringing the system to the lowest levels of photosynthesis and growth.

Between ~600 and 200 cal. yr BP, the coarser fractions and P contents slightly increase, although sheath:belowground ratio, productivity and OM accumulation show low values. This chronological interval is coeval with the establishment of terraced fields of olive trees and vineyards in the area (Franquesa i Codinach, 1995). Terraced agriculture would have limited soil erosion and hence the fluxes of sediments and nutrients into the bay, as attested by the decrease in the abundance of foraminiferal linings (Fig. 5; López-Merino *et al.*, 2017). This lower input of nutrients would explain the lower values of sheath:belowground ratio (Fig. 5).

Although sediment and nutrient inputs into the bay were reduced during phase III, this was not paralleled by a recovery in the productivity levels. The still low prevailing TSI may have kept productivity at its lowest levels, although the crossed threshold in the resilience of the meadow could have meant a change in the functioning of the ecosystem.

Phase IV: Low productivity despite better environmental conditions (~200 cal. yr BP-present)

During the last two centuries OM accumulation decreases, ecosystem productivity shows low values with no clear trend, the coarser fractions increase, and the sheath:belowground ratio shows higher values. Agriculture practices in the area were progressively abandoned since AD ~1850 due to phylloxera plague damaging the vineyards, and since AD 1956 after a damaging frost (Franquesa i Codinach, 1995). The progressive abandonment of the terraced fields could have enhanced catchment soil erosion, being the reason behind the increase in the coarser fraction, in P content and sheath:belowground ratio.

Briefly, during this phase, even though TSI is higher, the seagrass meadow does not recover its previous state of productivity. This might be because the trespassed threshold at CP-9.

The results of pRDA for the record of ecosystem productivity composite variable (PC4) show a quite equally distributed variability between local and large-scale factors as well as their interaction (Fig. 6). Therefore, during the last four millennia the ecosystem productivity have been affected by both human impact and climate, although their importance seems to have varied for the different phases. The long-term perspective of the mechanisms that control productivity in the *P. oceanica* ecosystem provided by the application of a palaeoecological approach on the seagrass mat, are coherent with the controls for the seasonal growth in this species in shallow environments, where local factors can play a major role when light availability is high (Alcoverro *et al.*, 1995).

6. Conclusions

The combination of biological and sedimentological proxies has provided long-term information on the functioning of the *P. oceanica* ecosystem. The multi-proxy analysis

has revealed millennial to centennial-scale seagrass ecosystem dynamics through changes in the OM accumulation in the mat, ecosystem productivity, nutrient supply and catchment soil erosion. Global (TSI and NH temperature) and local (anthropogenically-derived nutrient and sediment inputs) factors, as well as their interactions have played a role in the dynamics of the *P. oceanica* ecosystem throughout the last four millennia.

Although the multi-proxy approach has provided invaluable long-term information on ecosystem changes, the knowledge gaps on the relationships between the proxies used and the environmental factors they are supposed to represent should not be ignored. More integrated studies are needed in order to get a better understanding of catchment-bay interactions, since local factors in the catchment seem to be as important as the climate effects.

The results obtained here, together with the overall ecosystem trends identified, largely match with those found by Lopez-Merino *et al.* (2017) for another core at the same study area (150 m apart) and using another set of proxies. This reinforces our confidence in the robustness of the approach and in the usefulness of paleaeoecology as a tool for conservation. An overarching recommendation to be drawn from this study is the need of extending the observation level at the catchment scale if we do not want to overlook key factors that can bring coastal ecosystems close to crossing critical thresholds beyond their resilience.

Acknowledgements

This research was supported by a PhD scholarship funded by the Spanish Ministry of Science and Innovation to C. Leiva-Dueñas (FPU15/01934); the Spanish Ministry of Economy and Competitiveness, SUMILEN project (CTM2013-47728-R); the Spanish Autonomous Organism of National Parks, PALEOPARK project (ref. 1104/2014); the CSIRO Marine and Coastal Carbon Biogeochemistry Cluster. L. López-Merino was funded by The Leverhulme Trust towards an Early Career Fellowship (ECF-2013-530,

“*Posidonia* as environmental archive: long-term ecology and conservation views”). O. Serrano was supported by an ARC DECRA DE170101524. This is a paper of the Group of Benthic Ecology 2014 SGR 120.

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Tables

Table 1. Radiocarbon dates in the *P. oceanica* mat sediment Core 2000. The marine ^{13}C calibration curve was used for calibration and a local marine reservoir effect included ($\Delta R = 23 \pm 71$ yr). Radiocarbon dates are taken from Serrano *et al.* (2011).

Laboratory code	Material type	Depth (cm)	AMS ^{14}C date (yr BP)	Cal. yr BP (2 σ range)	Weighted mean age
OS-29665	<i>P. oceanica</i> sheaths	41	710 $\pm$ 45	160 - 400	289
OS-29666	<i>P. oceanica</i> sheaths	62	895 $\pm$ 45	343 - 555	461
OS-29667	<i>P. oceanica</i> sheaths	77	975 $\pm$ 40	468 - 666	569
OS-29668	<i>P. oceanica</i> sheaths	110	1430 $\pm$ 40	697 - 955	823
OS-29651	<i>P. oceanica</i> sheaths	145	1600 $\pm$ 45	913 - 1181	1045
OS-44491	<i>P. oceanica</i> sheaths	213	1710 $\pm$ 25	1269 - 1581	1425
OS-44492	<i>P. oceanica</i> sheaths	255	2120 $\pm$ 30	1572 - 1871	1721
OS-44493	<i>P. oceanica</i> sheaths	287	2270 $\pm$ 30	1821 - 2119	1967

OS-44494	<i>P. oceanica</i> sheaths	307	2500 ± 30	2005 - 2304	2152
OS-44497	<i>P. oceanica</i> sheaths	326	2560 ± 25	2184 - 2542	2345
OS-44498	<i>P. oceanica</i> sheaths	355	3130 ± 25	2570 - 2934	2771
OS-44499	<i>P. oceanica</i> sheaths	386	3320 ± 30	2947 - 3272	3111
OS-44502	<i>P. oceanica</i> sheaths	415	3500 ± 35	3236 - 3576	3406
OS-44504	<i>P. oceanica</i> sheaths	437	3850 ± 30	3473 - 3852	3663

Figure 1. (a) Location of the study area and the coring site of Core 2000 (red dot, this study) and Core 2006 (blue dot, López-Merino *et al.*, 2017) (Portlligat Bay, Girona, Spain). (b) Core 2000 shows a dense mat with abundant organic matter for the first forty centimeters, changing to sands (fine to coarse size) with rhizomes, roots and leaf sheaths more degraded in deeper sections.

940

941 **Figure 2.** Age-depth model of Core 2000 using Bacon.R software (Blaauw & Christen, 2011).
942 Fourteen radiocarbon dates were calibrated using the marine13 radiocarbon age calibration curve
943 (Reimer *et al.*, 2013) and corrected for a local marine reservoir effect ($\Delta R = 23 \pm 71$ years, Siani
944 *et al.*, 2000). The red dashed curve shows the “best” model based on the weighted mean age for
945 each depth. Individual radiocarbon dates are shown in probability density functions of calibrated
946 ages. The grey area indicates the uncertainty envelope of the age model with grey dashed curves
947 indicating 95% confidence intervals.

948

949 **Figure 3.** Descriptive variables: changes in bulk density, sediment organic matter (SOM), coarse organic matter (COM) and carbonate content, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C,
 950 N, P, C/N, C/P, organ debris distribution and grain size distribution along the *P. oceanica* mat sediment Core 2000 plotted against age. The percentage of
 951 organics is the sum of SOM (<1 mm) and COM (>1 mm) (i.e., the total organic matter content). Silicates correspond to the percentage of non-carbonate inorganic

952 sediments. Organic matter and carbonate contents are also expressed as MAR (see text for explanation). Stable isotopes and elemental composition were
953 analysed in the sheath debris.

Figure 4. (a) Factor loadings of the descriptive variables of Core 2000 used in the PCA. Numbers in bold indicate variables with factor loadings >0.6 and in bold italics are those with moderate factor loadings (0.5 to 0.6). The individual percentage of variance explained is given under each factor. Factor loadings represent correlation coefficients between the variables and the principal components. (b) Communalities. The communality accounts for the proportion of each variable's variance explained by the five extracted principal components. The total length of the bars is the communality of each element, while the sections

963 represent the proportion of variance allocated in each individual principal component.

Figure 5. Long-term ecological dynamics detected in the *P. oceanica* meadow of Portlligat Bay. Black dots correspond to the original data and horizontal lines are the noise estimation, which is the standard deviation of the unknown error (normal) distribution for a given data set. Thick red curves represent the average after 100,000 functions, while grey lines define 95% confidence interval ranges. The blue curve on the left shows the probability of the change-point [P(x)]. PC: Principal component, CP: Change Point. Horizontal grey bands highlight abrupt regime shifts with high probability. The change point functions are compared to Total Solar Irradiance (TSI), given as difference in W/m² to the value of the PMOD composite during the solar cycle minimum of the AD 1986 (1365.57 W/m²; Steinhilber *et al.*, 2012); Northern Hemisphere (NH) temperature, given as anomalies (°C) from AD 1961-1990 (Kobashi *et al.*, 2013); PC1m, considered to be related to anthropogenic activities in the catchment, and PC2m, related to metals with a lithogenic origin (Serrano *et al.*, 2011); sum of crops (*Cerealia*-t., *Cannabis/Humulus*-t., *Juglans*, *Castanea* and *Vitis*) is a palynological indicator of land-use change; foraminifera linings account for eutrophication of the bay waters and magnetic susceptibility indicates changes in the seagrass mat organic/inorganic content. Sum of crops, foraminifera linings and magnetic susceptibility

975 data are from Core 2006, a core obtained 150 m apart from Core 2000 (López-Merino *et al.*, 2017). On the right, the four phases identified in this study are
976 indicated as well as arid (yellow) and humid (blue) phases (Pérez-Sanz *et al.*, 2013).
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980 **Figure 6.** Percentage of partial explained variation and significance of individual terms (explanatory variables) assessed using Monte Carlo permutation tests
981 (999 permutations, levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.) in every partial RDA.

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984 **Figure 7.** Lomb-Scargle normalized periodograms (spectral power as a function of periodicity) of principal components PC1, PC3, PC4 and PC5.
985 The horizontal dotted line marks the significance level. Prominent periodicities are indicated with red lines. There was not any significant cycle
986 observed for PC2.

Figure 8. Sum of sinusoids fits using periods from Lomb-Scargle periodograms, showing ~1000 years cycles for the soil erosion record (PC3, this study); periods ~4000, ~2000 and ~1000 years cycles for PC1m (Serrano *et al.*, 2011) and period ~1100 for magnetic susceptibility (López-Merino *et al.*, 2017). Vertical grey bands highlight phases of high soil erosion which co-occur with high anthropogenic pressure (PC1m) and high terrestrial inputs (magnetic susceptibility).

996 **Figure 9.** Sum of sinusoids fits using periods from Lomb-Scargle periodograms, showing ~520, ~970 and ~2500 years cycles for the productivity
997 record (PC4) and ~980 and ~2300 years cycles for the Total Solar Irradiance series (Steinhilber *et al.*, 2012). Vertical grey bands highlight phases
998 of solar irradiance maximum, which co-occur with productivity maximum.

Supplementary material

Table 1. Results of Monte Carlo permutation tests (n=999) on pRDA models. Five pRDA models were run, one per PC, so one of the PC was the response variable in each of them. All models had the same four explanatory variables: TSI, NH temperature, PC1m and PC2m. All pRDA models had sample ages partialled out as a covariable. Monte Carlo permutation tests were used to test the significance of the model and of each predictor variable (999 permutations), obtaining the partial explained variation and the significance for every explanatory variable.

Levels of significance: *P≤0.05, **P≤0.01, ***P≤0.001.

Response variables	% variance explained	Model P value	Significant terms	% variance explained by each term in the model	Terms P value
PC1 (OM accumulation)	15.3	0.001	TSI	2.87	0.001***
			PC1m	8.72	0.001***
			TSI*NH	1.94	0.007**
PC2 (sheath/belowground organs)	10.5	NS			
PC3 (soil erosion)	36	0.001	TSI	7.6	0.001***
			PC1m	13.57	0.001***
			PC1m*PC2m	4.03	0.002**
			TSI*NH	1.71	0.017*
			TSI*PC1m	1.36	0.042*
			NH*PC1m	2.05	0.011*
			TSI*NH*PC1m	1.86	0.017*
PC4 (productivity)	21.1	0.001	TSI	3.16	0.014*
			PC1m	5.04	0.001***
			TSI*NH	3.33	0.008**
			TSI*PC1m	3.58	0.001***
			NH*PC1m	2.03	0.043*
			PC1m*PC2m	1.82	0.043*
PC5 (phosphorus availability)	23.7	0.001	NH	1.93	0.043*
			PC2m	4.14	0.004**
			PC1m	4.9	0.005**
			NH*PC2m	7.11	0.001***
			PC1m*PC2m	2.38	0.029*

TSI stands for Total Solar Irradiation, given as the difference respect to the value of the Physikalisch-Meteorologisches Observatorium Davos (PMOD) composite during the solar cycle minimum of the year 1986 AD (1365.57 W/m²; Steinhilber *et al.*, 2012)

NH is the Northern Hemisphere temperature anomalies in °C. It is ice-core-derived and from the base year of 1961–1990 (Kobashi *et al.*, 2013).

PC1m and PC2m are principal components from heavy metal abundances in sheaths analysed also in Core 2000 (Serrano *et al.*, 2011). PC1m, considered to be related to anthropogenic activities in the catchment, and PC2m, related to metals with a lithogenic origin.