An ecological status indicator for all time: Are AMBI and M-AMBI effective indicators of change in deep time?

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Abstract

Increasingly environmental management seeks to limit the impacts of human activities on ecosystems relative to some ‘reference’ condition, which is often the presumed pre-impacted state, however such information is limited. We explore how marine ecosystems in deep time (Late Jurassic)are characterised by AZTI’s Marine Biotic Index (AMBI), and how the indices responded to natural perturbations. AMBI is widely used to detect the impacts of human disturbance and to establish management targets, and this study is the first application of these indices to a fossil fauna. Our results show AMBI detected changes in past seafloor communities (well-preserved fossil deposits) that underwent regional deoxygenation in a manner analogous to those experiencing two decades of organic pollution. These findings highlight the potential for palaeoecological data to contribute to reconstructions of pre-human marine ecosystems, and hence provide information to policy makers and regulators with greater temporal context on the nature of ‘pristine’ marine ecosystems.

Key words: baseline; palaeoecology; deoxygenation; AMBI; environmental monitoring; reference conditions

1. Introduction

There is increasing recognition of the value of marine ecosystems, the services they provide (Costanza et al., 2014; de Groot et al., 2012; United Nations, 2005) and the threats to their continued delivery (United Nations 2017). Attempts to manage these threats (e.g. pollution, fisheries, shipping, climate change (Breitburg et al., 2018; FAO, 2016; Frid and Caswell, 2017; IPCC, 2014; United Nations, 2005)) have often been hampered by a lack of clear information on the state of the system and how this relates to the pressures imposed (Carpenter et al., 2009; Lubchenco and Petes, 2010). This has led to the development of a plethora of indices of 'environmental health' that seek to inform regulatory bodies and wider society about the state of the environment and in turn support the management of impacting activities (Birk et al., 2012; Borja et al., 2016; Niemi and McDonald, 2004).

In adopting an 'ecosystem approach' to environmental management many jurisdictions have sought to incorporate metrics of 'system level' health/status within their regulatory frameworks (e.g. EU, US, Canada)(Borja et al., 2008; Niemeijer and de Groot, 2008; United Nations, 2005). However, finding indicators that are 'reliable' (see ICES 2001a for a discussion of the properties of an ideal indicator) when applied to systems other than those for which they were developed has proved challenging (ICES, 2001b; Rice et al., 2012; Rice and Rochet, 2005; Rossberg et al., 2017; Van Hoey et a. 2010).

Seafloor sediments represent the second largest habitat on Earth and those organisms that inhabit the seafloor (the benthos) are often monitored and used as the basis for assessments of marine ecosystem health (Díaz et al., 2004). The benthos tends to have high site fidelity and moderate (multiple year) longevity so that they serve to integrate short-term fluctuations in environmental conditions, and so are representative of the local environmental status. They also occupy a critical role in many marine food webs such as those upon which commercial fisheries depend. These attributes of the benthos have been recognised for decades and the monitoring of benthic fauna has been a key aspect of many estuarine and coastal monitoring programs (e. g. Gray et al., 1990). One of the most widely applied measures of marine benthic 'health' has been the AZTI's Marine Biotic Index (AMBI) family of indices which were originally developed to measure the impacts of enrichment, deoxygenation and pollution within estuaries and coastal waters (Borja et al., 2000). Developed for the EU Water Framework Directive (European Commission 2000) these metrics are now used for the remediation assessments in the Marine Strategy Framework Directive (European Commission 2008, Borja et al. 2011). To form the basis of a regulatory response both a strong response to pressures and an understanding of the nature of the un-impacted or baseline system are needed.

The effects of these pressures on natural systems are hard to predict (HELCOM, 2010) and require reference conditions or baselines for determining change from what is normal or typical for an ecosystem (ICES, 2001a, b). Knowledge of the undisturbed state of marine ecosystems, in terms of structure, functioning and dynamics, are generally lacking and the data used within management frameworks are rarely 'true' baselines in that they do not describe a state prior to anthropogenic pressures (Jackson et al., 2001; Pauly, 1995). Although management baselines describe the last few decades of change, they neglect the long history of marine exploitation that spans centuries to millennia (Jackson et al., 2001; Lotze et al., 2006; Pandolfi et al., 2003; Rick and Erlandson, 2008), some of the consequences of which are yet to manifest (Jackson et al., 2001). The reliability of forecasting and the evidence-base for management could be improved by a better appreciation of the reference conditions for anthropogenically-induced change (Van Hoey et al., 2010). However, these baselines have been shown to shift with the temporally limited knowledge-base of the observer, the baseline continually shifts to reflect a more and more degraded state moving further from the 'natural' reference state (Dayton et al., 1998; Kittinger et al., 2015; Pauly, 1995). The shifting baseline phenomenum makes it difficult to discern natural from anthropogenic change, and can obscure long-term change and natural variability (Klein and Thurstan, 2016).

To manage the pressures on marine ecosystems successfully there is a need to understand the changes, natural and anthropogenic, which have occurred to date and prepare for those that may occur in the future (Cheung et al., 2009; Pauly et al., 2000; Pereira et al., 2010; Stock et al., 2011). Information on the nature of historic healthy ecosystems and ecosystem resilience is needed to determine reliable targets (Lotze, 2010). This information can be acquired from environmental history (Klein and Thurstan, 2016), but whilst being an improvement over more recent 'baseline data', these reference conditions still incorporate some degree of anthropogenic impact (e. g. Pinnegar and Engelhard, 2008). Using the fossil record of ecological change (or 'palaeoecological' change) allows consideration of the ecosystem prior to human activities. Although the taxa present differ, to some degree, they occupy very similar ecological niches and have equivalent ecological roles (Caswell and Frid, 2013). These palaeoassemblages therefore have the potential to provide ecological and functional baselines for 'pristine' seafloor communities, and may also provide reference conditions for regional and global perturbations within coastal ecosystems that were driven by wholly natural processes (e.g. volcanism, plate tectonics, clathrate dissociation, or wildfires)(Bond and Grasby, 2017; e. g. Jenkyns, 2010). In this study we investigate the record of regional palaeoecological change from Late Jurassic deposits of the Kimmeridge Clay Formation in Dorset, UK, as an example of changes in coastal benthic systems experiencing natural organic enrichment and associated deoxygenation.

This study examines whether disturbances in past marine ecosystems can be measured using biotic indices developed to assess contemporary ecosystem status under human disturbance. In principle, benthic community indices such as AMBI and M-AMBI (Muxika et al., 2007) should reflect environmental changes (e.g. deoxygenation, and climate) whether they be natural or human induced (Borja et al., 2015). We test whether relatively well-preserved fossil deposits that have undergone substantial natural environmental (as indicated by geochemical and geological proxies) and ecological changes are analogous to the changes occurring in the modern oceans in response to anthropogenic activities. To date, these indices have only been applied to assemblages of live taxa and recently to death assemblages ((i.e. skeletal components only) of molluscs that have great potential value for benthic assessments (Dietl et al., 2016; Leshno et al., 2016), however they have not previously been applied to fossil assemblages.

2. Methods

2.1. Study site and data sources

Data for this study originate from the sedimentary deposits of the Kimmeridge Clay Formation (KCF) that are exposed in the south-east UK on the Dorset coast near Kimmeridge, UK (50°36’58”N, 2°7’14”W), Westbury pit, south Wiltshire and Black Head near Osmington and Weymouth (Fig. 1). The formation consists of up to ~540 m of vertical section of cyclically alternating fine grained organic-rich sediments and limestones (Morgans-Bell et al., 2001). The total organic carbon content (TOC) of the deposits is very high at some levels (up to ~50 wt%) and the stratigraphy and geochemistry have been well-studied (e. g. Morgans-Bell et al., 2001; Tyson, 2004; van Kaam-Peters et al., 1997). The palaeoassemblage data analysed in the present study are based on the species composition and abundance data (number, expressed as percentage, per 0.2 m^3 of rock sampled) collected by Wignall (1988, 1990) from these exposures of the KCF. Samples were collected approximately every 1 m vertically throughout the section and were classified into 31 unique associations on the basis of their ranked species-abundance distributions (sensu Wignall, 1990), hereafter referred to as palaeoassemblages, many of which recur throughout the stratigraphic section (Supplementary Material (SM) Fig. S1). The palaeoassemblages spanned between 0.05 m–24.4 m of vertical rock and so persisted on average for 0.90 m equivalent to a temporal duration of ~7000 years based on the cyclostratigraphic timescale of Weedon et al. (2004), totalling around 4 million years.

On the other hand, a contemporary data set has been used to compare the response of the benthic assemblages to environmental changes. We have used data from the Nervión estuary (North of Spain), which has been modified by urban, mining, industrial and port settlement; these have occupied practically the whole of the valley, during the last 150 years (Cearreta et al., 2004). The estuary received historically high volumes of wastewater discharges, resulting in extremely low concentrations of dissolved oxygen in the waters and high organic matter and pollution content, leading to deterioration of benthic communities (Borja et al., 2006). Reductions in the volumes of wastewater discharged began in the late 1980s, the physico-chemical waste treatment began in 1991, and biological treatment started in 2001 (Pascual et al., 2011). Data on the benthic macrofaunal composition, oxygen and organic matter in the Nervión estuary were obtained from a monitoring program carried out since 1989 (Borja et al., 2006). In order to have two contrasting benthic assemblages, we selected two out of the eight sampling stations with differing levels of enrichment: (i) station 5, located in the inner part of the estuary, in a water depth of 8–10 m near to the discharge point; and, (ii) station 110, close to estuary mouth, in 25–30 m water depth. Data for these two stations span 1989 to 2012.

2.2. AMBI and M-AMBI determination

One of the challenges in assessing the status of palaeoecological assemblages is the assignation of species to one of the five ecological groups (EG) on which AMBI is based: EGI: sensitive species; EGII: indifferent species; EGIII: tolerant to organic enrichment; EGIV: second order opportunistic species; and EGV: first order opportunistic species (Borja et al., 2000). The ecological group classifications consider feeding type, life habit, body-size, life history and response to disturbances (i.e. organic enrichment)(Borja et al. 2000). This information may be acquired for a fossil fauna by: direct measurement, functional morphology, use of extant analogues, and the associations of fossil taxa (i.e. determined from distribution and/or abundance, nature of the palaeoenvironmental and the palaeoecological associations). In the SM we have included the complete list of taxa, with the feeding type, life habit, body-size, mode of reproduction, distribution, associations and the source literature, for each taxon, upon which we have based the assignation of the ecological groups (Table S1). To avoid circular reasoning each taxa was classified using independent evidence (Table S1), which shows the response of the taxa to environmental disturbances. After taxa assignation to ecological groups, AMBI values were calculated using the formula in Borja et al. (2000), with the software available at http://ambi.azti.es. The threshold values used for AMBI classification were:

undisturbed <1.2; slightly disturbed 1.2–3.3; moderately disturbed, 3.3–5.0; heavily disturbed 5.0–6.0; and extremely disturbed 6.0–7.0.

The M-AMBI determination included information on the ecological groups (from AMBI), taxa richness and diversity, and it uses information from both undisturbed and severely disturbed communities as reference conditions to assess biological status. For the undisturbed reference conditions an AMBI value of zero was used (total dominance of sensitive species), and for richness and diversity values that were slightly higher than the highest values in the dataset (55 for taxonomic richness and 4.5 bits ind^{-1} for diversity). Conversely, the disturbed reference conditions were selected using azoic sediments with an AMBI value of 6 (extremely disturbed) and for richness and diversity we used zero.

M-AMBI was calculated using the same software as for AMBI, based on factor analysis (Bald et al., 2005; Muxika et al., 2007). At 'high' ecological status, the reference condition may be regarded as an optimum where the M-AMBI approaches 1, whilst at 'bad' ecological status, the M-AMBI approaches 0. The threshold values used for the M-AMBI classification were 'high' ecological quality, >0.77; 'good', 0.53-0.77; 'moderate', 0.38-0.53; 'poor', 0.20-0.38; and 'bad', <0.20 (Borja et al., 2007; 2009).

2.3. Relationships between environmental conditions and biotic indices

The links between the changes in the AMBI and M-AMBI score of the palaeoassemblages from Kimmeridge (21 of the total 31) were investigated using data on the TOC and the ratio of the elemental abundances of Thorium: Uranium (Th/U), measured from bulk rock samples, collected from the Kimmeridge Clay Formation exposed on the coast (i.e. the same sections as those from which the palaeontological data were collected) and two nearby boreholes sections (Morgans-Bell et al., 2001; Fig. 1b). TOC may be indicative of organic carbon supply to the benthos, and so primary production (e. g. Tyson, 2004) and/or redox state. The elemental ratio of Thorium: Uranium (Th/U) abundances may be a proxy for palaeoredox (Arthur and Sageman, 1994; Morgans-Bell et al., 2001). The relationships between the indices, and between the biotic indices and environmental factors/proxies for palaeoenvironmental change were determined using Spearman's rank order correlation or linear regression.

3. Results

3.1. The palaeoassemblages

The palaeoassemblages included a total of 129 taxa, mostly true species, with taxa richness of the individual assemblages varying between six and 42. The assemblages were dominated by bivalve molluscs, but also contained gastropods, brachiopods, bryozoans, crustaceans, scaphopods, echinoderms and annelids (serpulid worms). AMBI showed that the 31 palaeoassemblages ranged from 'slightly' to 'heavily disturbed' (Table 1, Fig. 2a). Two palaeoassemblages were heavily disturbed (E1a and E2a), 14 were moderately disturbed and the remaining 15 were slightly disturbed (Table 1). In turn, M-AMBI showed that the ecological status of the assemblages varied from 'bad' to 'good' (Table 1, Fig. 2b) with one assemblage having bad ecological status (E2a), six poor, six moderate and the remaining 18 were good, with two (A7 and A10) near the boundary of good–high status (Fig. 2b). Thus, classifications of the 31 palaeoassemblages by AMBI and M-AMBI differed, and overall M-AMBI described a broader range of states than AMBI. The results from the two indices classified palaeoassemblages A1, A10, A11 and E3 as being of better state (based on their relative groupings with the other palaeoassemblages; Table 1) with M-AMBI rather than AMBI, whereas E9 and A5 received a lower classification with M-AMBI (Table 1). These differences in classification seemed to be primarily attributable to differences between the number of taxa present in the assemblages, which are used in the determination of M-AMBI but not AMBI (Fig. 2?).

The 31 palaeoassemblages were composed of varying proportions of the five ecological groups (Fig. 2). Under high TOC (e.g. >4%) for most palaeoassemblages ≥50% of the taxa were first and second order opportunists (ecological groups V and IV, respectively; Fig. 2). E4 and E9 were exceptional in having both high TOC and lower proportions of first and second order opportunists (Fig. 2c). Of the lower TOC (<4%) palaeoassemblages B1–B5 were dominated by disturbance-tolerant taxa (ecological group III) with relatively equal proportions of taxa from the other four ecological groups. Palaeoassemblages A2–A9 and A/E1 were composed mostly of taxa that were indifferent to disturbance, disturbance-tolerant and second order opportunists: with <3% of taxa being first order opportunists. Assemblages A1 and A10–A11 were similar to A2–A9 and A/E1, but had larger proportions of first order opportunists. Assemblages E3, E8 and A7 had the highest proportions of taxa that were sensitive to disturbance (Fig. 2).

Linear regression showed that both the AMBI and M-AMBI scores of the 21 palaeoassemblages from the outcrops near Kimmeridge were correlated with the mean TOC content of the deposits within which each palaeoassemblage was preserved (AMBI $R^2 = 0.22$, $p<0.05$; M-AMBI $R^2 = 0.52$, $p<0.001$; Fig. 3). Once E2a, considered an outlier, was removed both correlations became stronger (AMBI $R^2 = 0.25$, $p < 0.05$; M-AMBI $R^2 = 0.64$, $p < 0.001$). AMBI was also correlated ($R^2 = 0.22$, $p<0.05$) with mean Th/U suggesting a direct or indirect link with palaeoredox.

Amongst all palaeoassemblages E2a is unique in being dominated >90% by first order opportunists (Fig. 2) and having the highest AMBI and the lowest M-AMBI scores suggesting heavy disturbance (although it does not have the highest TOC; Fig. 2c).

For the remaining 10 palaeoassemblages (A2–A11), collected from locations other than Kimmeridge Bay, TOC and Th/U data were not available but AMBI values indicated slight disturbance and M-AMBI indicated good ecological status for A2–A9; and, A10–A11 were moderately disturbed although had good M-AMBI status (Table 1). Palaeoassemblage A5 had distinctly higher AMBI and lower M-AMBI (Fig. 2a) than the other 9 palaeoassemblages and was dominated, >80%, by second order opportunists (*Isocyprina* spp.; Fig. 2a). A comparison of the abundances of the different ecological groups (I–V) in the palaeoassemblages from Kimmeridge with those from the other two sites (Weymouth and Westbury) showed that the mean abundance of first order opportunists were five times more abundant at Kimmeridge (t-test, $t = 2.54$, $p = 0.017$) than for the 10 palaeoassemblages from the other two sites combined.

3.2. Comparison of palaeoassemblages with present-day benthos

The palaeoassemblages from the KCF were compared with the benthos of the Nervión estuary between 1989 and 2016 (Table 1, Figs 2 and 4-5) that has received human waste (sewage and industrial discharges) for >150 years and so has experienced large organic loads (Figs 4–5). The Nervión assemblages ranged between slightly and extremely disturbed within the inner reaches, and from undisturbed to slightly disturbed in the outer reaches of the estuary (Table 1). Furthermore, the assemblages in the inner reaches of the Nervión estuary remained disturbed (Table 1; Fig. 4e) for a number of years despite improvements in oxygenation.

The species richness of the palaeoassemblages were comparable with the benthos from the Nervión estuary which ranged from 0–50 species per site (Figs 2c, 4c, 5c). With the exception of palaeoassemblages E2a, E8 and A6–A7, the KCF benthos most closely resembled those present in the inner reaches at Nervión after 2001 when oxygen saturation increased from 50% to >80% (Figs 1 and 3). In most years these assemblages ranged from slightly to moderately disturbed (with good–high M-AMBI status in the inner reaches; Figs 1a–c and 3a, Table 1). At times the entire assemblage in the inner reaches of the estuary consisted of 2–3 species of first order opportunists only, whereas in the KCF this was never the case (although some barren possibly azoic intervals occurred; Wignall 1988, Figs 2 and 4). The most disturbed palaeoassemblage E2a resembled those in the inner reaches of the Nervión estuary prior to the initiation of physico-chemical water treatment in 1991 (Figs 1 and 3) where bottom water oxygen concentrations were <40% saturation (Figs 4b-c).

Contrastingly, in the outer reaches of the Nervión estuary bottom water oxygen saturation exceeded ~80% in all years (Fig. 5) and the range of AMBI scores were approximately three-fold lower than those from the inner reaches (Figs 4a and 5a). These assemblages were classified as either undisturbed or slightly disturbed (Table 1) and in most years >70% of taxa were sensitive or indifferent to disturbance (Figs 4a and 5a). Thus, overall the palaeoassemblages were more similar to the benthos of the inner reaches of the estuary in terms of their AMBI, M-AMBI and ecological group composition (Figs 2, 4 and 5). However, E8 and A6–A7 had more similar ecological group composition and AMBI scores (although lower M-AMBI scores) to the benthos in the outer reaches, being mostly composed of ecological groups I–III, from 1989–1990 before water treatment began. In general, the KCF palaeoassemblages seem to have been less disturbed than the benthos within the inner reaches of the Nervión estuary, but they were not as healthy as the benthos inhabiting the outer reaches of the estuary.

The AMBI scores of assemblages from the inner reaches of the Nervión estuary were strongly negatively correlated ($R^2 = 0.75$, $p<0.001$) and the M-AMBI were positively correlated ($R^2 = 0.78$, $p<0.001$) with bottom water oxygen saturation. In the outer reaches of the estuary the environmental gradients were less distinct (Fig. 5) and only the M-AMBI score was correlated with dissolved oxygen concentrations ($R^2 = 0.20$, $p<0.05$). Although no direct relationship with oxygen content can be established for the KCF palaeoassemblages the correlations between M-AMBI and AMBI with TOC and Th/U shows there were at least indirect links between the degree of ecological disturbance and palaeoredox conditions (Fig. 3).

Comparisons of the ecological group composition, AMBI, and M-AMBI scores of palaeoassemblages from Westbury and Weymouth, for which there are no geochemical proxy data, with sites in the Nervión estuary (Figs 1–4, Table 1) provides some basis for interpretation of the palaeoenvironment. Palaeoassemblages A10–A11 were comparable with those present in the inner reaches of the estuary when full water treatment began (in 2001), and A2–A5 were comparable to the benthos a decade or so afterwards (Figs 2a–b and 4a–b) and so seem to have been less enriched/deoxygenated. Palaeoassemblages A6–A7 were most similar to the benthos in the outer reaches of estuary in 1989–1990 (before water treatment began) and so although they may have received some organic enrichment they were also well-oxygenated (Figs 2a–c and 5a–e).

The relationships between AMBI, M-AMBI scores and species richness were similar for the present-day and Jurassic datasets (Fig. 6a-c) and correlations were stronger for the present-day data (Fig. 6a–c) perhaps because of preservational loss from the fossil assemblages. The nature of the relationship (i.e. the slope) between species richness and M-AMBI varied for each dataset, an equivalent increase in M-AMBI corresponded to a greater increase in species richness in the KCF and the outer reaches of the estuary compared with the inner reaches. These differences are probably attributable to environmental differences (with station 5 being upriver and so in a different salinity regime and thus less diverse even when 'recovered' from the organic enrichment).

The abundances of all ecological groups except one were correlated with both AMBI and M-AMBI at station 5 and in the KCF (Table 2, $p<0.005$). For AMBI all correlations were negative except for the first order opportunists (EG V) and for M-AMBI the opposite was the case. At station 110 taxa that were sensitive or indifferent decreased whereas second order opportunists increased with AMBI score ($p<0.05$); and, the abundances of sensitive and indifferent taxa (EG I-II) were correlated with M-AMBI ($p<0.01$).

Although the benthic diversity of the KCF is comparable with the Nervión estuary (Figs 1b, 3b, 4b), the generally weaker correlations for the palaeofauna compared with the present-day benthos (Fig. 6a–c) may indicate preservational loss from the fossil assemblages. The weaker correlations between AMBI and species richness (Fig. 6c) and the ecological group abundances (Table 2) might be due to a lack of soft-bodied first and second order opportunists (EG IV-V) such as polychaetes with low preservation potential.

3.3. Temporal changes

Throughout the *c.* 4 million years the majority of taxa were second order opportunists (Fig. 7), followed by first order opportunists, tolerant taxa, and those that were indifferent or sensitive to enrichment formed the smallest proportions.

Comparison of the AMBI, M-AMBI and ecological group composition with the benthic assemblages in the outer reaches of the Nervión estuary (Figs 5-6) that were mostly normoxic show how the palaeoassemblages compared with a typical present-day undisturbed benthos. These changes corresponded to fluctuations in the TOC of the sedimentary deposits with periods of higher TOC generally having a greater proportion of first order opportunists and periods of low TOC having more tolerant (EG III), indifferent (EG II) and sensitive taxa (EG I). As time progressed there were fewer second order opportunists, and taxa that were tolerant, indifferent or sensitive became a larger proportion of the benthic assemblage (Fig. 7a). AMBI showed a general decrease and M-AMBI an increase through time (Fig. 7b-c) suggesting that conditions improved from being heavily to moderately disturbed (AMBI; Fig. 7b) or from moderate to good ecological status (M-AMBI; Fig. 7c).

4. Discussion

To continue accessing the ecosystem services that marine systems provide we need to effectively manage impacts of anthropogenic pressures up on ecosystems (United Nations, 2005). To do so requires an understanding of the ecosystem changes that have occurred in the past in order to prepare for those that may occur in the future under continuing human pressures (Cheung et al., 2009; Elliott et al., 2015; Pereira et al., 2010; Stock et al., 2011). Our understanding of the (human) pressure - (ecosystem) state relationship is hampered by the quality of our ecosystem baselines most of which are not truly natural (Dauvin and Ruellet, 2009; Elliott and Quintino, 2007; Jackson et al., 2001; Klein and Thurstan, 2016; Pauly, 1995). In this study we applied contemporary biotic indices of ecosystem health to fossil assemblages during a period of past natural environmental change in order to compare the ecological response and determine whether such palaeontological records have utility as wholly natural baselines for changes in the marine benthos. One hundred and fifty million years ago organic enrichment, caused by changes in regional ocean circulation patterns (Miller, 1990)(Fig. 1c-d), drove palaeoecological change in much the same way that anthropogenic organic enrichment does locally and regionally today (e. g. Caswell et al. 2018; Diaz and Rosenberg, 1995; Diaz and Rosenberg, 2008; Pearson and Rosenberg, 1978; Rabalais et al., 2010; Seitz et al., 2009; Sturdivant et al., 2014). While these changes are attributable to entirely natural processes they represent discrete and severe environmental events, and therefore might be seen as excursions from what we define as ‘healthy baseline conditions’.

Overall, the palaeocommunities from the Late Jurassic Kimmeridge Clay Formation, UK were considered to be ‘disturbed’ using the benthic community health indices AMBI and M-AMBI that were developed for assessing the response of present-day benthic assemblages (e. g. Borja et al., 2000). Changes in the palaeoassemblages as described by the two indices were correlated with the total organic carbon content (TOC) of the sedimentary deposits: at higher TOC both AMBI and M-AMBI indicated greater disturbance. Above 4% sedimentary TOC AMBI classified communities as at least 'moderately disturbed', and M-AMBI as 'moderate' or 'poor' ecological status. Under the Water Framework Directive (European Commission, 2000) present-day benthic communities classified as in moderate ecological status (e.g. M-AMBI <0.53, in Spain), or worse, require remediation action (European Commission, 2018). So these communities were perturbed, by natural events, and the severe organic enrichment triggered changes in the benthos that were analogous to those seen in organically-polluted modern systems (e. g. Birchenough and Frid, 2009; Borja et al., 2006; Caswell et al. 2018; Diaz and Rosenberg, 2008; Pearson and Rosenberg, 1978; Rees et al., 2006). This confirms that whilst the species inventory was completely different between the Jurassic and the present-day, the ecology, life history and other taxa attributes were comparable and responded in the same way. This suggests that periods in deep time for which the indices report healthy/good status could potentially serve as true 'baselines' for the assessment of marine environmental health (if preservational loss is also considered).

Within the palaeoecological time series the decrease in M-AMBI and AMBI status through time (Fig. 7) corresponded with an increasingly arid climate, shifting from humid to semi-arid, that developed across the Laurasian continent approximately 4.5 Myr, after/above the base of the KCF (in the *huddlestoni* ammonite Zone; Hesselbo et al., 2009; Wignall and Ruffell, 1990). Further confirming the utility of the AMBI indices to identify periods of changing ecological 'health' and hence their potential for use in constructing baselines or reference configurations, such as those required for climate change scenarios e.g. due to shifts in aridity (IPCC, 2013).

Comparisons with data from benthic assemblages in the inner and outer reaches of the formerly polluted Nervión estuary in Bilbao, Spain (Borja et al., 2006) provided further basis for the interpretation of the prevailing palaeoenvironmental conditions. The palaeoecological group composition and the AMBI and M-AMBI scores in the 21 palaeoassemblages from Kimmeridge Bay when compared with the benthos from the inner reaches of the Nervión estuary (Borja et al., 2006) showed that palaeocommunities A/E1, A1, B1–B5 and E8 had some organic enrichment but were probably oxygenated for considerable periods (Fig. 2). Whereas the palaeoassemblages with high AMBI scores (>3.3) and low M-AMBI scores (<0.53) were disturbed and regularly deoxygenated (Fig. 2a, E1a–E7) which is consistent with the geochemical proxy data that show elevated organic enrichment and deoxygenation (Fig. 2d)(Morgans-Bell et al., 2001; Pearce et al., 2010). Some discrepancies existed between AMBI and M-AMBI scores (usually higher classifications with M-AMBI), presumably due to differences in species richness (Borja et al., 2007), but overall the assessments of past ecological status were consistent with previous interpretations for most of the Kimmeridge Bay palaeoassemblages (Caswell and Frid, 2013; Wignall, 1990). The exception was E8, an assemblage classified as deoxygenated by Wignall (1990) with a relatively high TOC (3.8%) (Morgans-Bell et al. 2000), indicating the AMBI/M-AMBI scores only ‘slight disturbance’ or ‘good’ status, with an ecological group composition similar to assemblages in the outer Nervión estuary. However, palaeoassemblage E8 also had a unique taxonomic and biological trait composition compared with all of the other palaeoassemblages (Caswell and Frid 2013).

Although there were no environmental proxy data for palaeocommunities A2–A11, documented from locations other than Kimmeridge Bay, the interpretation of their oxygenation state based on the lithology (rock type) of the deposits (Wignall 1988) is consistent with most of the AMBI and M-AMBI scores and ecological group representation that indicated slight disturbance in A2 to A9. Moderate disturbance in A10-A11 as suggested by Wignall (1988), based on the presence of several suspected hypoxia tolerant taxa, is confirmed by AMBI (Fig. 2a–c). However, palaeoassemblage A5, dominated by the second order opportunist *Isocyprina* spp. (Fürsich and Thomsen, 2005), had AMBI and M-AMBI scores (Fig. 2a) indicative of moderate disturbance and poor ecological status which conflicts with its interpretation as oxygenated by Wignall (1988).

Overall, the most impoverished palaeoassemblage was E2a that was classified as being of bad ecological status and heavily disturbed, E2a was comprised of >90% first order opportunists although it did not have exceptionally high TOC (Fig. 2d)(Morgans-Bell et al., 2001). This palaeoassemblage was not unusual in taxonomic or biological trait composition (Caswell and Frid, 2013) although it was dominated by opportunistic bivalves and conditions were sometimes euxinic (Pearce et al., 2010).

The organic enrichment and deoxygenation recorded in the Kimmeridge Clay Formation resulted in significant changes in the composition of the marine benthos. For example, decreased species richness, the disappearance of echinoderms, crustacean and scaphopods, reductions in burrowing depth (Caswell and Frid 2013), and increased proportions of first and second order opportunists. However, none of the palaeocommunities were classified as being extremely disturbed (AMBI > 6), completely undisturbed (AMBI ≤ 1.2), or of high ecological status (M-AMBI >0.77). There are several possible explanations for this:

(i) That the benthic conditions remained sub-optimal throughout the entire 3 Myr period. The geochemical proxies showed that regional deoxygenation persisted between 2.4 to 5.6 Myr (Fig. 7a)(Pearce et al., 2010), and these regional changes were accompanied by global increases in the intensity of reducing conditions at that time (Pearce et al., 2010) increasing the likelihood for local/regional deoxygenation to develop.

(ii) The M-AMBI reference conditions and the boundaries between quality classes, used for this data may have been inadequate and need refining (Birk et al., 2013) since the boundaries were established for contemporary benthic communities (Borja et al., 2012).

(iii) Alternatively, this could be an artefact of incomplete preservation (e. g. Behrensmeyer et al., 2000), which biased species composition and so the AMBI and M-AMBI classifications. Although fossil assemblages can reliably be used to reconstruct palaeoassemblage diversity and composition, among other attributes, this potential varies between groups of taxa (Greenstein, 2007; Kidwell, 2013; Miller, 2011; Terry, 2010). For instance, Kidwell and Tomasovych (2013) and Kidwell (2015) showed that the fidelity of fossil and subfossil death assemblages with living shelled fauna is very good, with 83-95% site and 75-98% habitat fidelity. However, it seems unlikely that there were so few soft-bodied taxa in the palaeocommunity, such as polychaetes that form a significant component of modern healthy and enriched benthic assemblages (Diaz and Rosenberg, 1995; Levin, 2003; Rees et al., 2006). For instance, in the inner reaches of the Nervión estuary the "*Capitella capitata*" species complex dominated, however in the outer reaches *Tellina* and *Venus* bivalves dominated (Borja et al., 2006). Soft-bodied taxa such as polychaetes have low preservation potential and are often under-represented in the geological record (Briggs, 2003). The inclusion of information on trace fossils that record organism behaviour, e.g. tracks, burrows or resting traces, could provide information on the extent and nature of the missing fauna, and its contribution to ecosystem functioning (e. g. Caswell and Frid, 2017). Unfortunately, detailed information is lacking for the KCF at the present time.

(iv) The final reason that the scores for the palaeoassemblages and the undisturbed contemporary benthos in the outer reaches of the Nervión estuary may differ is due to time averaging. A degree of time-averaging is inherent to almost all fossil, or subfossil, assemblages, information might be averaged over weeks, years, centuries or millennia. The samples from Nervión were collected annually whereas an individual sampling point in the Kimmeridge Clay represents a period that approximates a century (based on the timescale of Weedon et al. 2004). These temporal differences may result in short-term variations becoming obscured (Kidwell and Tomasovych 2013), and the greater period of time represented by the palaeoassemblages may have inflated the apparent species richness above that in the original life assemblages (Kidwell, 2013). Although the differences in timescale must be considered in any comparison with the present-day fauna, time-averaging can capture superior information, than that from non time-averaged data, and this includes information on rare species, regional diversity, species range changes, habitat preferences, and species turnover (Kidwell and Tomasovych, 2013; Kidwell 2015).

AMBI has previously been applied to both whole benthic assemblages and selected taxonomic groups, such as polychaetes (Cheung et al., 2008) or molluscs (Dietl et al., 2016; Leshno et al., 2016; Nerlovic et al. 2011). A recent meta-analysis (Dietl et al. 2016) showed that analyses of partial assemblages, i.e. the mollusc component only, share many features with death assemblages, and so this is a viable method for determining changes in ecological status. The AMBI scores of death assemblages and mollusc-only assemblages were comparable with those for complete live assemblages (in ~80% of cases the AMBI ecological status assignments were the same; Dietl et al. 2016). This suggests that, even if the Kimmeridge assemblage was incomplete, the results probably do not differ much from those expected if the fossil assemblage was complete (Dietl et al. 2016, Leshno et al. 2016). Dietl et al. (2016) showed that partial assemblages, i.e. of molluscs only, slightly overestimated the AMBI values for assemblages with high ecological status and underestimated AMBI for those with low ecological status: this might explain the lack of Kimmeridge assemblages classified as being extremely disturbed (AMBI>6).

Comparison of contemporary faunas with palaeoassemblages from a greater range of palaeoenvironments (as determined from lithology and geochemical proxies) and/or from those that are exceptionally preserved e. g. Lagerstätte (e.g. the Solnhofen limestone (Barthel et al., 1990), Burgess Shale (Conway Morris, 1998) or Chengjiang Maotianshan Shales (Hou et al., 1999)) will help to determine whether the differences in AMBI and M-AMBI values between present-day and the fossil assemblages are environmental or preservational. Such work would also supply valuable ecological information required to establish better baselines for ecosystem state prior to human disturbance, and so will help refine the reference conditions used by tools such as AMBI (Borja et al., 2012, Dietl et al. 2016). Study of naturally perturbed (i.e. pre-human) systems can improve understanding of pressure-impact relationships such as functional changes and ecological threshold-effects (Birk et al., 2012; Caswell and Frid, 2013; Frid and Caswell, 2015). Furthermore, death assemblages whether fossils or subfossil, may provide an integrated temporal picture, as opposed to the snapshots usually acquired by ecologists, that is more likely to describe the ecological status of a region. Such information is sorely needed (Van Hoey et al., 2010) and could be a great asset for defining the thresholds of 'good environmental status' upon which regulation is implemented (e.g. European Commission 2008, Dietl et al. 2016, Leshno et al. 2016).

This study has shown that even when applied to marine benthic assemblages from deep time that contain no species in common with modern systems, and those that underwent wholly natural ecological change the AMBI indices are able to distinguish between perturbed and unperturbed systems. This in turn allows for both a fuller analysis of the impacts of large-scale 'natural' perturbations that are analogous to systems subjected to anthropogenic pressures, and/or those that will be impacted in the future (IPCC, 2014; United Nations, 2005). It also highlights the potential of palaeoecological datasets more generally for developing reconstructions of past community structure and functioning in pre-human marine ecosystems (e. g. Caswell and Frid, 2013; Caswell and Frid, 2017; Dietl et al., 2015; Kidwell, 2013). In this way palaeoecological data could provide information to policy makers and environmental regulators with greater temporal context that reveals the true or 'pristine' nature of marine ecosystems prior to human impacts.

5. Conclusions

The AMBI and M-AMBI indices, are extensively used in many countries across the World to assess benthic habitat quality in response to a range of different human pressures (Borja et al., 2015). Organic enrichment and deoxygenation during the Late Jurassic, although natural, produced considerable changes in the ecological structure and functioning of benthic palaeocommunities that could be detected using the AMBI and M-AMBI indices. Despite the considerable differences in temporal scale, these changes were consistent with the response of the present-day benthos to organic enrichment and deoxygenation in the inner and outer reaches of the polluted Nervión estuary in Bilbao, Spain. We have shown that the application of biotic indices, such as these, to palaeontological data could be used to (i) provide information on reference conditions and for the structure and functioning of benthic communities prior to human impacts that could be used to determine "good ecological status"; and (ii) help identify and/or confirm the ecological impacts of past perturbations (in Earth history) on marine benthos, by comparison with indices from present-day systems, particularly when palaeoenvironmental information is missing or incomplete.

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Table 1

Table 1. AMBI and M-AMBI classifications for the 31 Late Jurassic benthic palaeoassemblages (from the Kimmeridge Clay Formation), and comparison with the benthic assemblages from the different years in the inner and outer reaches of the Nervión estuary, Bilbao, Spain (from 1989-2016).

Classification	**Benthic assemblages**		
	Kimmeridge Clay Fm	**Nervión estuary: inner**	**Nervión estuary: outer**
AMBI:			
Undisturbed			92, 97–98, 01, 04, 06–08
Slightly disturbed	A/E1, A2–A4, A6–A9, B1-B5, E8–E9	03-04, 06, 09–10	89–96, 99–00, 02–03, 05, 09–12
Moderately disturbed	A1, A5, A10–A11, E1b, E2b–E2e, E3–E7	98, 01, 05, 07–08, 11–12	
Heavily disturbed	E1a, E2a	90–97, 99–00	
Extremely disturbed		89	
M-AMBI:			
High		03–06, 09–12	89–04, 06–12
Good	A/E1, A1–A4, B1–B5, E3, E8, A6–A11	02, 07-08	05
Moderate	E2b–E2d, E4–E5, E9	98	
Poor	A5, E1a–E1b, E2e, E6–E7	00–01	
Bad	E2a	89–97	

Table 2. Correlations between ecological group (ecol. group) abundance and AMBI, or M-AMBI for all three datasets. Empty cells = no significant correlation ($p>0.05$). Ecological group classifications: I = taxa sensitive to disturbance, II = taxa indifferent to disturbance, III = disturbance-tolerant taxa, IV = second order opportunists, V = first order opportunists.

Ecol. group	**AMBI**			**M-AMBI**		
	KCF	**Station 5**	**Station 110**	**KCF**	**Station 5**	**Station 110**
I	-0.37, p<0.001	-0.60, p<0.001	-0.76, p<0.001	0.20, p<0.05	0.97, p<0.001	0.31, p<0.01
II	-0.57, p<0.001	-0.43, p<0.001		0.15, p<0.05	0.59, p<0.001	-0.51, p<0.005
III	-0.17, p<0.05	-0.57, p<0.001	-0.60, p<0.001	0.31, p<0.005	0.44, p<0.001	
IV	0.20, p<0.05	-0.43, p<0.001	0.22, p<0.05		0.37, p<0.005	
V	0.49, p<0.001	0.59, p<0.001		-0.37, p<0.001	-0.58, p<0.001	

Figure 1

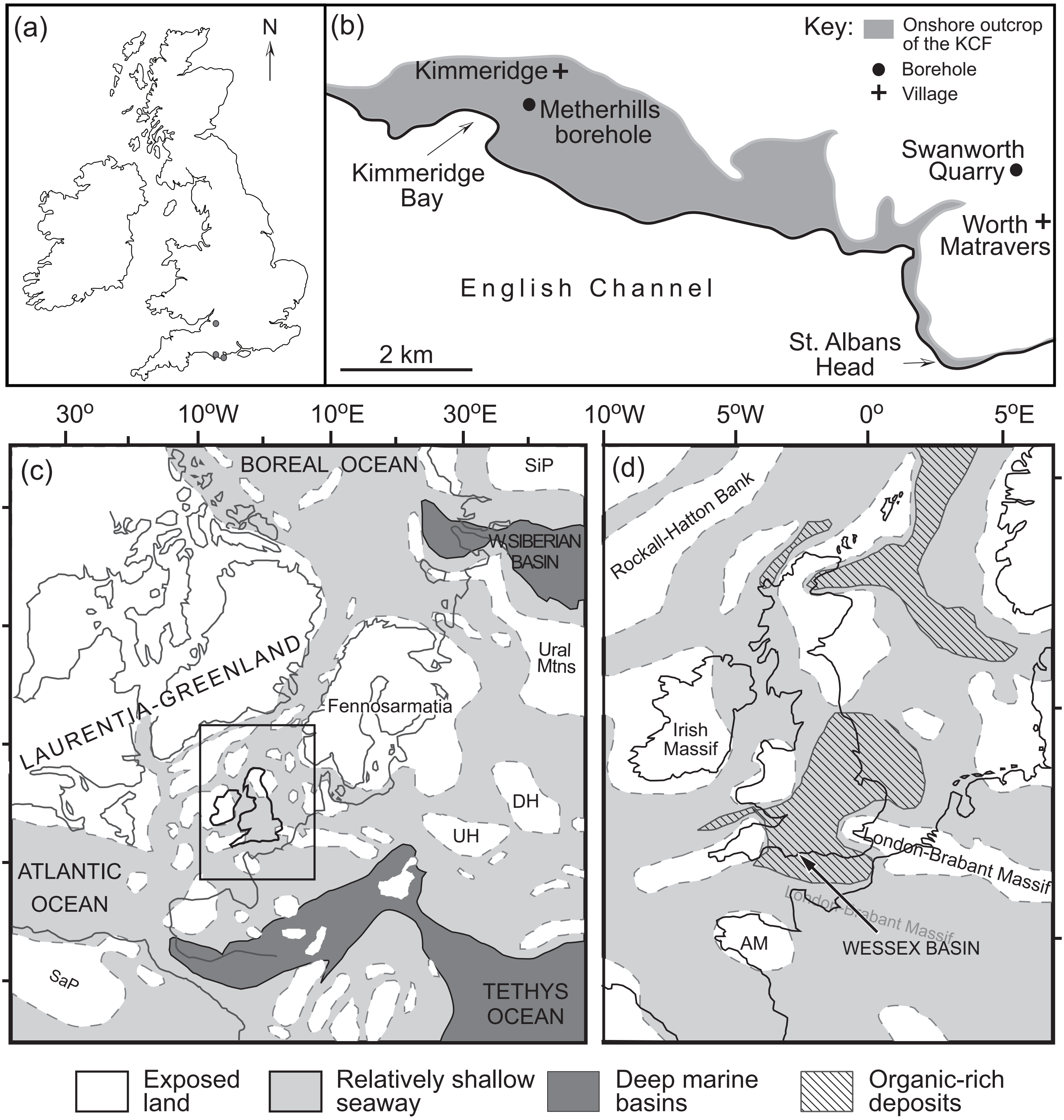

Fig. 1 Caswell, Frid, Borja 2018

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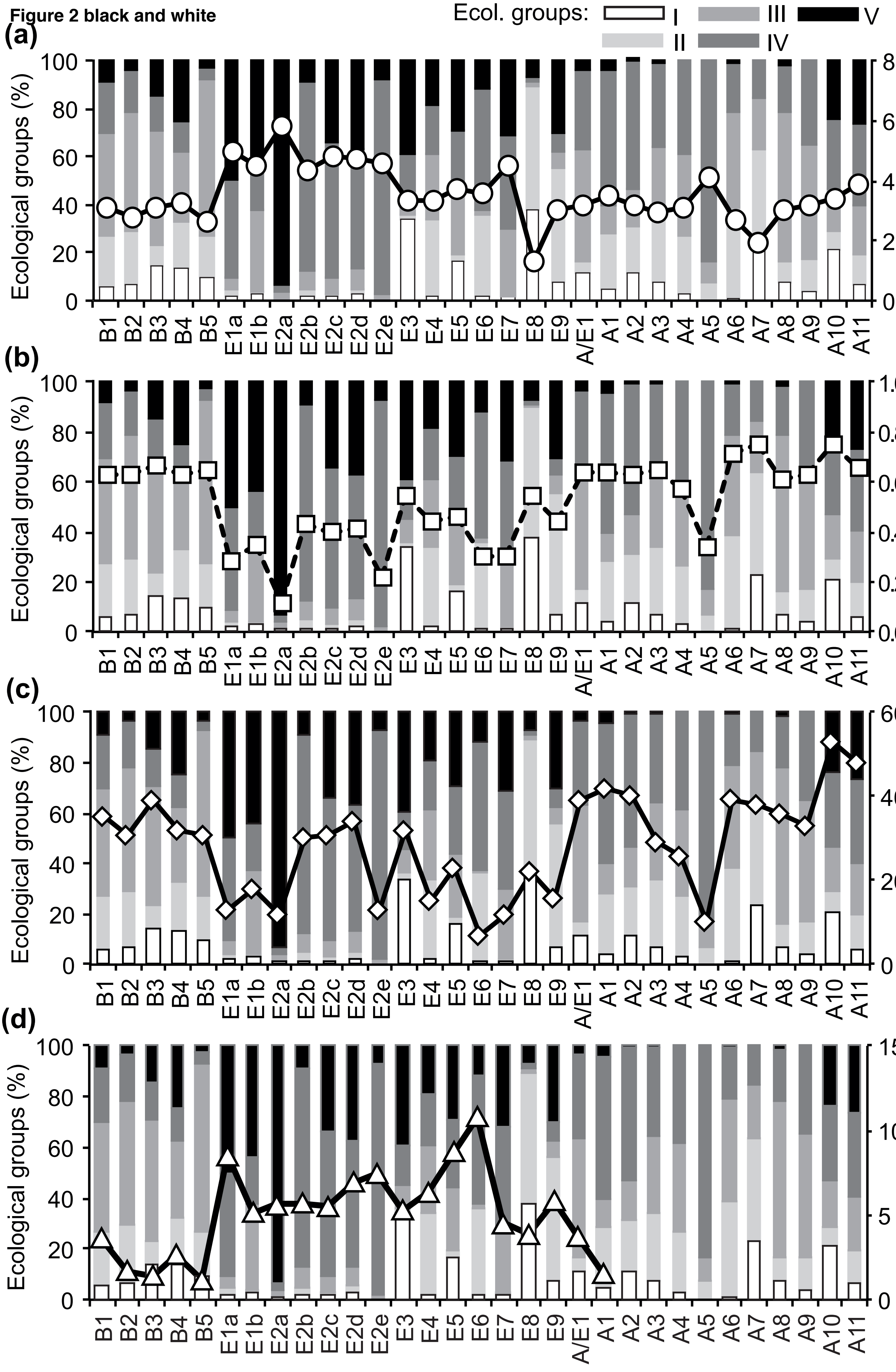

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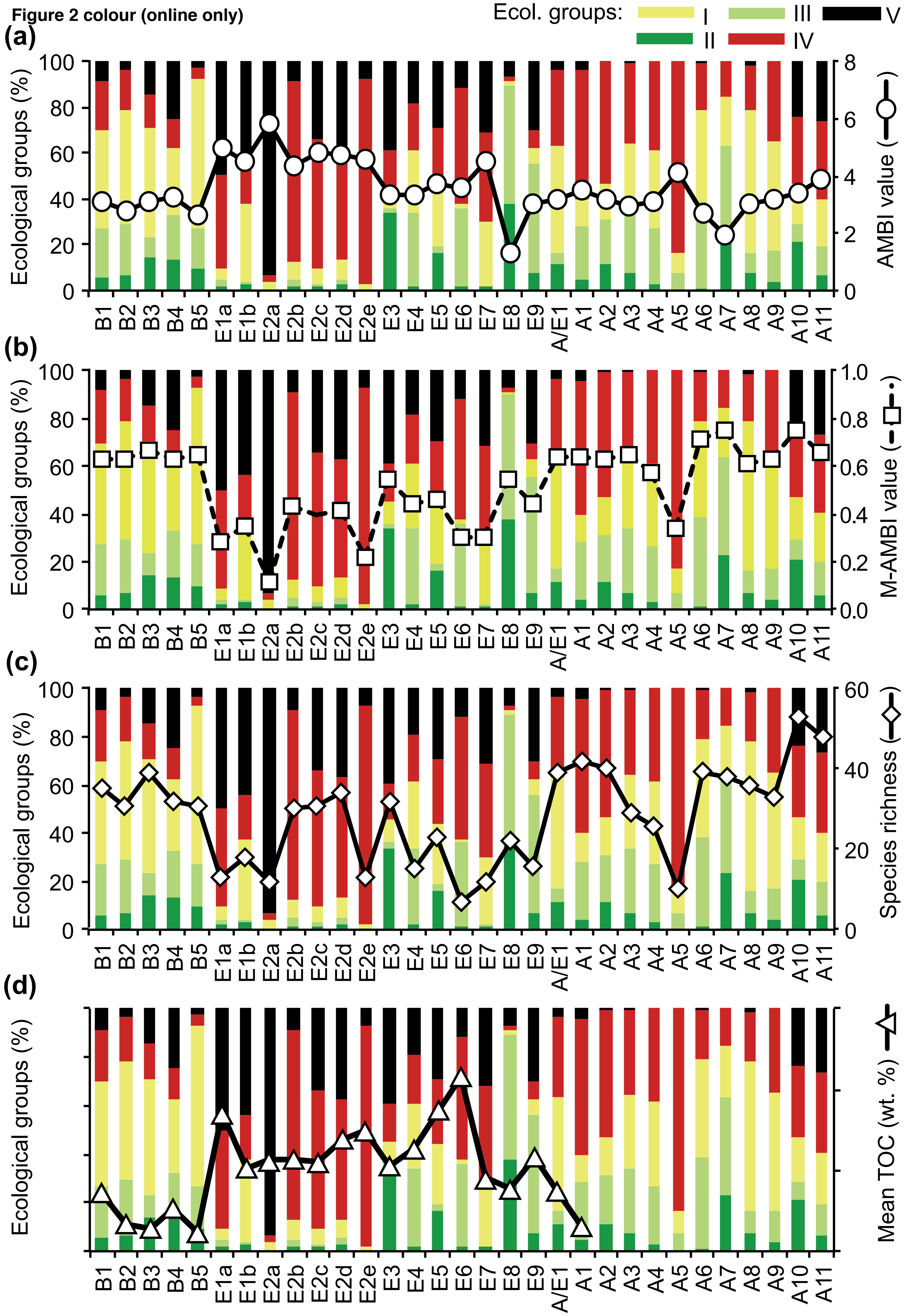
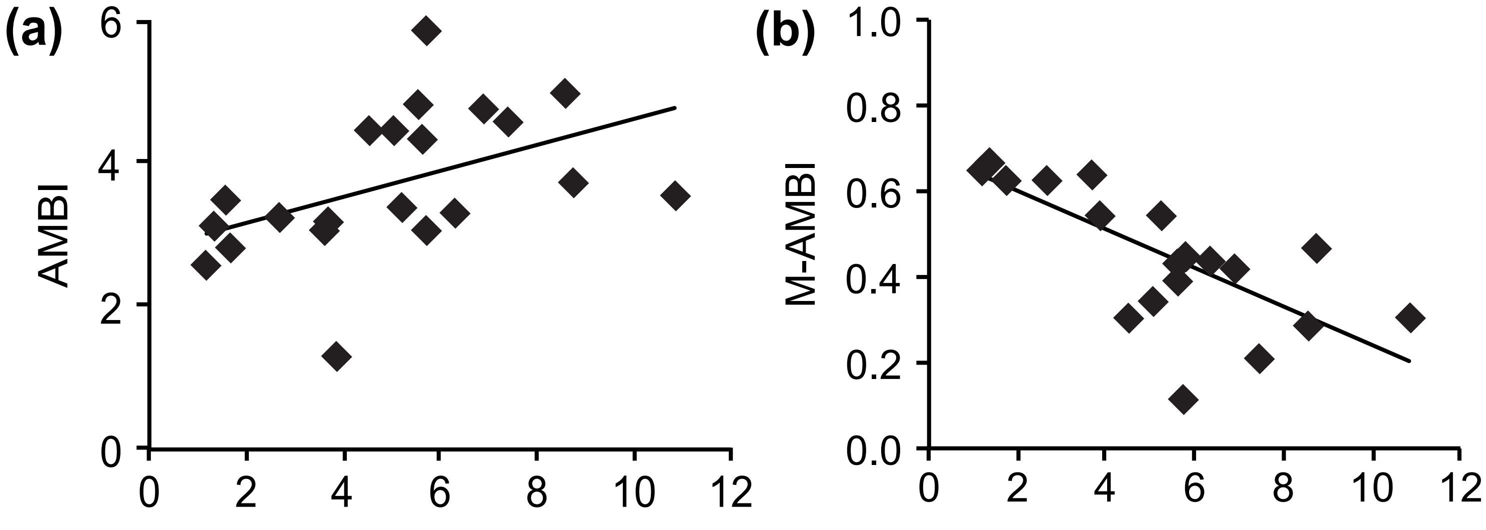


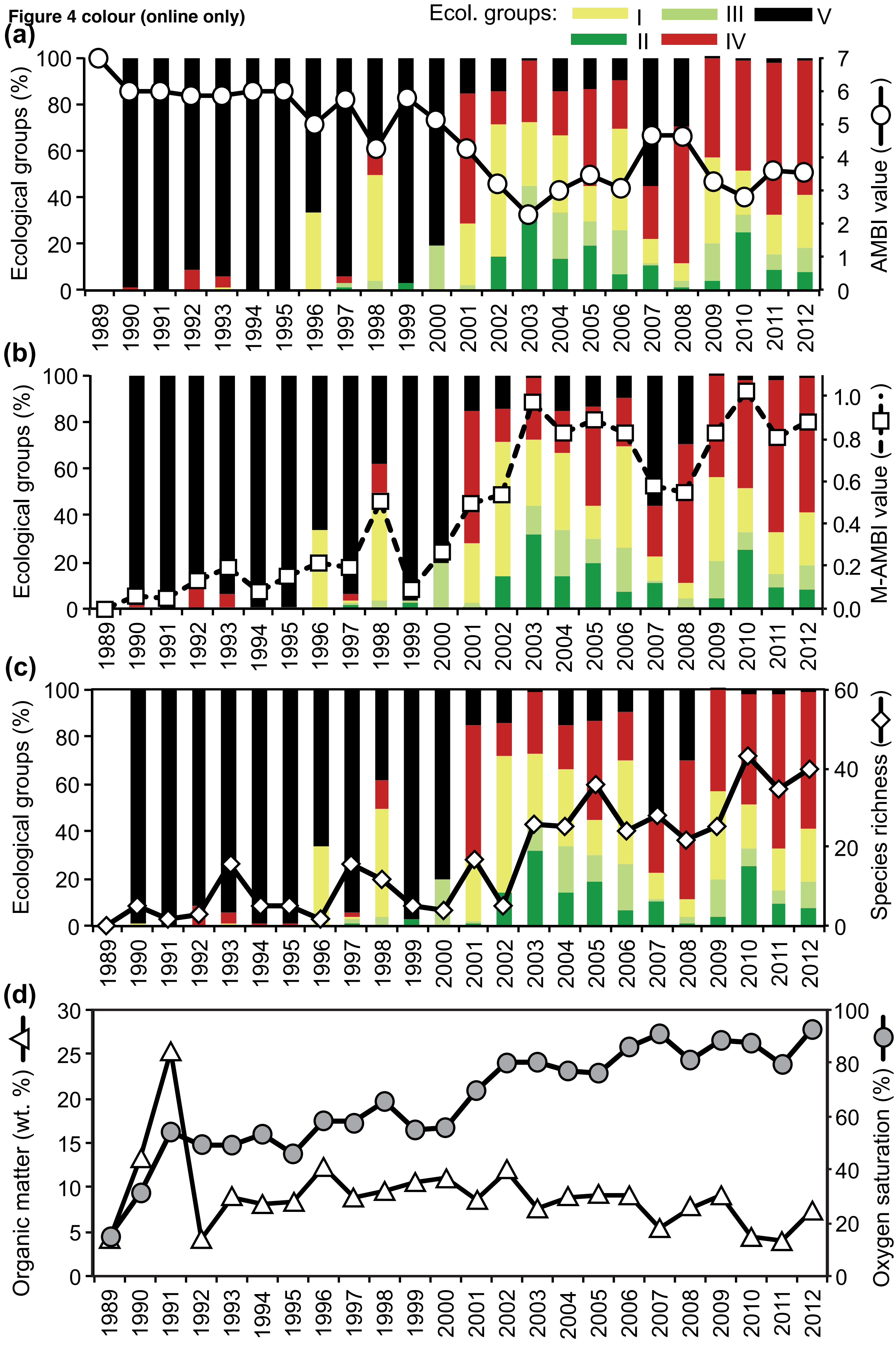
Caswell, Frid and Borja 2018 Figure 2 colour

Figure 3



Caswell, Frid, Borja 2018 Figure 3

Figure 4 colour (online only)



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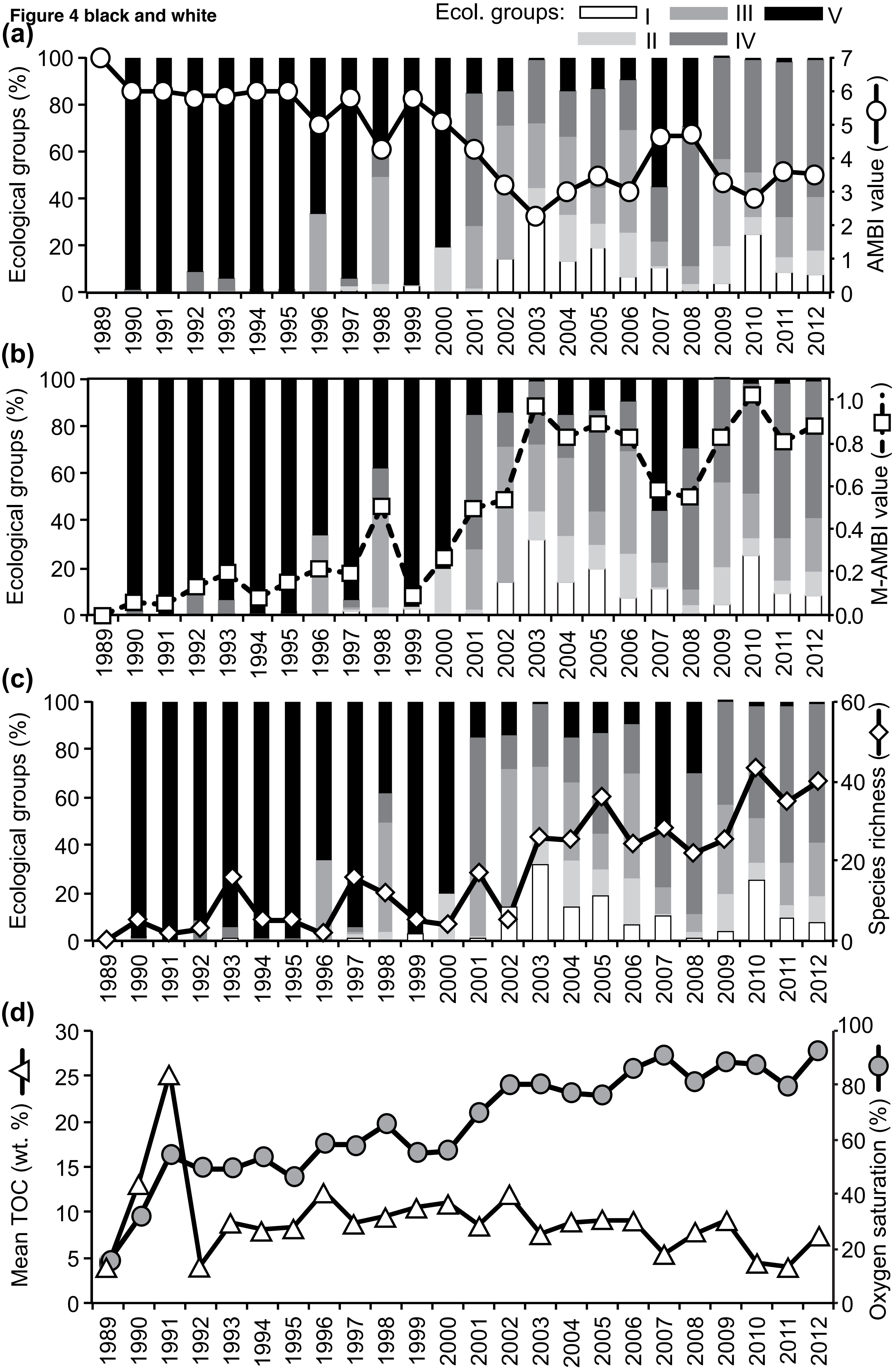

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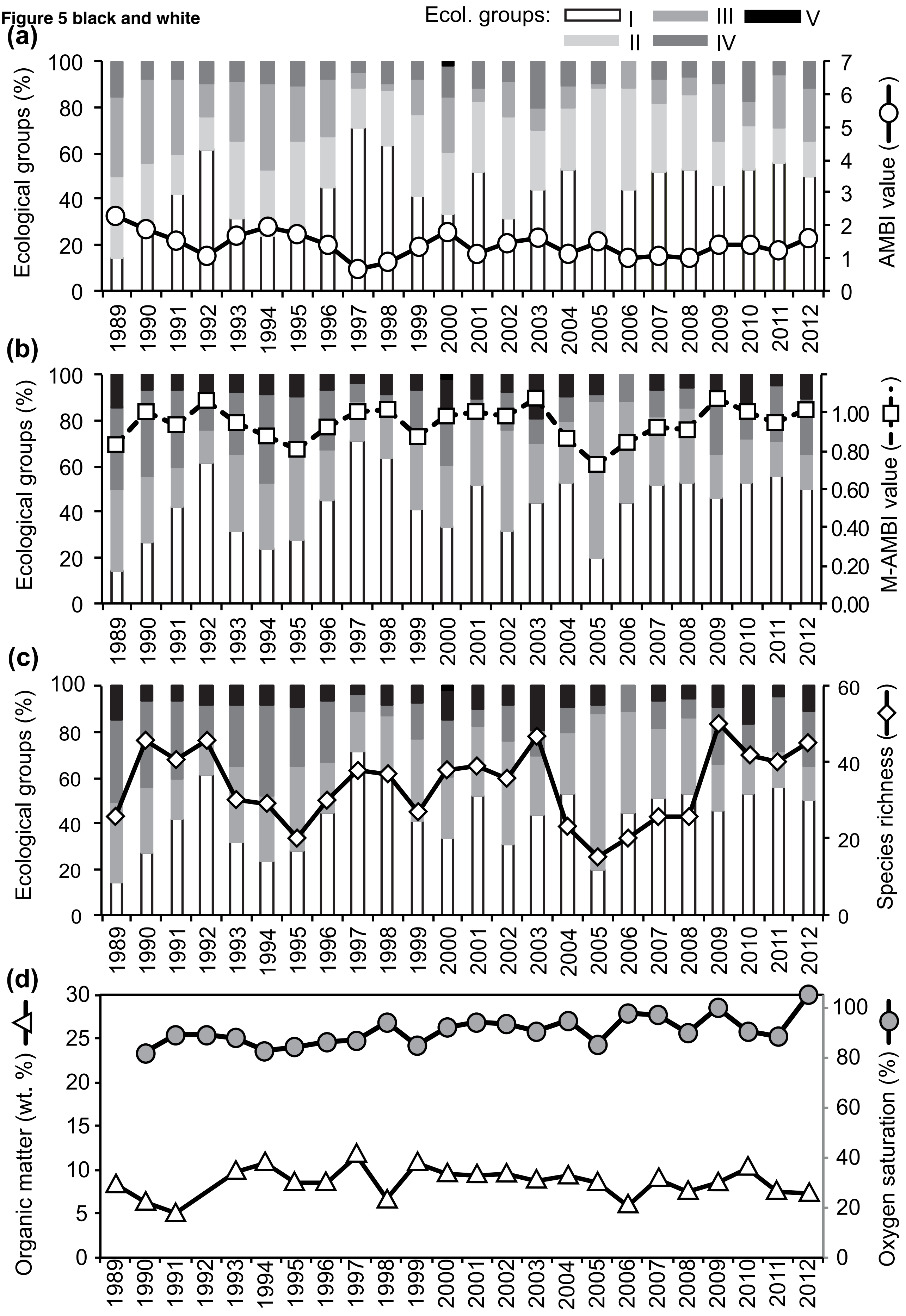
Figure 5 black and white



Caswell , Borja, Frid 2018 Figure 5 colour

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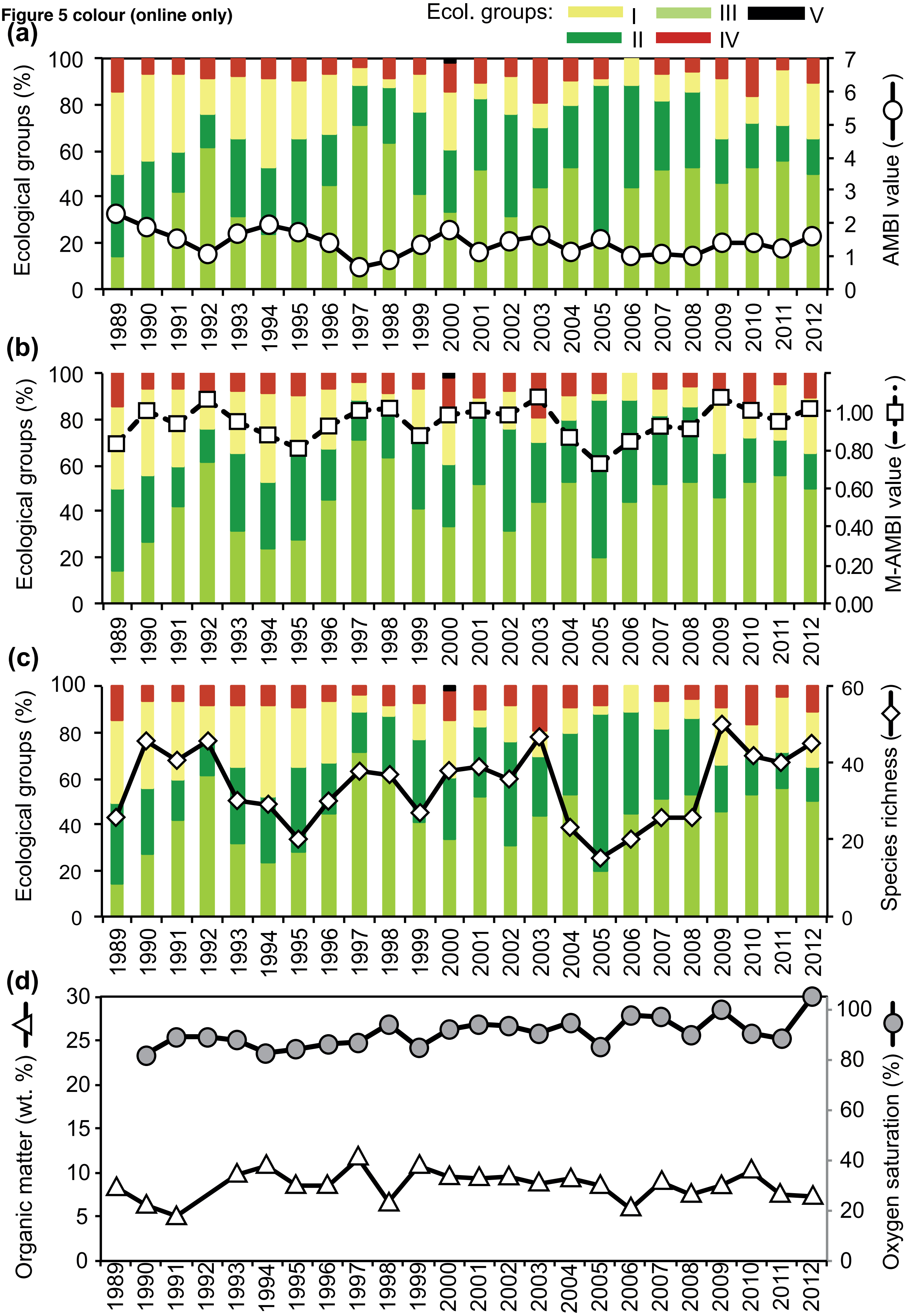
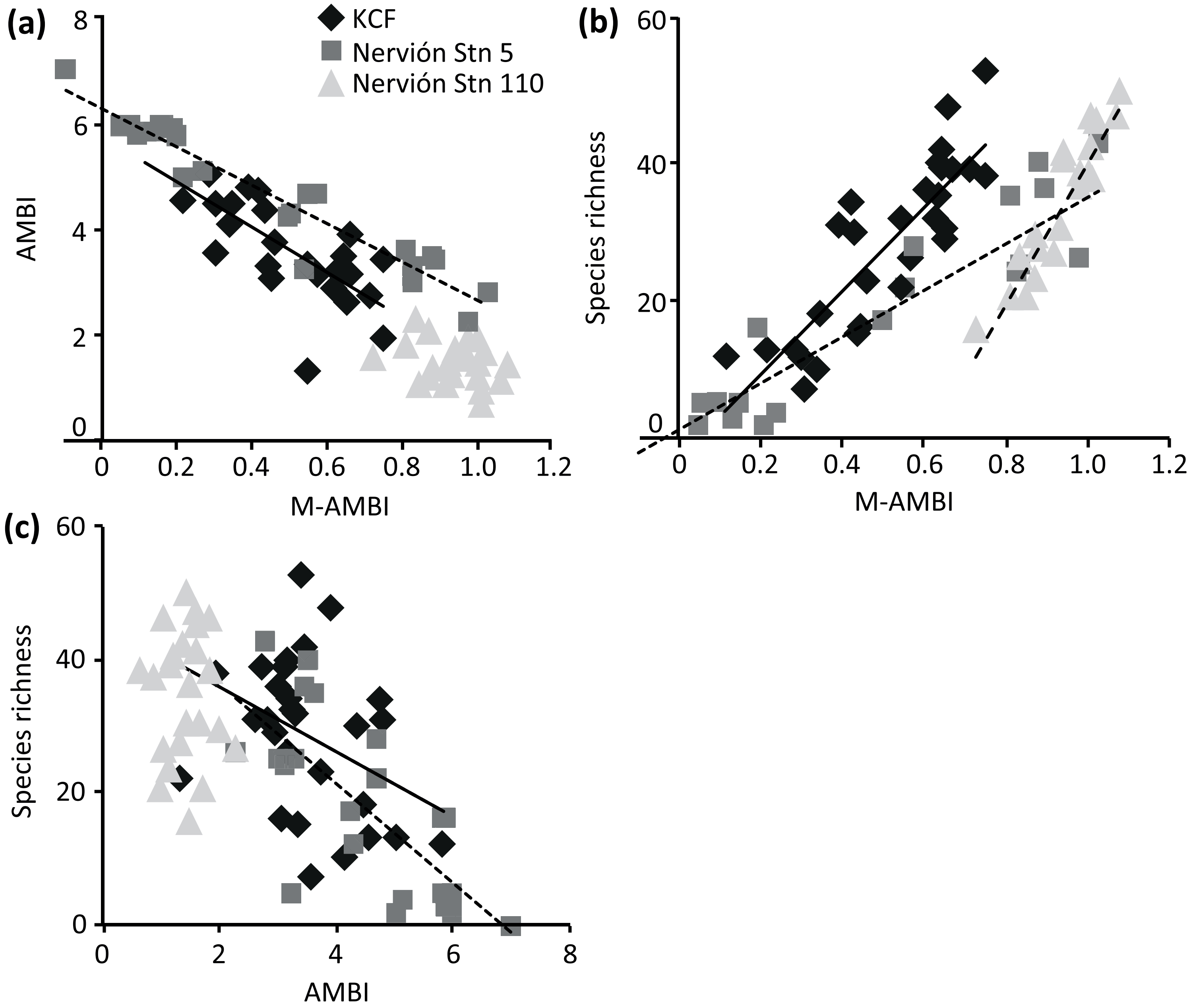


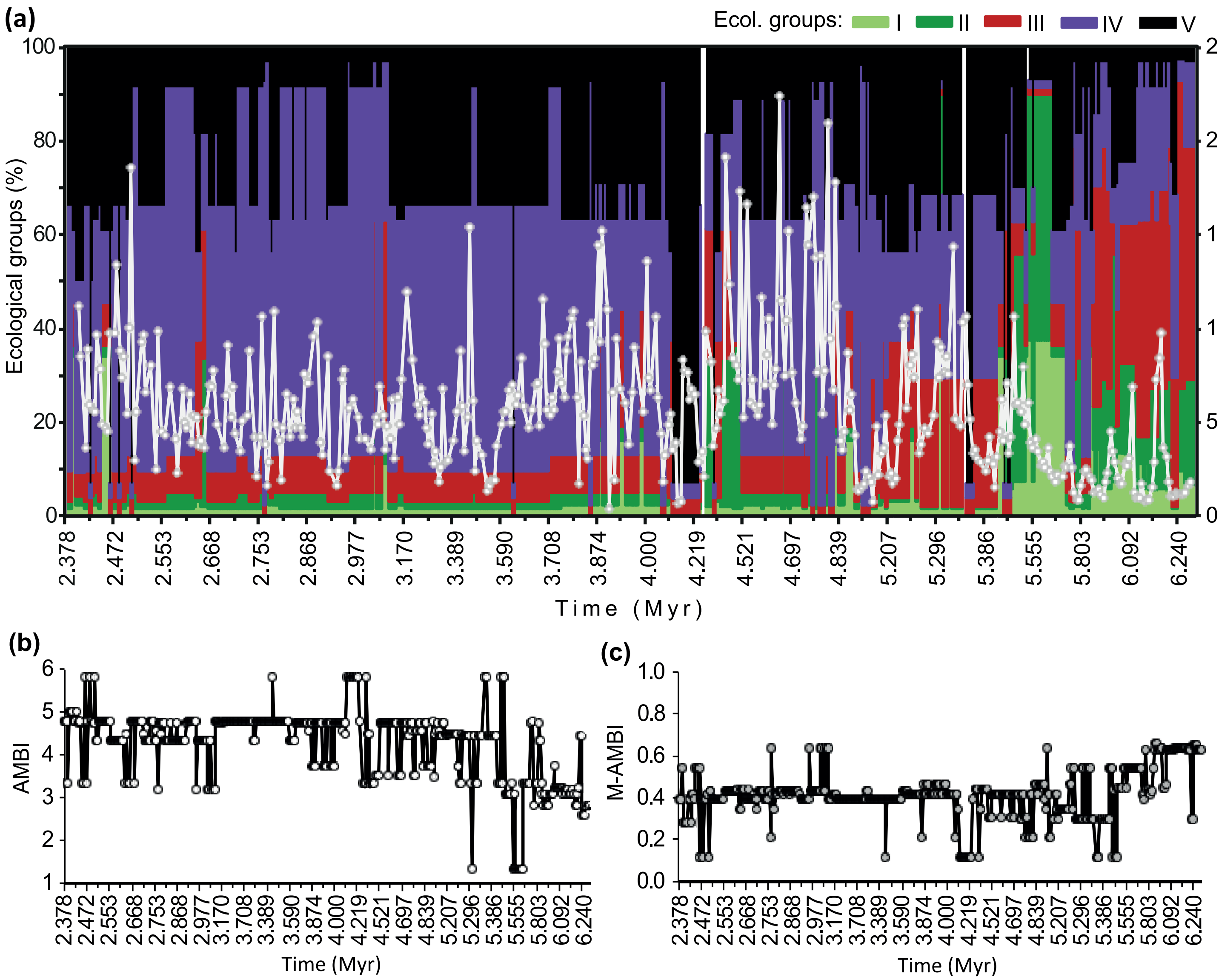
Caswell , Borja, Frid 2018 Figure 5 colour

Figure 6



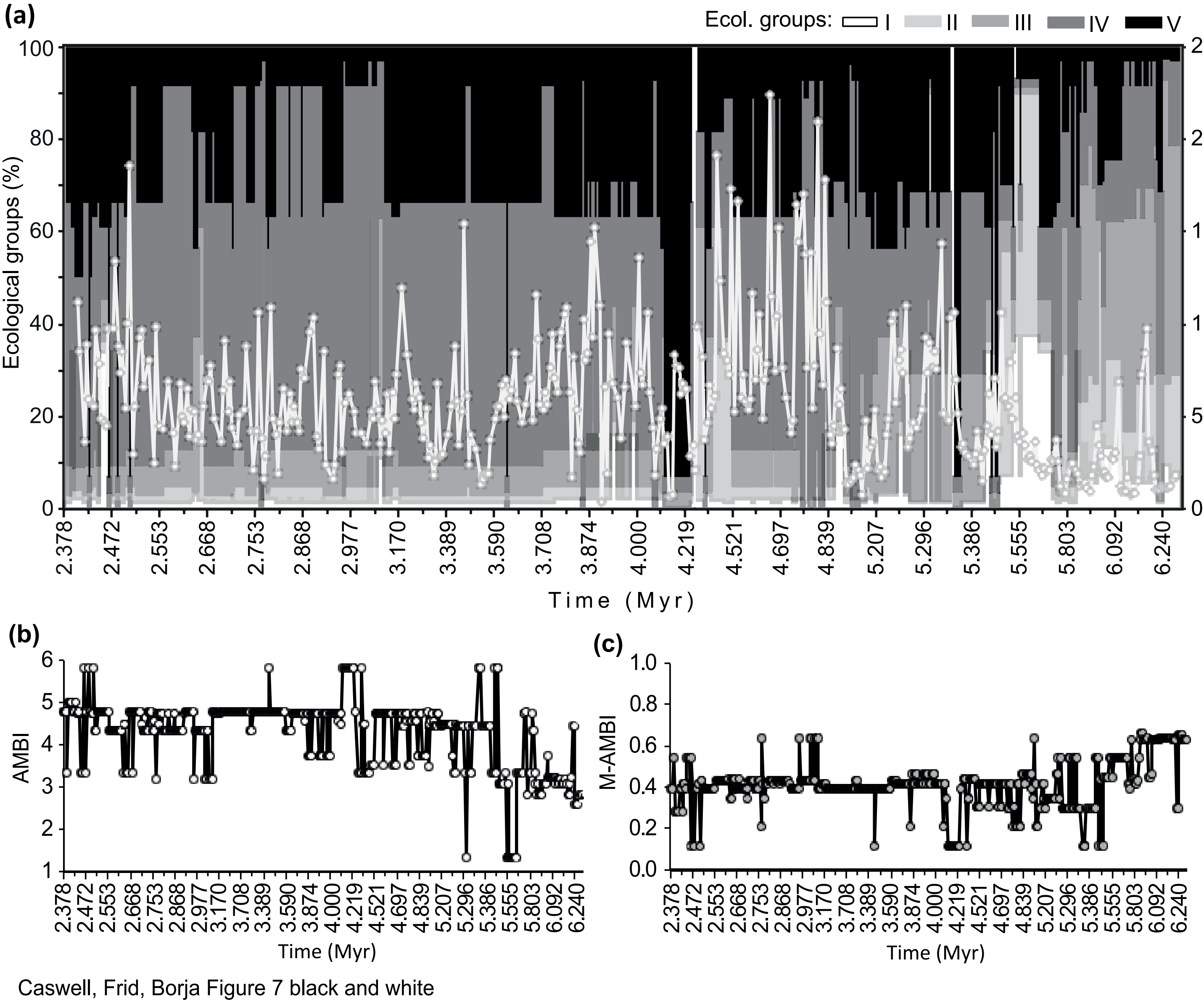
Caswell, Frid, Borja 2018 Figure 6

Figure 7 colour (online only)



Caswell, Frid, Borja 2018 Figure 7

Figure 7 black and white



Caswell, Frid, Borja Figure 7 black and white

Supplementary Table S1

Supplementary Fig. S1