Managing for resilience: an information theory-based approach to assessing ecosystems

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Summary

1. Ecosystems are complex and multivariate; hence, methods to assess the dynamics of ecosystems should have the capacity to evaluate multiple indicators simultaneously.

2. Most research on identifying leading indicators of regime shifts has focused on univariate methods and simple models which have limited utility when evaluating real ecosystems, particularly because drivers are often unknown.

3. We discuss some common univariate and multivariate approaches for detecting critical transitions in ecosystems and demonstrate their capabilities via case studies.

4. *Synthesis and applications*. We illustrate the utility of an information theory-based index for assessing ecosystem dynamics. Trends in this index also provide a sentinel of both abrupt and gradual transitions in ecosystems.

Key-words: ecosystems, Fisher information, indicators, indices, information theory, leading indicators, multivariate, regime shifts, resilience

Introduction

Resilience is the capacity of a system to absorb change and maintain a similar set of processes and structures (Holling 1973). When an ecosystem exceeds this capacity, the system can shift into a new regime characterized by a different set of processes and structures (Allen *et al.* 2014). Ecosystems that exhibit this dynamic behaviour are characterized by multiple regimes (Gunderson & Holling 2002) and have the capacity for nonlinear change (Garmestani, Allen & Gunderson 2009), which may shift these systems into new regimes that do not provide a full suite of desired ecosystem goods and services.

Empirical evidence for multiple regimes in ecosystems has been accumulating for some time (Beisner, Haydon & Cuddington 2003; Kortsch *et al.* 2012; Randsalu-Wendrup *et al.* 2012), and multiple regimes have been identified in many ecosystems, including lakes, coral reefs and rangelands (e.g. Beisner, Haydon & Cuddington 2003; Dakos *et al.* 2012a). Regime shifts are typically associated with significant consequences (e.g. coral reef

collapse, loss of water quality) resulting in transboundary problems that are not easily accommodated in existing legal and governance frameworks (Garmestani, Allen & Benson 2013; Green *et al.* 2014). Regime shifts do not always require abrupt tipping points and can result from long periods of system reorganization (Spanbauer *et al.* 2014). Because of the potential for serious negative consequences associated with shifting to an undesirable regime, developing methods to identify regime shifts before they occur (i.e. leading indicators) is a critical area of scientific research (Brock & Carpenter 2006; Biggs, Carpenter & Brock 2009; Dakos *et al.* 2012a,b; Scheffer *et al.* 2012; Eason, Garmestani & Cabezas 2014).

Researchers have used increasing variance, skewness, kurtosis and autocorrelation to investigate the behaviour of ecosystems close to a threshold (e.g. Scheffer *et al.* 2009; Dakos *et al.* 2012a). However, most of these analyses focused on a single or a few variables that the researchers knew would respond to their experimentation (Carpenter *et al.* 2011). Most proposed methods for detecting leading indicators involve univariate analyses, which have limited utility when assessing ecosystems where the driving variable in the ecosystem is unknown (Bestelmeyer *et al.* 2011);

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Brock & Carpenter (2012) describe this limitation as a 'fundamental problem'. Perretti & Munch (2012) found that variance, skewness, kurtosis, spectral density and critical slowing down (defined by the lag 1 autocorrelation coefficient, AR1) all performed poorly when applied to a three-species model under conditions likely to be experienced in a field study. Thus, it is necessary to develop and test multivariate methods for assessing ecosystem dynamics (Perretti & Munch 2012; Eason, Garmestani & Cabezas 2014).

Measures of variance have intuitive appeal for signifying potential regime shifts because they provide a sense of system stability. Systems with low variance tend to exist near the mean suggesting a stable system, whereas rising variance indicates an increasing tendency to exist in regimes further from the mean, possibly foretelling relocation to a new regime. The variance index (VI) and Fisher information (FI) are two measures for assessing ecosystem variance using multivariate data (Eason, Garmestani & Cabezas 2014). The VI captures the dominant variance component (the largest eigenvalue) in a multivariate system and has been used to monitor pollutant dispersion and subsequent impacts on ecosystem dynamics (Brock & Carpenter 2006). FI is a more integrative measure than the VI, reflecting the overall variance of a multivariate system as opposed to just the dominant variance component. Fisher information was developed by Sir Ronald Fisher (1922) as a measure of the amount of information on a parameter (e.g. community structure) that is available in observable data. It is rooted in statistical estimation theory and has been adapted into a means of assessing patterns in ecosystem dynamics (Cabezas et al. 2003; Mayer, Pawlowski & Cabezas 2006; Karunanithi et al. 2008). The fundamental idea of this approach is the ability to evaluate system behaviour by assessing changes in variables that characterize its condition. It is closely related to other information theory-based approaches that have proven useful for understanding ecosystem function, structure and complexity (Ulanowicz 1997; Anand & Orlóci 2000; Svirezhev 2000; Fath & Cabezas 2004). The index is inversely related to the system variance (Eason, Garmestani & Cabezas 2014); accordingly, when comparing FI and VI, note that VI tends to peak and FI declines prior to a transition (Eason, Garmestani & Cabezas 2014).

Recent work involves using FI to assess critical transitions and explore subsequent implications for resilience in human and natural systems (Eason & Cabezas 2012; Eason & Garmestani 2012; Eason, Garmestani & Cabezas 2014; Spanbauer et al. 2014). In this paper, we review several studies and present a new study (phytoplankton dynamics in Tablas de Daimiel National Park) using both univariate indicators and multivariate methods to assess ecosystem dynamics. Our results reveal the complementary nature of the methods and highlight the utility of multivariate approaches.

Materials and methods

We selected four case studies to compare and assess the utility of univariate indicators and multivariate methods. Time series were compiled from previous studies to assess: (i) phosphorous inflows into a shallow lake (Karunanithi et al. 2008; Eason, Garmestani & Cabezas 2014), (ii) regional climate and biological variables in the Bering Strait (Hare & Mantua 2000; Karunanithi et al. 2008; Eason, Garmestani & Cabezas 2014), (iii) diatom assemblages in a ~7000-year high-resolution palaeoecological record (Spanbauer et al. 2014); and (iv) climate-strained (drought-impacted) phytoplankton community dynamics (Alvarez-Cobelas, Sánchez-Carrillo & Cirujano 2007; Angeler et al. 2013). Furthermore, we explored methods of identifying underlying drivers of ecological change. All of the indicators and indices were computed in MATLAB (2014b) (Release 2014b, Mathworks, Inc.).

FISHER INFORMATION

The form of FI used in this work is based on the probability of observing various conditions (states, s) of the system, $p(s)$ (Fath, Cabezas & Pawlowski 2003; Mayer et al. 2007). Here, ecosystem states are defined as a function of the variables that characterize ecosystem condition which may change due to fluctuations in internal dynamics or in response to external perturbation.

$$I = \int \frac{ds}{p(s)} \left[\frac{dp(s)}{ds} \right]^2 \qquad \text{eqn1}$$

Equation 1 reflects proportionality between FI and the change in the probability of observing an ecosystem state ($dp(s)$) versus the change in state ds (i.e. $\propto \frac{dp(s)}{ds}$). The utility of this principle can be understood by exploring two dynamic extremes (see Appendix S1 in Supporting information). The first case is a system that oscillates within a limited range in a regime from one observation to the next. In this case, the overall condition is (relatively) predictable, the patterns in the system are evident and FI tends towards infinity. Conversely, if there are no clear patterns in system behaviour, there is equal probability of the system being observed in any state, and FI is zero (Fath, Cabezas & Pawlowski 2003).

Given the fundamental idea that different ecosystem regimes are controlled by distinct processes and exhibit unique patterns, interpreting FI involves assessing how the index changes through time (Karunanithi et al. 2008). Regimes are identified as periods in which FI is nonzero and relatively stable (i.e. dFI/dt ≈ 0). While rising FI indicates increasing dynamic order and therefore movement towards more stable patterns, declining FI signifies that the patterns are degrading (greater fluctuations in the variables) and may serve as a warning signal of an impending transition (Eason, Garmestani & Cabezas 2014). A local minimum in FI between two regimes typically denotes a regime shift. Note that there is no guarantee that a shift from one regime to another is a transition to a more desirable system condition (e.g. a lake shifting from an oligotrophic to a eutrophic regime). Variables that characterize the system must be evaluated to determine the condition of the system (Eason & Garmestani 2012). A higher FI value is typically associated with a greater degree of dynamic order (stable patterns). However, the level of dynamic order is not as important as the ability of the system to remain within a desirable regime. Hence, a resilient system regime has a relatively high mean FI (μFI) and low standard deviation in FI (σFI) (Gonzalez-Mejia 2011; Eason & Garmestani 2012).

Variance, skewness and kurtosis are computed using standard statistical functions, and the lag 1 autocorrelation coefficient is used to estimate critical slowing down (Dakos *et al.* 2008). These indicators are calculated for each system variable over time. VI is defined as the largest eigenvalue of the covariance matrix (Brock & Carpenter 2006), and a small algorithm was developed to calculate it. Appendix S1 contains derivation information, the basic computation algorithm and a simple example of calculating FI. Because of the difficulty of doing the FI computation (particularly for large-scale data sets) by hand, the algorithm for computing FI has been coded in MATLAB. Further details on the procedure and the core components of the MATLAB code are provided in Cabezas & Eason (2010). For the sake of consistency, all univariate indicators and FI were computed using the same moving window size (defined in each study).

Results

CASE 1: SHALLOW LAKE

A classic example of a bifurcation-type regime shift is that of a shallow lake, which undergoes a regime shift in response to a slow-changing driver (the inflow of phosphorus). Shallow lakes have been studied extensively to understand the behaviour of a system as it approaches a critical transition (e.g. Carpenter, Ludwig & Brock 1999; Wang *et al.* 2012; Dakos, van Nes & Scheffer 2013). We used a simple model to capture system dynamics as the conditions shift from oligotrophic to eutrophic (Karunanithi *et al.* 2008; Pawlowski & Cabezas 2008). Equation 2 defines the concentration of phosphorus (x) at time t as a function of the phosphorous inflow rate (a) and the rate of removal (b) through sedimentation, flushing or biomass sequestration:

$$x_{t+1} = x_t + a - bx_t + \frac{x_t^2}{1 + x_t^2} \qquad \text{eqn 2}$$

The model was simulated for 2500 time steps with b set to 0·58 and a varied to define: three stable periods [i.e. (0–200) = 0·02, (210–500) = 0·08 and (1800–3000) = 0·14] and two distinct shift periods (Karunanithi *et al.* 2008; Eason, Garmestani & Cabezas 2014):

$$200 < t < 210 \qquad a = 0·02 + \left(\frac{t - 200}{10}\right) \times 0·06 \qquad \text{eqn 3}$$

$$500 < t < 1800 \qquad a = 0·08 + \left(\frac{t - 500}{1300}\right) \times 0·06$$

Figure 1 is a plot of the concentration of phosphorus (Fig. 1a) and corresponding indicator results computed over a 100-time-step moving window (hwin = 100). The univariate indicators (Fig. 1b–e) and FI (Fig. 1g) typically exhibited signals consistent with the shifts (e.g. increasing

variance) and VI (Fig. 1f) was zero for the entire period because only one variable was used to define the system (hence, no covariance). FI displayed tiered trends reflecting changes in system dynamics and provided warning of the impending regime shift (i.e. declining up to the shift point and increasing consistently with the rate of change in the phosphorous level as it moved towards stability).

CASE 2: BIOLOGICAL AND CLIMATE SHIFTS IN THE BERING STRAIT

Climate and biological variation have spurred years of research on the Bering Strait (McGowan, Cayan & Dorman 1998; Hare & Mantua 2000; McGowan *et al.* 2003; Grebmeier *et al.* 2006). Researchers cite atmospheric conditions related to the Pacific Decadal Oscillation as a key factor contributing to a sudden and lengthy transition (20–35 years) in physical conditions (Hilborn *et al.* 2003). These changing conditions resulted in regime shifts in 1977 and 1989 (Hare & Mantua 2000). Previous FI studies were successful in detecting these shifts using aggregated analytical and numerical FI approaches (Mayer *et al.* 2007; Karunanithi *et al.* 2008; Eason, Garmestani & Cabezas 2014). Here, we build upon those studies to include all the univariate indicators, as well as VI and FI.

Bering Strait conditions from 1965–1997 were captured using 65 biological and climate variables compiled from a study by Hare & Mantua (2000). The variables encompass a variety of information on the Bering Strait (e.g. climate indices, surface temperature, stream flow, biomass of species and fish catch) and were used to compute the indicators over a 10-year moving window (hwin = 10). Plots of the time series, indicators and indices demonstrate the difficulty in evaluating complex system dynamics (Fig. 2). Since the univariate indicators were calculated separately for each of the 65 variables, it was difficult to draw any general conclusions about the dynamics of the system over the 30+-year timespan of the data (Eason, Garmestani & Cabezas 2014). Accordingly, the multivariate nature of the system made it challenging to identify signals of an impending regime shift using univariate approaches (Spanbauer *et al.* 2014). VI and FI provided evidence of changes in ecosystem dynamics, yet presented different stories. VI peaked several times but these peaks did not coincide with known regime shifts (Fig. 2c). FI declined 43% from 1972 to 1977 (4·78–2·74) and about 16% from 1987 to 1989 (4·15–3·51). These local minima are consistent with known regime shifts (1977 and 1989), and the decreases prior to the regime shifts serve as warning of the impending transition ahead.

CASE 3: PALAEOECOLOGICAL RECORD OF DIATOM ASSEMBLAGES ON FOY LAKE (MONTANA, USA)

Researchers studying regime shifts typically focus on transitions occurring over short periods (i.e. decades), yet the variables and mechanisms may operate at longer
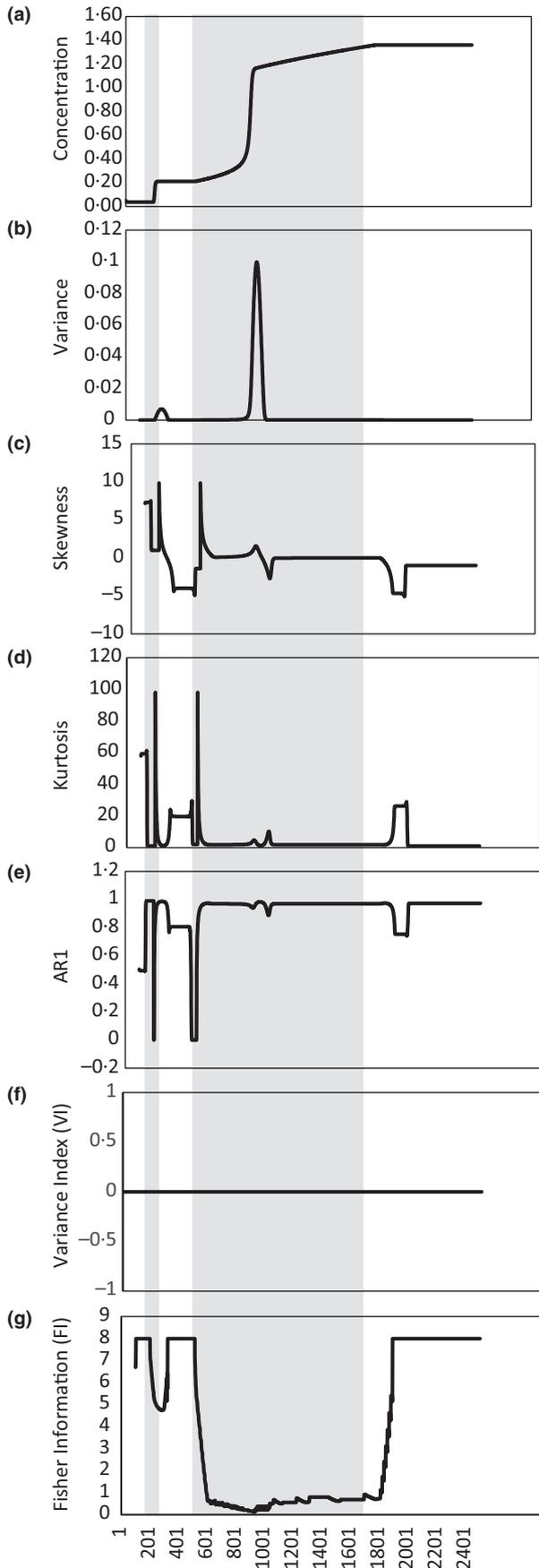
Fig. 1. Dynamics of the shallow lake model. Shaded regions indicate where the (a) concentration of phosphorus dynamics changed and how this is reflected in (b) variance, (c) skewness, (d) kurtosis, (e) AR1: proxy for critical slowing down, (f) VI: variance index and (g) FI: Fisher information.
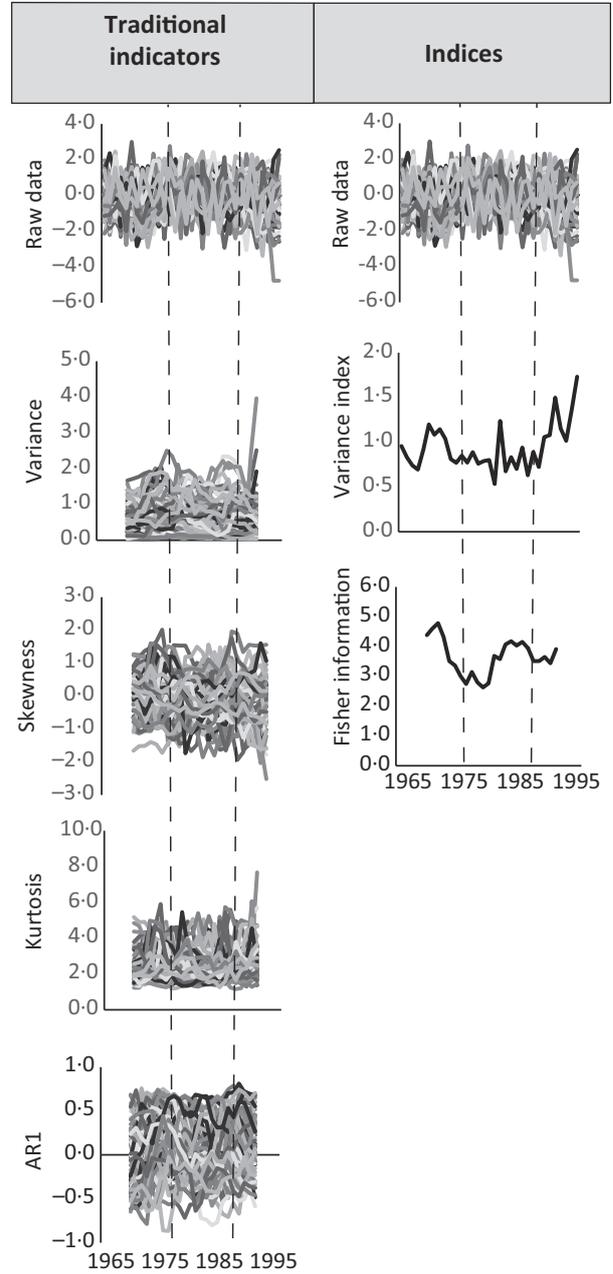

Fig. 2. Trends in indicators for the Bering Strait. While traditional indicators have little to no utility when assessing multivariate systems and variance index (VI) peaks do not correspond with known shifts, the local minima in Fisher information (FI) are consistent with shift periods. Declines in FI provide warning of the transition many years ahead.

time-scales (e.g. climate), heightening the difficulty of identifying the key drivers of ecological change. It is widely recognized that both slow- and fast-moving vari-

ables can alter system dynamics and accordingly may be culpable in diminishing resilience. The ability to capture these impacts is often hampered by data availability, and hence long-term time series are highly coveted. Spanbauer *et al.* (2014) compiled nearly seven thousand years of data from a sediment record at Foy Lake (Montana, USA) which characterizes diatom community dynamics. The data consisted of percentage abundance of 109 diatom species over 763 time steps. In this study, indicators and indices were computed (hwin = 10) to capture signals of system dynamics in this high-resolution palaeoecological record. As in the Bering Strait example, the univariate indicator results were difficult to interpret as they often displayed conflicting patterns; hence, we focused on the multivariate index results. While there were a number of peaks in VI, an increasing trend emerges from ~4 to 2 ka (ka: thousands of years) before 1950 AD (Fig. 3b). This pattern is similar in FI, which declined (57%) for thousands of years prior to reaching a local minima at ~2 ka and then increasing and stabilizing at ~1·3 ka (Fig. 3c). These results were consistent with ecological and climate patterns for Foy Lake in which a long period of instability was characterized by a shallow, benthic flora-domi-
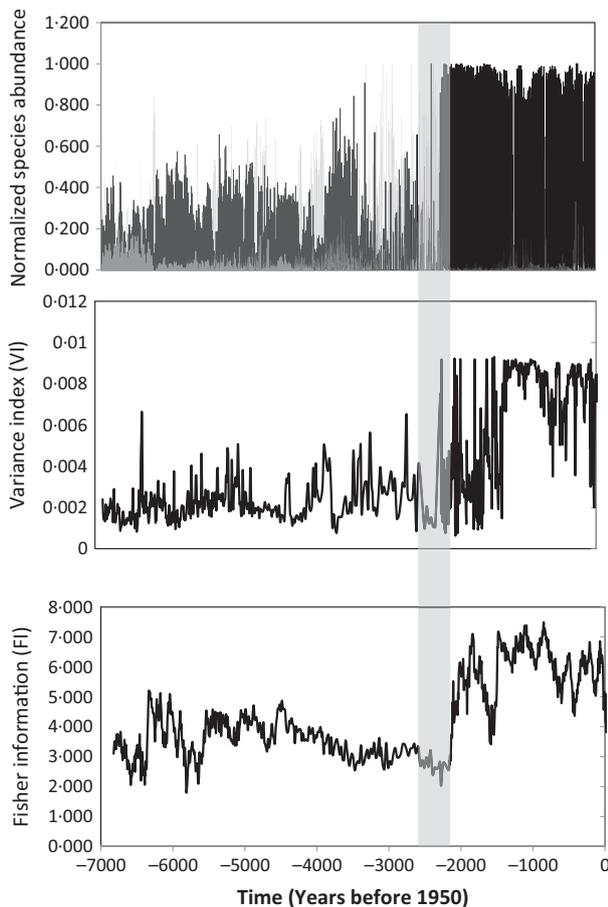
nated lake and severe mid-continental drought (Booth *et al.* 2005; Spanbauer *et al.* 2014). Prior to that period, the lake was relatively deep and exhibited greater diversity in the planktonic and benthic flora.

CASE 4: PHYTOPLANKTON DYNAMICS IN TABLAS DE DAIMIEL NATIONAL PARK

One of the consequences of climate change is the increased frequency and duration of drought events, which can have negative ecological and economic repercussions. Droughts are considered protracted disturbances where ecosystem impacts gradually worsen as the drought persists and harm often does not become evident until a critical threshold is passed (Lake 2000). Recent studies have focused on assessing the resilience of ecosystems, particularly to determine whether drought conditions push ecosystems into climate-induced alternative states (Angeler *et al.* 2013). We analysed phytoplankton time series in a floodplain wetland in Spain. Phytoplankton was useful in this study because it responds rapidly to environmental perturbation. Our analysis focused on community dynamics during a period (1996–2002) when climate conditions transitioned from an interannual wet state to a period of prolonged drought, reflecting alternative climate regimes. We also explored the relationships between patterns in various taxonomic species groups to discover whether the FI computed from any of the groups was highly correlated with the FI of the overall system. Such a result may suggest key drivers of systemic change.

Data were gathered from the Tablas de Daimiel National Park (TDNP), a 1675-ha floodplain located in central Spain (39°08′N 3°43′W). TDNP is shallower in the north-east and deeper in the south-west (Fig. 4). With a 0·91-m average depth, the wetland is hypertrophic as a result of heavy nutrient loadings since 1980 and the high productivity of both emergent vegetation and

Fig. 3. Shifting patterns in long-term diatom assemblages are reflected by increases in the variance index (VI) and declining Fisher information (FI).
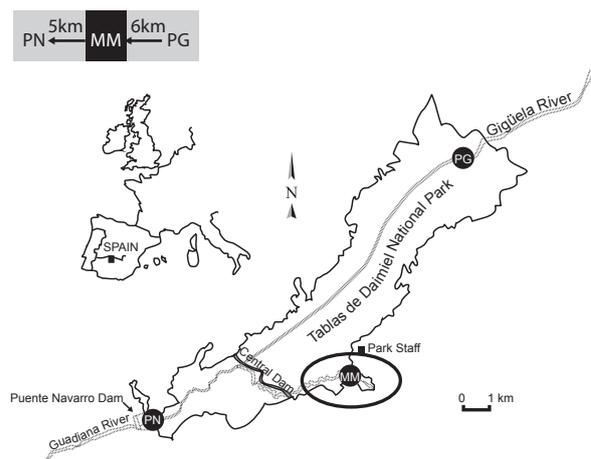

Fig. 4. Wetland: Las Tablas de Daimiel National Park (adapted from Angeler *et al.* 2013). Data used in this study are from the Molemocho site (circled).

phytoplankton. Further information on the wetland can be found in Alvarez-Cobelas & Cirujano (1996), Alvarez-Cobelas, Sánchez-Carrillo & Cirujano (2007), Sánchez-Carrillo & Angeler (2011) and Angeler *et al.* (2013).

Since our goal was to evaluate whether there was a shift in community structure from the wet to dry period, we focused on phytoplankton dynamics in a deeper and wider area located in the middle of the wetland, called Molemocho (MM). Monthly flooding and biovolume of phytoplankton species (Fig. 5a,b) were used to capture the community dynamics from the wet period (shaded: 1996–1998) in which the sites are considered hydrologically connected (flooding level >1500 ha) to the period of prolonged drought conditions (1999–2002). The biovolume of each of the 159 species (from nine taxonomic species groups) was treated as a separate variable, and the indicators and indices (hwin = 10) were used to assess ecosystem dynamics.

Temporal variance peaks for a few species (e.g. *Anabaena* sp.1 and *Peridinium willei*) prior to the end of the wet period (Fig. 5a,b), but this signal is not found in most of the other species or traditional univariate indicators. When comparing the behaviour of the indices (VI and FI) in the two hydrological periods, distinctive patterns emerge (Fig. 5c,d). A single VI spike occurs before the end of the wet season and FI remains relatively stable with a slight decreasing trend signalling the impending transition. A local FI minimum occurs in April 1998 and then FI abruptly increases as the system transitions. FI declines through the onset of the dry season (47% decrease from September 1998 to December 2000), stabilizes for a period and then declines further as the drought persists. VI peaks multiple times during the dry season, yet rather than signifying transition points, the index displays shifting trends reflected by spikes of increasing magnitude as the system moves deeper into the drought. Furthermore, we found that the mean VI and standard deviation in FI essentially tripled from the wet to the dry period signifying greater variability in community dynamics as drought conditions persisted.

To identify possible drivers of the changes in community structure, FI was computed for each taxonomic group except those represented by few species or where data were only available for a short period (e.g. xanthophytes and conjugatophytes). Then, the FI from each taxonomical group was compared to each other, the FI of the overall system (all species) and time, using Spearman rank order correlations (SROC). Declining FI trends were found in the overall system and some of the taxonomic groups (Table 1). The trends in the overall system were highly correlated with the euglenophytes, conjugatophytes and diatomophytes. These correlations with the overall system suggest that species from these three groups may be the main drivers of change and vulnerability in phytoplankton community dynamics related to the flood–drought transition. The declining FI trends in these species indicate highly variable patterns in species biovolume
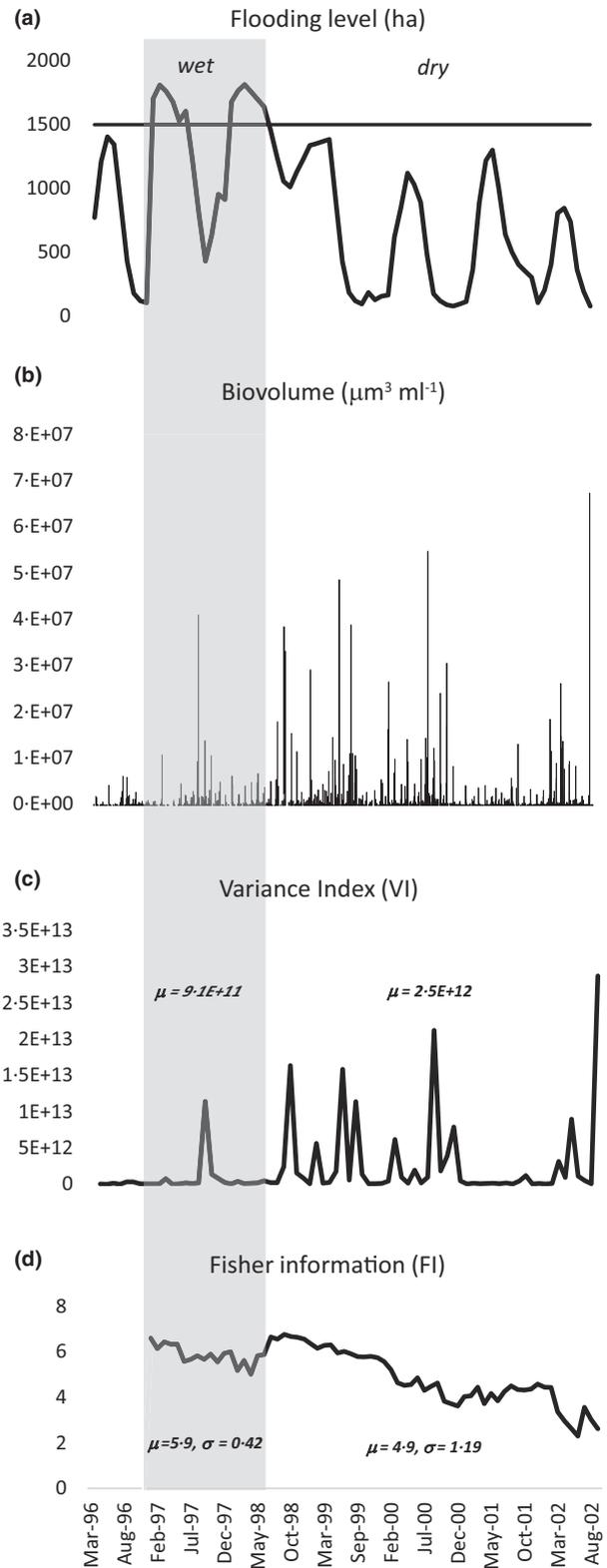

Fig. 5. (a) Flooding area at Molemocho (MM) in Tablas de Daimiel National Park from 1996–2002, (b) phytoplankton biovolume, (c) variance index (VI) and (d) Fisher information (FI) trends are relatively stable during the connectivity period (wet period: shaded) and severely decline as Molemocho settles deeper into the drought (dry period). The drought period is also characterized by multiple VI peaks of increasing magnitude.

over time and therefore volatility in community structure during the drought period. The FI of dinoflagellates displayed a positive correlation with time (rho = 0·65, $P < 0.05$), implying that this group of algae has remained relatively resistant to the drought conditions. An inverse relationship was found between dinoflagellates and diatomophytes, and the trends for diatomophytes, chrysophytes and chlorophytes were positively correlated.

Distinctive patterns emerge when focusing on FI dynamics in the wet and dry periods separately (Table 2). Chlorophytes had a strong correlation with the overall trends in the system for both periods; however, different taxa (cyanobacteria in the wet period and euglenophytes in the dry period) complement these relationships in each period. The FI of the diatomophytes reflected strong temporal dynamics in the wet season. This is due to the fact that the diatoms consist of centric microalgae which are strictly planktonic and need a certain thickness of the water layer in which to live (Reynolds 2006; Rojo *et al.* 2012). Declining FI trends for multiple taxonomic groups (i.e. cryptophytes, chrysophytes and cyanobacteria) indicate greater instability during the drought. Multiple statistically significant correlations between the FI of taxonomic groups are present during the drought period, suggesting more interdependence between the taxonomic groups.

Analysis of the plankton biovolume in MM provided a continuous picture of the impact of the transition from the wet to prolonged drought period. Previous studies confirm that there is increased species richness and diversity from wet to dry periods in TDNP (Rojo *et al.* 2012; Angeler *et al.* 2013); however, drought conditions resulted in reduced species evenness. Angeler *et al.* (2013) used multivariate time-series modelling and found that phytoplankton dynamics tended to be more stochastic during the dry period; hence, their models had lower explanatory power during this time. Accordingly, more species richness did not imply greater resilience (Angeler *et al.* 2013). Importantly, our study corroborates this unexpected finding in Angeler *et al.* (2013), thanks to the ability of FI to detect structural shifts in phytoplankton community dynamics.

Table 1. Statistically significant Spearman rank order correlations: Fisher information (FI) overall vs. FI of the taxonomical groupings from 1996–2002 ($P < 0.05$)

	Time	All	Cyanobacteria	Dinoflagellates	Euglenophytes	Cryptophytes	Chrysophytes	Diatomophytes	Chlorophytes
Time	X	−0·82		0·65	−0·43		**−0·86**	**−0·72**	**−0·84**
All		X		−0·49	**0·71**		0·67	0·78	0·97
Cyanobacteria			X	0·47	0·46				
Dinoflagellates				X			−0·53	**−0·73**	−0·55
Euglenophytes					X				0·61
Cryptophytes						X			
Chrysophytes							X	0·69	**0·73**
Diatomophytes								X	0·78
Chlorophytes									X

Bolded values indicate strong correlation (rho > 0·7).

Table 2. Spearman rank order correlations for the wet (grey: 1996–1998) and dry periods (2000–2002): (rho > = 0·7, $P < 0.05$)

	Time	All	Cyanobacteria	Dinoflagellates	Euglenophytes	Cryptophytes	Chrysophytes	Diatomophytes	Chlorophytes
Wet period: 1996–1998									
Time	X							0·81	
All		X	0·98						**0·95**
Cyanobacteria			X						**0·90**
Dinoflagellates				X					
Euglenophytes					X				
Cryptophytes						X			
Chrysophytes							X		
Diatomophytes								X	
Chlorophytes is									X
Dry period: 2000–2002									
Time	X		**−0·81**			−0·74	−0·74		
All		X			0·74				**0·95**
Cyanobacteria			X			0·79			
Dinoflagellates				X					0·78
Euglenophytes					X				0·74
Cryptophytes						X	0·95		
Chrysophytes							X		
Diatomophytes								X	
Chlorophytes									X

Bolded values indicate strong correlation (rho > 0·7).

Studying FI trends in phytoplankton assemblages afforded the ability to assess changes in community structure linked to a strong climatic shift, and the analysis highlighted the differences in community dynamics within each hydrological period. Our analysis helps to demonstrate the utility of multivariate approaches which might translate into a tool that can help ecologists and managers assess ecosystem dynamics, thereby providing useful information for aquatic resources management.

Discussion

Numerous measures including variance, skewness, autocorrelation and kurtosis have been proposed as potential leading indicators of regime shifts in ecosystems (e.g. Dakos *et al.* 2008; Scheffer *et al.* 2012). Researchers have catalogued warning signals and examined the relationship between many of the proposed regime shift indicators (Scheffer *et al.* 2012; Eason, Garmestani & Cabezas 2014). Although it is commonly believed that traditional measures rise, warning of an impending transition, it has been shown that different conditions (e.g. slowing, flickering) may be present as a system nears a bifurcation point (Seekell, Carpenter & Pace 2011; Dakos *et al.* 2012a; Seekell *et al.* 2012). Hence, researchers have found asymmetric responses when using traditional measures (Batt *et al.* 2013; Dakos, van Nes & Scheffer 2013). Much of the work on leading indicators involves speculative assessments of simulated system behaviour or a few variables from real data sets; however, critical variables driving system transitions are typically unknown. Brock & Carpenter (2012) cite this lack of knowledge about ecosystem characteristics as a core issue for traditional indicators. Furthermore, the assessment of real ecosystems involves simultaneously tracking multiple variables and work is still needed to determine whether traditional univariate methods can be adapted to assess changes in these complex systems (Scheffer *et al.* 2009; Dakos *et al.* 2012a).

It is possible for traditional indicators to perform fairly well for simple systems defined by few variables (e.g. shallow lake model); however, Dakos *et al.* (2012a) and Seekell, Carpenter & Pace (2011), Seekell *et al.* (2012) cite evidence of conflicting patterns in autocorrelation, variance and skewness as a system approaches a regime shift. The need for alternative methods is truly highlighted when evaluating multivariate systems (e.g. ecosystems), which are hampered by the use of univariate approaches because they provide unclear signals about complex system behaviour (Eason, Garmestani & Cabezas 2014; Spanbauer *et al.* 2014). The detection of leading indicators of regime shifts is often complicated by a lack of long-term time-series data, and sampling of data is typically conducted in a manner that avoids temporal autocorrelation, a factor that some contend (Dakos *et al.* 2012a) is necessary for the assessment of leading indicators. Given data of varying lengths (up to nearly 7000 years), the case studies we reviewed (e.g. Bering Strait,

diatom community structure in Foy Lake) and our new analysis (drought-impacted phytoplankton dynamics) demonstrate that univariate indicators offer little insight when evaluating complex systems.

Multivariate methods present great promise in meeting this research need, although different methods offer varying degrees of utility. VI affords the ability to track many variables at once, but its signals are sometimes unclear, possibly due to the fact that all systems do not increase in variance as they approach a regime shift (Batt *et al.* 2013). FI measures how much system conditions vary, yet does not simply focus on the component of maximum variance or the direction of change (e.g. increase), affording the ability to capture both abrupt and subtle changes in system dynamics. This information theory-based approach examines trends in ecosystem variables to discern patterns useful for understanding system behaviour and subsequent drivers. In our new study (Case 4), FI allowed us to not only distinguish natural community seasonality from variation that is likely arising from anthropogenic climate change (supraseasonal climate states), but also offered utility in assessing signals of ecosystem change. Moreover, Spearman rank order correlations of the FI trends allowed us to determine that patterns in euglenophytes, conjugatophytes and diatomophytes were primarily responsible for the trends in the overall ecosystem. Such information is useful for selectively prioritizing monitoring efforts and developing management strategies.

An additional benefit of this approach is that declines in FI provide evidence of a loss of dynamic order and resilience. As such, Eason, Garmestani & Cabezas (2014) proposed that FI be explored as a warning signal of critical transitions because it can be used as a management tool for monitoring shifting conditions. While VI signals are not always clear, when used in concert with FI, interesting and harmonious trends may emerge (see Case 3 and Case 4). The ultimate goal of this growing field of study is to provide methods to detect signals of impending transitions that can facilitate policy and management actions.

Ecosystem management is very challenging as managers are operating under the possibility of multiple regimes and abrupt change in social–ecological systems (Garmestani & Benson 2013). In light of increasingly rapid environmental change, managers and policymakers will need to manage for resilience in social–ecological systems (Allen *et al.* 2011; Bestelmeyer *et al.* 2011). Given the growing connectivity between systems affected by and contributing to global environmental change, there is a premium on approaches that afford the ability to identify patterns in data particularly when prior knowledge of ecosystem behaviour and corresponding mechanisms is unknown. Thus, there is a critical need to develop better tools for the task, as there are significant consequences (e.g. coral reef collapse, loss of water quality) associated with regime shifts. Information theory-based approaches offer great promise for such applications and are well sui-

ted for assessing a broad range of data and systems (Frieden 2007). Univariate methods of assessing ecosystems are limited when applied to real ecosystems, and while multivariate methods (e.g. information theory-based approaches) are promising, they have their own limitations (Spears *et al.* 2015). We posit that using multiple quantitative approaches may provide a 'preponderance of evidence' in the search for methods to facilitate management in the face of global environmental change.

While the results presented in this paper are a step forward, quantitative methods are just one tool that will be necessary to manage for resilience (Allen *et al.* 2011; Garmestani 2014). We have yet to develop and may never have the full capacity to quantify the 'resilience' of a social–ecological system. Thus, resilience-based management requires a suite of tools (e.g. quantitative methods, legal reform, scenario planning, market mechanisms), in order to move closer to system-based management of ecosystems. Ecosystem management is of great importance moving forward in the Anthropocene, and we hope that the methods discussed in this manuscript move us closer to solving the problem.

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Data accessibility

Data are available from the University of Valencia repository RODERIC: http://hdl.handle.net/10550/48062.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Fisher information derivation, basic calculation algorithm and simple example.

Table S1. Sample data for simple example.

Table S2. Dividing data into overlapping windows.

Table S3. Computing absolute differences

Table S4. Testing the size of states criteria.

Table S5. Amplitude for each window.

Fig. S1. Fisher information and the probability of observing system states.

Fig. S2. Plot of sample data for simple example.

Fig. S3. Bulls-eye plot of binning points.

Fig. S4. Probability density for each window.

Fig. S5. Gradients of the amplitude.

Fig. S6. Fisher information for simple example.