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Paper:

Seddon, A., Froyd, C., Witkowski, A. & Willis, K. (2014). A quantitative framework for analysis of regime shifts in a Galapagos coastal lagoon. *Ecology*, 95(11), 3046-3055.

<http://dx.doi.org/10.1890/13-1974.1>

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A quantitative framework for analysis of regime shifts in a Galápagos coastal lagoon

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Abstract. Regime shifts are often used to describe sharp changes between two or more ecological states, each characterized by their own dynamics, stochastic fluctuations, or cycles. Ecological theory indicates they can occur either as a result of an abrupt environmental forcing (extrinsic regime shift), or be indicative of complex responses to local-scale dynamics and thresholds (intrinsic regime shift). One important area of ecological research is to develop quantitative tools to analyze regime shifts, but there are few studies that have applied these methods to the long-term ecological record. In this study, we introduce a framework to investigate regime shifts in diatom assemblages and mangrove ecosystem dynamics in a coastal lagoon from the Galápagos Islands over the past 2600 years. The framework integrates a set of established statistical methodologies for investigating regime shift dynamics in long-term ecological records. We use these methods to (1) identify the presence of regime shifts; (2) test for a series of hypothetical relationships (i.e., linear through to threshold) between ecological response and environment using nonlinear regression; and (3) investigate the relative importance of intrinsic and extrinsic dynamics in response to environmental perturbations. The transitions in the diatoms closely track the sequence of disturbance, recovery, and habitat shifts that have occurred in the lagoon over the past 2600 years, demonstrating extrinsic responses to environmental forcing. In contrast, the shift from a mangrove- to a microbial mat-dominated system ~945 cal yr BP provides potential evidence of an intrinsic regime shift. Our framework enables robust interpretations into the underlying dynamics of regime shifts in the paleoecological record and is widely applicable for investigating abrupt ecological changes in a range of systems.

Key words: abrupt ecological change; diatoms; extrinsic and intrinsic ecological dynamics; generalized nonlinear least squares; mangroves; microbial mats; paleoecology; regime shifts.

INTRODUCTION

Regime shifts are sharp changes between two or more ecological states, each characterized by their own dynamics, fluctuations, and/or cycles (Scheffer 2009). In ecology, much theoretical understanding of regime shifts has arisen from experimental studies on closed systems (Wissel 1984, Veraart et al. 2011), but finding ways to detect, define, and understand these dynamics in observational data remains a major challenge (Scheffer and Carpenter 2003). The paleoecological record (i.e., the long-term ecological record of sub-fossilized remains preserved in sedimentary archives) can play a particularly important role in understanding the processes behind regime shifts, because it enables the reconstruction of processes occurring over decadal–centennial

timescales or longer. Paleoecological data can be used to identify the existence of ecological thresholds, and to investigate the long-term environmental processes that can lead to loss of resilience and abrupt transitions between alternate states (Dearing 2008, Willis et al. 2010).

Current understanding suggests that a regime shift may be the product of two very different processes. Extrinsic regime shifts are abrupt ecological transitions occurring at the same time as a large environmental forcing. In contrast, intrinsic regime shifts occur when an abrupt ecological change occurs in response to a gradual environmental driver, implying the importance of local-scale dynamics and thresholds (Williams et al. 2011). Therefore, an important line of ecological research is to identify the processes behind regime shifts and to understand whether their underlying dynamics are intrinsic or extrinsic in nature.

Williams et al. (2011) proposed a conceptual model for determining the relative importance of intrinsic vs. extrinsic dynamics within changes in biological commu-

Manuscript received 15 November 2013; revised 25 February 2014; accepted 8 April 2014; final version received 29 April 2014. Corresponding Editor: F. S. Hu.

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nities by (1) identifying linear, unimodal, or threshold relationships between biological and environmental variables, and (2) testing whether major trends in these paleoecological assemblages occur at the same time as major changes in environment (and are therefore intrinsically or extrinsically driven). For example, major vegetation transitions that occurred synchronously across North America over the Younger Dryas period (12 900 cal yr BP–11 700 cal yr BP) were proposed to represent extrinsically forced dynamics occurring in response to the abrupt climate cooling and warming at this time (e.g., Steffensen et al. 2008). In contrast, the heterogeneous response of vegetation to slow changes in aridity during the end of the African Humid period was inferred to indicate intrinsic ecological change due to the presence of local, site-specific thresholds (Kröpelin et al. 2008).

In recent years, a number of statistical techniques have been developed to enable quantitative detection of regime shifts in observational records (e.g., Rodionov 2004, 2006, Carstensen and Weydmann 2012), and which can also be adapted for multivariate ecological data sets (Nicholls 2011). Randsalu-Wendrup et al. (2012), for example, used nonlinear regression to identify two regime shifts in diatom assemblages from a Swedish lake. Although they did not apply statistical modeling to the environmental drivers, diatom regime shifts occurring around a well-documented, abrupt cooling event 8.2 K years ago were suggested to be extrinsically forced. One important contribution to improve these methods, therefore, is to integrate a set of quantitative tools into the conceptual model proposed by Williams et al. (2011). This would enable robust interpretation of the relative role of intrinsic and extrinsic dynamics driving abrupt ecological change.

In this study we adapt the model proposed by Williams et al. (2011) and introduce a quantitative framework to (1) identify the presence of regime shifts in a paleoecological data set; (2) test for a series of hypothetical relationships (i.e., linear through to threshold) between ecological response variable and environment; and (3) investigate the relative importance of intrinsic and extrinsic dynamics in responses to environmental perturbations. We apply this framework to a data set from a coastal lagoon in the Galápagos Islands (Seddon et al. 2011a), and contrast the ecological responses of diatoms (microscopic organisms whose silica frustules are well preserved in lake sediments), and local-scale mangrove ecosystem dynamics to environmental variability over the past 2600 years. The framework integrates established statistical methodologies (Rodionov 2004, Nicholls 2011, Carstensen and Weydmann 2012) for investigating regime shift dynamics in long-term ecological records, and applies techniques to enable testing on the unevenly spaced samples commonly observed in paleoecological data sets. By using independent environmental data we are able to build on these past studies, both by introducing a formal test of the trends in control variables, and by testing for

a series of hypothetical relationships (i.e., linear through to threshold) between ecological response variable and environment.

MATERIAL AND METHODS.

Paleoecological data

We use diatom assemblage, $\delta^{13}\text{C}$, and trace-element geochemistry data (see Seddon et al. 2011a) to investigate the presence and dynamics of ecological regime shifts in a coastal lagoon from the Galápagos Islands (Appendix A). A 4.9-m core from a coastal lagoon in the Diablas wetland complex located on the south coast of Isabela Island (0.952° S, 90.986° W) was collected in August 2005 (Seddon et al. 2011a). The core chronology is based on eight AMS radiocarbon dates, with the age–depth model estimated using a smooth-spline function in clam (Blaauw 2010). This age model has been updated by calibrating with the IntCal13 Southern Hemisphere calibration curve for this study (Hogg et al. 2013) (Appendix B). Dating of samples directly above and below an abrupt sediment transition ~ 945 cal yr BP has confirmed that there have been no major hiatuses in sedimentary deposition. For further details of all the laboratory methods used, we refer the reader to Seddon et al. (2011a).

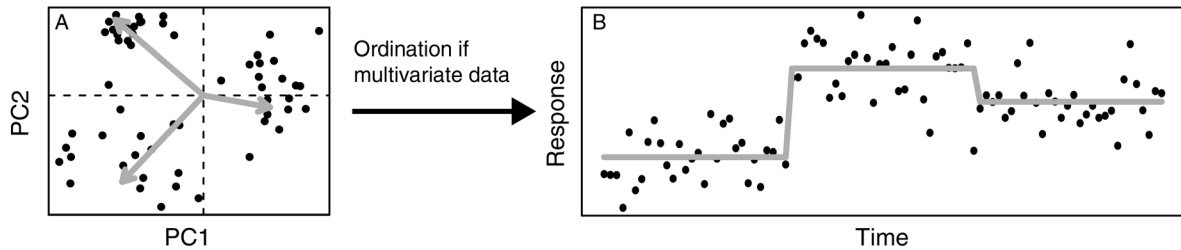
The diatom assemblage data were obtained by extracting 1-cm³ subsamples of sediment at 4-cm resolution, and were prepared following standard methodology (Battarbee et al. 2001). Analysis of stable carbon-isotope composition ($\delta^{13}\text{C}$) of the bulk sediment from the Diablas core showed that mangroves in the Diablas lagoon preferentially assimilate the lighter isotope ¹²C from the atmosphere and have more negative $\delta^{13}\text{C}$ values (–26.4 to –22.9‰) compared to the microbial-dominated organic material present in the lagoon today (–16.0 to –10.7‰) (Seddon et al. 2011a). Variability in the $\delta^{13}\text{C}$ signature can therefore be used as an indicator of mangrove–microbial mat dynamics in the coastal lagoon over the past 2600 years.

Element geochemistry data (Ti influx) were obtained using Inductively Coupled Plasma-Atomic Emission Spectrometer (ICP-AES), and are interpreted here as evidence of high-energy tidal disturbance events (Seddon et al. 2011a). Variability in Ti was found to be closely correlated with other minerogenic elements such as Al and Fe, and the down-core trends in Ti therefore likely reflect allogenic input (e.g., erosional inwash) into the basin (Boyle 2001). Geochemistry samples had been taken 1 cm below the diatom samples, and so were linearly interpolated to the same core depths. Concentrations of Ti (in parts per million) were transformed by sediment accumulation rates to influx (in micrograms per square meter per year).

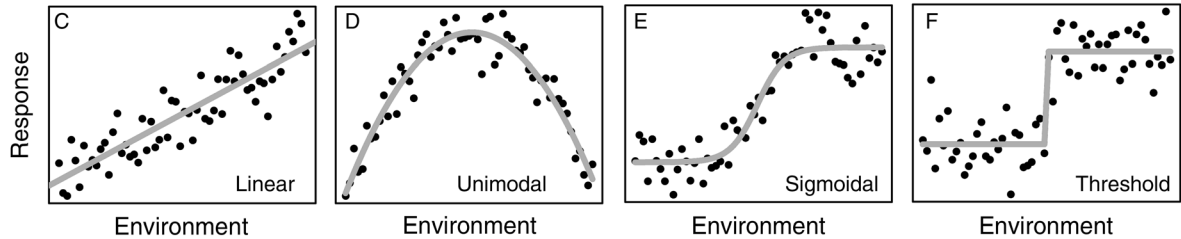
Statistical approaches

Step 1: Regime shift detection.—The Sequential T-test Analysis of Regime-Shifts algorithm (STARS) devised by Rodionov (2004, 2006) was combined with classical

Step 1: Regime shift detection



Step 2: Investigate response functions



Step 3: Test for intrinsic vs. extrinsic dynamics

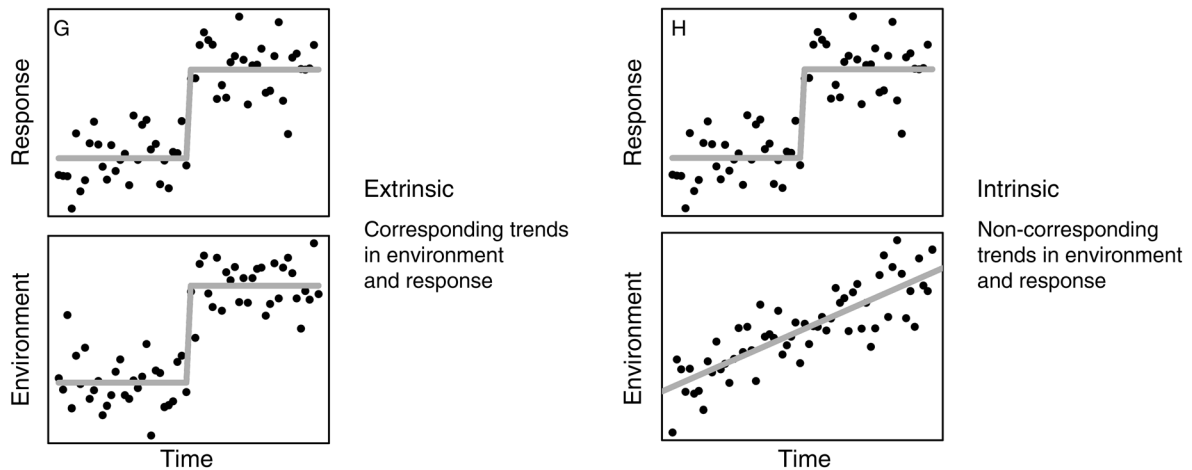


FIG. 1. Framework used to identify intrinsic vs. extrinsic regime shifts used in this study. The approach follows that outlined by Williams et al. (2011), but instead applies a set of quantitative statistical methods. Step 1 uses change point analysis to identify potential regime shifts. For multivariate data, an ordination is required, first (A) before the regime shift detection methods (B) are applied to relevant ordination axes. Step 2 uses generalized nonlinear least squares to test for (C) linear, (D) unimodal, (E) sigmoidal, and (F) threshold relationships between response and environment. Step 3 uses generalized nonlinear least squares to investigate trends in mean and variance in each of the variables over time, and to test for (G) extrinsic and (H) intrinsic dynamics.

multivariate techniques to identify statistically significant changes in the mean of the paleoecological (i.e., diatoms, $\delta^{13}\text{C}$) temporal series (Nicholls 2011). For univariate data (e.g., $\delta^{13}\text{C}$), the STARS algorithm could be applied directly; for the multivariate diatom assemblages, a principal components analysis (PCA) was first used to extract major components in assemblage variation, and the algorithm was applied to the first and second principal component axes (PC1 and PC2) (Fig. 1A, B). The diatom data had been Hellinger transformed to reduce the influence of abundant species (Legendre and Gallagher 2001, Legendre and Birks

2012). Each temporal series had been sorted into 40-year bins, standardized by the mean and standard deviation, and were passed through a white-noise filter using the ordinary least-squares method outlined in Rodionov (2006). We set the P value to 0.05 and the window size was 15. As a further regime-shift detection technique, constrained and unconstrained cluster analyses were also run on the diatom data using a Bray-Curtis dissimilarity matrix. Significant zones were identified by comparison with the broken stick model (Bennett 1996) using the “rioja” package in R (Juggins 2012). Following these regime-shift detection techniques, it was

TABLE 1. Change points (cal yr BP) in diatom assemblage data identified by different regime shift detection techniques (see also Figs. 2–4).

Diatom assemblages	Change Point 1	Change Point 2	Change Point 3
Constrained cluster analysis (diatoms)	2015	1605	945
Cluster analysis (diatoms)	1975	1590	945
PC1 STARS (diatoms)	2140	...	940
PC2 STARS (diatoms)	2020	1580	...
$\delta^{13}\text{C}$ STARS (mangrove–microbial mat)	940

possible to create individual subsets of data, each separated by an abrupt transition (Table 1).

Step 2: Response functions.—For each transition point, we used nonlinear regression (e.g., Carstensen and Weydmann 2012) to investigate the relationship between response and predictor variables by testing for linear (Fig. 1C), unimodal (Fig. 1D), sigmoidal (Fig. 1E) and threshold (Fig. 1F) relationships using the nlme package in R (Pinheiro et al. 2013). For the diatoms, a PCA was rerun on the samples belonging to zones both before and after each change point, and the geochemistry data (Ti) were log transformed to account for the fact that low values would have low variance in comparison to high values. Following the interpretation of Seddon et al. (2011a), we investigate the relationship between tidal disturbance (i.e., Ti influx) and local mangrove ecosystem dynamics ($\delta^{13}\text{C}$). For the diatom assemblages, we tested the relationship between assemblage and both tidal disturbance (Ti influx) and local habitat change driven by the changing dominance of mangrove vs. microbial mat substrata ($\delta^{13}\text{C}$). The best model was identified using the Akaike Information Criterion (AIC) and the residuals of the best model were checked for temporal autocorrelation using Moran's *I* statistic (Dutilleul et al. 2012). To do this we calculated the Moran's *I* correlation of the residuals at 20-year increments and then fitted an exponential curve to these estimates to model the degree of autocorrelation in the samples (see Appendix C). The trend was reanalyzed with the autocorrelation formulated as part of the covariance matrix of the observations, using an exponential model if required. This procedure enables us to include an autocorrelation term in the models used on paleoecological data, which commonly contain samples unevenly spaced in time, as suggested by Bolker (2008).

Step 3: Intrinsic vs. extrinsic responses.—Finally, to assess the relative importance of intrinsic and extrinsic dynamics across each of the transitions, a second set of models representing changes in mean state and variance were fitted to the environment and response series using generalized nonlinear least squares regression. These are the same models described by Carstensen and Weydmann (2012), but we also included a sigmoidal model to represent a smooth-step response to changes in mean. The best models were assessed using AIC, and the same methods were used to estimate the potential impact of temporal autocorrelation in the residuals and to correct for this if required. For any given transition, the

differences between the two models were assessed (Williams et al. 2011). Corresponding functions (i.e., step-change driver and step-change response) represented extrinsically driven regime shifts (Fig. 1G). In contrast, non-corresponding responses (e.g., the environmental driver was linear and the assemblage response was nonlinear) were interpreted as evidence of the importance of internal dynamics (Fig. 1H).

RESULTS

Diatom assemblage changes

Both constrained and unconstrained cluster analysis showed that the diatom assemblages could be separated into four zones, with change points identified at ~2000, 1600, and 945 cal yr BP (Fig. 2A and Table 1). The first zone contains opportunistic, fast-reproducing species such as *Fragilaria* cf. *subsalina* (Grunow) Lange-Bertalot and *Pseudostaurosiraopsis geocollegarum* (Witkowski and Lange-Bertalot) Morales, in addition to a number of naviculoid benthic taxa that, to date, have only ever been found to occur within this section of the Diablas lagoon core (Seddon et al. 2011b, 2014). The second zone contains an assemblage dominated by *Achnanthes submarina* Hustedt, which was replaced by a *Fragilaria* cf. *subsalina* assemblage between 1570 and 945 cal yr BP. This second *Fragilaria* assemblage also contained *Navicula atwateri* Seddon, Witkowski and Hemphill-Haley, *Nitzschia palea* (Kützing) W. Smith, and *Nitzschia nana* Grunow. The final assemblage change identified by the cluster analysis occurred at 945 cal yr BP. Over this period *N. galapagoensis* Seddon and Witkowski and *Amphora acutiuscula* Kützing were initially dominant, while *A. caroliniana* Giffen became established at ~600 cal yr BP.

Results from the STARS algorithm on PC1 and PC2 complemented the cluster analyses (Fig. 2B–E). The first two ordination axes (PC1 and PC2) explained 34% of the variation in the diatom data set. High PC1 scores are associated with the early *Fragilaria* assemblage, and the lowest scores with the *Amphora/Navicula* assemblages at the top of the record (Fig. 3B, F). In contrast, variations in the gradient of PC2 reflect the transition into and out of the *Achnanthes*-dominated assemblage between ~2000 and 1570 cal yr BP (Fig. 3D, F). PC1 transition points were identified at 2140 and 940 cal yr BP, while in PC2 the transition points were identified at 2020 and 1580 cal yr BP (Table 1).

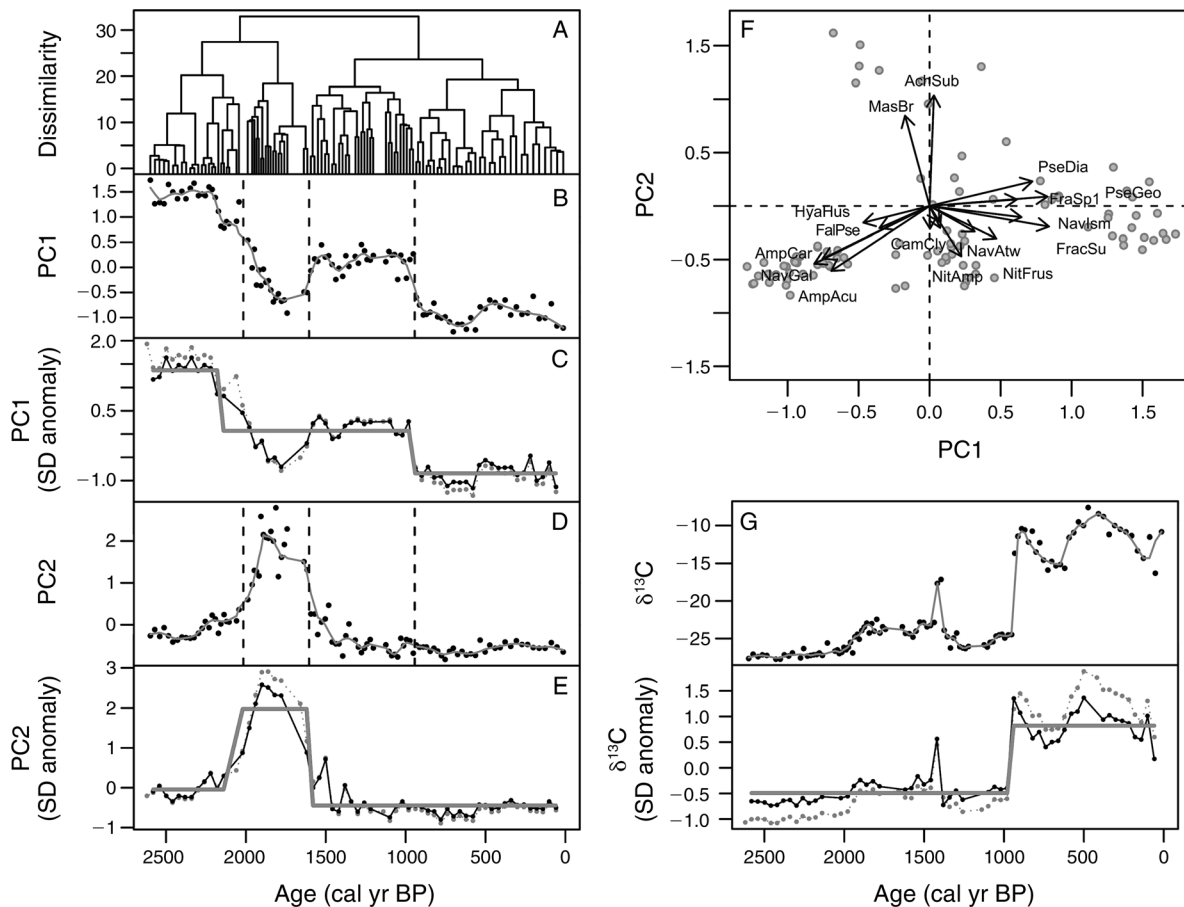


FIG. 2. Change point detection methods and ordination results to determine major trends in the diatom assemblage and $\delta^{13}\text{C}$ data (Step 1 in the framework outlined in Fig. 1). (A) Constrained cluster analysis on the diatom assemblages. Temporal series of (B) PC1 and (D) PC2 of the diatom assemblages plotted against time, with a lowess smoother fitted to the PC scores to demonstrate the main trends in assemblage composition. The dotted lines indicate the major transitions identified by the constrained cluster analysis. Changes in diatom assemblage composition identified using the STARS algorithm (Rodionov 2004, 2006) on (C) PC1 and (E) PC2. The gray dashed lines represent the standardized, 40-year binned data; the black lines are the white-noise filtered series, while the thicker dark-gray line depicts the changes in mean identified by the STARS algorithm over the course of the record. (F) The PCA plot on which these change point detection methods are based. A list of species codes is provided in Appendix E. (G and H) The temporal series of the $\delta^{13}\text{C}$, with (G) the same lowess smoother and (H) STARS identified changes in mean.

Mangrove–microbial mat dynamics

The stable carbon isotope signature from the core shows low and stable values between 2600 and 2000 cal yr BP (mean = -27.1‰), slightly higher and more variable values between 2000 and 1350 cal yr BP (mean = -23.7‰), and a major shift (mean = -12.0‰) at 945 cal yr BP (Fig. 2G). This major shift at 945 cal yr BP was the only transition identified in the mangrove data set over the past 2600 years (Fig. 2H). Since it corresponds with obvious changes in core lithology, it represents an abrupt transition from a mangrove-dominated ecosystem to the microbial mat found present in the lagoon at the present day (Seddon et al. 2011a).

Therefore, using this approach we identified three distinct periods of change in diatom assemblage or mangrove–microbial mat dynamics over the past 2600 years: Regime Shift 1 (RS1), 2600–1610 cal yr BP;

Regime Shift 2 (RS2), 1990–950 cal yr BP; and Regime Shift 3 (RS3), 1590 cal yr BP–present (Table 1).

Non-linear regressions

Across RS1, the best model (lowest AIC) used to describe changes in both $\delta^{13}\text{C}$ and diatom assemblages was a sigmoidal change around 2000 cal yr BP (Fig. 3A, B) (exponential terms in both models significant at $P = 0.05$). In contrast, the best model used to describe the changes in Ti influx was a double step change in mean, with break points at 2300 and 1920 cal yr BP (Appendix D: Table D.1). A linear relationship found between Ti influx and diatom assemblages across this transition was removed after correcting for autocorrelation (Appendix D: Table D.4), but a smooth-sigmoidal relationship was observed between PC1 of the diatom assemblage and $\delta^{13}\text{C}$ (Fig. 3G) (exponential term significant at $P = 0.05$).

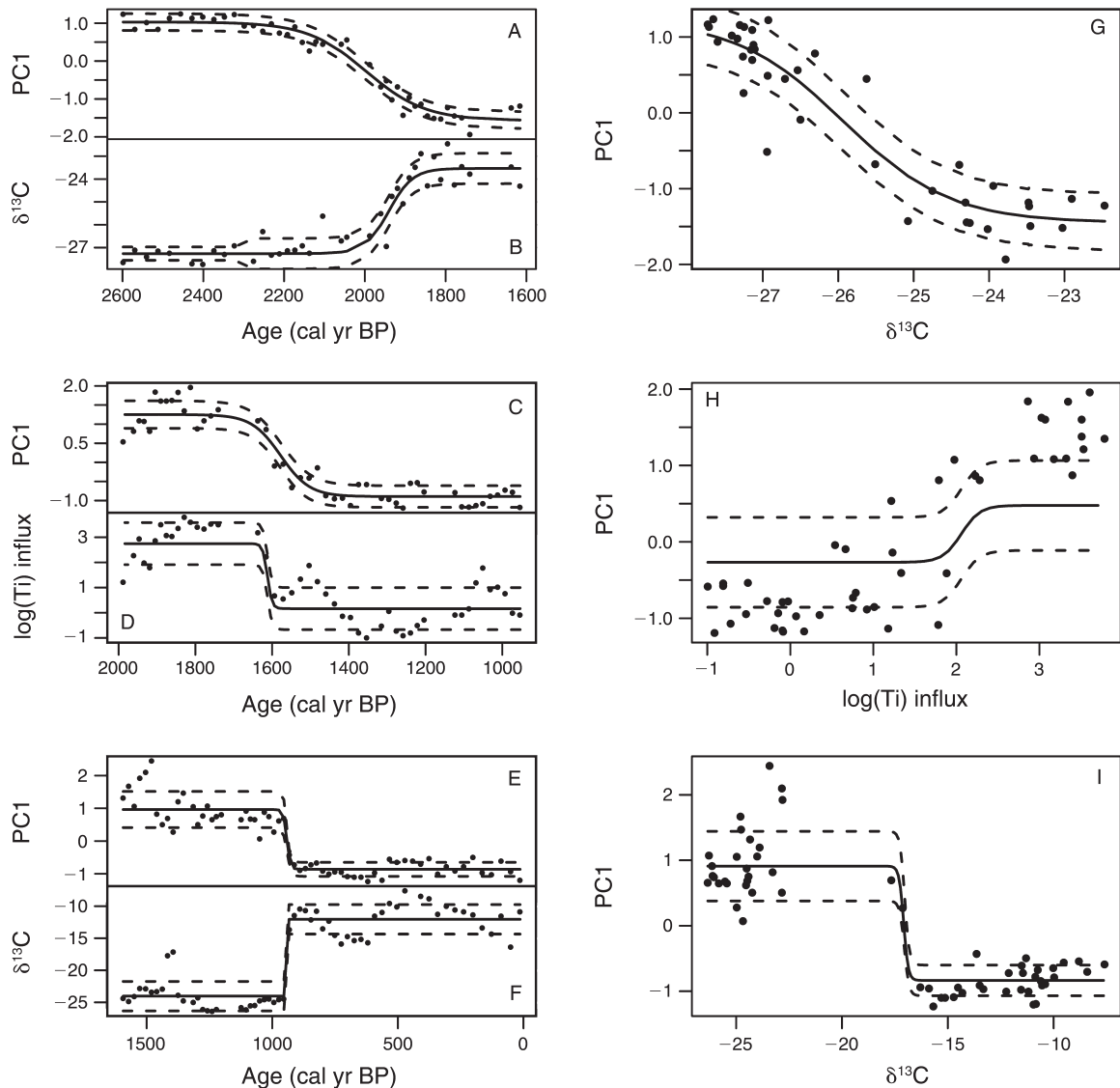


FIG. 3. Results of the nonlinear regressions run on the three major assemblage transitions identified in the diatom-assemblage data (Steps 2 and 3 of the framework presented in Fig. 1). Diatom assemblages (PC1) are in panels A, C, and E, environmental variables are in B, D, F. The best models to describe the shifts in the temporal series were estimated using nonlinear regression. Response plots (G, H, I) demonstrate the relationship between the environmental variables and diatom assemblage over the three regime shifts. Dashed lines represent ± 1 standard error estimates.

In RS2 a step-like sigmoidal drop in Ti influx (difference in means at break points using step model significant at $P=0.05$) was complemented by a smooth-step change in PC1 around 1600 cal yr BP (Fig. 3C, D) and a sigmoidal relationship was observed between the two variables (Fig. 3H), although the uncertainty estimates for the exponential term in this model were large following correction for temporal autocorrelations (3.3 ± 3.1 , (± 1 SE), $P=0.28$).

Across RS3, sharp changes in both PC1 of the diatom assemblage and $\delta^{13}\text{C}$ signature were observed at 945 cal yr BP (Fig. 3E, F), in contrast to a very small (sigmoidal) drop in Ti influx at 900 cal yr BP (Fig.

4A, B). The relationship between PC1 and the $\delta^{13}\text{C}$ signature was best modeled as a sharp-sigmoidal (i.e., threshold response) (differences in mean across break-points, significant at $P=0.05$) (Fig. 3I). In contrast, a quadratic function was selected as the best model between $\delta^{13}\text{C}$ and Ti influx, although all three models tested here demonstrated poor fit. Once an autocorrelation term had been added, this model failed to converge, and no appropriate model was found for this response function. Therefore, we further split these data into two subsets (i.e., pre- and post-transition point), and fitted individual linear models separated by the change in lithology at 945 cal yr BP although the trends

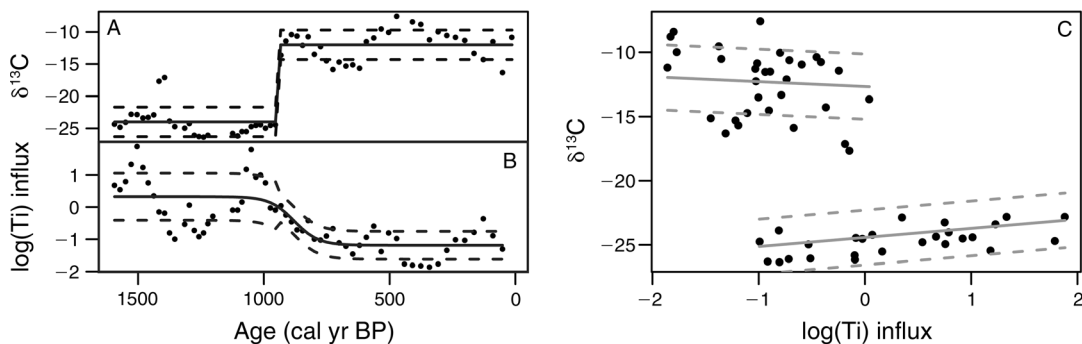


FIG. 4. Results of the nonlinear regressions run on the change point identified in the stable carbon-isotope ($\delta^{13}\text{C}$) data (mangrove-microbial mat dynamics). Stable isotope data are in panel (A), environmental data (Ti influx) are in panel (B). The best models to describe the shifts in the temporal series were estimated using nonlinear regression. The response plot (C) demonstrates the relationship between Ti influx and local mangrove dynamics over the regime shifts. All models had a poor fit in the response plot in panel (C), so we split the data at 945 cal yr BP and fit two separate linear models (grey lines). Original units for Ti influx are $\mu\text{g}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$. Dashed lines represent ± 1 standard error estimates.

in these individual models remained nonsignificant at $P = 0.05$ (Fig. 4C).

DISCUSSION

Environmental variability in Diablas lagoon

A detailed discussion of the environmental changes occurring in Diablas lagoon was published in Seddon et al. (2011a); here we provide a brief description for context. Between 2600 and 2000 cal yr BP, low $\delta^{13}\text{C}$ values indicate a stable environment in which sedimentation was dominated by the accumulation of mangrove leaf litter on the surface of the lagoon (Fig. 2G). Thus, a mangrove community was likely locally present within the lagoon at this time. The diatom assemblages found in this period are opportunistic, fast-reproducing taxa typical of coastal-lagoon environments with brackish-euryhaline waters, and are similar to those observed, for example, in the Baltic Sea (Stabell 1985, Weckström and Juggins 2006).

The first major environmental disturbance event occurred ~ 2000 cal yr BP, when step increases in Ti influx indicate a period in which the basin was more susceptible to tidal disturbance. Peaks in Ti influx were also shown to occur in line with peaks in grain-size data from a nearby lake sediment core, which act as a proxy for increases in the strength and intensity of the El Niño Southern Oscillation (ENSO) (Conroy et al. 2008). Since this occurred around the same time as increases in the inferred salinity derived from a diatom salinity transfer-function, down-core variability in Ti may be linked to changes in ENSO via increased storm-surge activity (Seddon et al. 2011a).

The diatom assemblages and mangrove ecosystem dynamics exhibited responses to this set of disturbance events (Fig. 3A). A shift to higher, more variable $\delta^{13}\text{C}$ values likely indicate a small amount of microbial mat growth, and the fragilarioid diatom assemblage was replaced by one dominated by *Achnanthes submarina*. Other taxa in this zone are associated with higher

salinity conditions, and have been found living in euryhaline microbial mats on other locations on Galápagos (Seddon 2010, Seddon et al. 2011b). Thus, we interpret these data to represent a change in diatom habitat conditions linked to the opening of the mangrove canopy and increases in salinity driven by increased tidal influence. The diatom assemblages tracked the environmental changes in the lagoon when these conditions were alleviated (Fig. 3C, D).

At 945 cal yr BP, the stable isotope evidence points to a major transition from a mangrove community to a microbial mat (Fig. 4A). Microbial mats are predominantly composed of cyanobacteria and develop either in open shallow marine littoral or intertidal zones subject to water level changes (Witkowski 1990, Krumbein et al. 2003). They are often associated with dryer conditions (Sachs et al. 2010). Prior to this major shift there were two small peaks in the Ti influx data at 1500 and 1050 cal yr BP, reflecting potential minor tidal disturbances, but these were an order of magnitude lower than the peaks in Ti influx after 2000 cal yr BP and in general, the very low values in Ti influx after 1500 cal yr BP indicate reduced influence of disturbances at this time (Fig. 4B). The diatom assemblages were dominated by *Navicula* and *Amphora* taxa after 945 cal yr BP and tracked the habitat shifts related to the microbial mat transition.

Extrinsic vs. intrinsic regime shifts

The framework developed for this study enables a robust interpretation of the ecological responses to environmental change in the Diablas lagoon. For the diatoms, statistical modeling of both the ecological and environmental paleoecological time-series provides evidence that the three major changes in assemblage structure closely tracked either (1) changes in tidal disturbance regime, or (2) changes in habitat conditions related to mangrove-microbial mat dynamics (Fig. 3). Since step changes in an ecological variable occurred at the same time as a step changes in the environmental

TABLE 2. Summary of dynamics of regime shifts identified in the coastal lagoon.

Period	Ecological variable	Ecological dynamics	Environmental variable	Environmental dynamics	Relationship	Forcing
RS1	diatoms	sigmoidal	$\delta^{13}\text{C}$	sigmoidal	smooth sigmoidal	extrinsic
RS2	diatoms	sigmoidal	Ti influx	sharp-sigmoidal step	sigmoidal	extrinsic
RS3	diatoms	sharp-sigmoidal step	$\delta^{13}\text{C}$	step	sharp-sigmoidal threshold	extrinsic
RS3	mangroves	sharp step	Ti influx	minor sigmoidal	dual relationship	intrinsic

drivers, we conclude that diatom assemblage changes represent extrinsically forced regime shifts (Table 2).

In RS1, for example, the transition to the *Achnanthes submarina*-dominated assemblage was related to the shift to slightly higher $\delta^{13}\text{C}$ values that are indicative of the opening of the mangrove canopy (Fig. 3A, B, G). This, in turn, appears to be associated with increased rates of erosional influx into the basin (i.e., Ti influx), and indicates a set of major environmental disturbances occurring in the lagoon at this time. The alleviation of these conditions occurring in RS2 (represented by a step change in Ti at 1600 cal yr BP) was also closely followed by a slightly smoother, step change in diatom assemblages in RS2 (Fig. 3C, D, H) as these conditions alleviated. The smoothed-sigmoidal relationships (i.e., close to linear) observed between $\delta^{13}\text{C}$ and diatom assemblages in RS1 provide further evidence of the simple, extrinsically forced dynamics in this regime shift. Note that although a sharp threshold-type relationship was observed between diatom assemblage PC1 and the mangrove–microbial mat transition (Fig. 3I), it is clear this transition was also extrinsically forced.

Our evidence of extrinsically forced dynamics in diatom assemblages from a paleoecological record contrasts with a number of recent studies suggesting that they are possible examples of intrinsic regime shifts. For example, it has been suggested that abrupt changes in diatom assemblages from Baldeggersee, Switzerland (Lotter 1998) reflected transitions between alternative stable states (Scheffer 2009). Similarly, a study from Lake Erhai in China reported increases in variance in the ordination axis of a diatom assemblage in response to nutrient loading (Wang et al. 2012). Although this was cited as possible evidence of a critical regime shift, numerical support for this interpretation remains inconclusive at present (e.g., Carstensen et al. 2013). Our study, which tested both response and control variables over the regime shift periods, indicates that the diatom assemblages likely responded in line with large environmental perturbations, rather than a set of internal biological feedbacks and locally driven factors linked to intrinsically driven ecological change. This follows from other studies in which the abrupt changes in diatom communities were found to be driven by large, external forcing (e.g., Bradshaw et al. 2005, Sayer et al. 2006, Randsalu-Wendrup et al. 2012). These results are likely the result of the rapid generation times of diatoms relative to the timescales observed in the paleoecological

record, enabling fast responses to external drivers in the coastal lagoon (Hsieh and Oman 2006).

The mangrove–microbial mat dynamics provide a contrasting example to the diatom assemblage responses observed here. The step change in $\delta^{13}\text{C}$ at 945 cal yr BP represents the transition from a mangrove to microbial mat-dominated community at the present lagoon site. Although a sigmoidal-step change in Ti influx data was identified between ~ 1000 –900 cal yr BP, the magnitude of these changes was rather small compared to those observed earlier in the record. Aside from the small tidal disturbances to which the mangrove–microbial mat dynamics appeared to respond indirectly at 1600 and 1050 cal yr BP, evidence from the sediment record presented here indicates that, despite the major transition in sediment type from mangrove to microbial mat, environmental conditions remained relatively stable at this time.

Given this evidence, there are two possible explanations for the major shift in ecological dynamics over this period. The first is that an alternative driver, not measured by the variables used here, was responsible for the abrupt mangrove–microbial mat shift. Conroy et al. (2009), for example, documented a period of cooler sea surface temperatures in the Eastern Tropical Pacific after 1000 cal yr BP, which would have resulted in drier conditions in the coastal regions of Galápagos. However, a salinity reconstruction from the same core indicates only very gradual increases in conditions across this period (Seddon et al. 2011a), and extensive evidence of regional-scale cooling is not present in this record. In addition, a large-scale climatic driver might be expected to have driven similar large responses in lagoon sites nearby. This is not the case in a record from San Cristobal Island (Seddon 2010), while sediments collected from cores from a network of sites around the Diablas wetlands indicates that the major mangrove–microbial mat transition was only present at our coring site (D. Nelson, *personal communication*). Therefore, there remains limited evidence for a regional-scale ecosystem response to a large external driver at this time. One cannot rule out, however, another local-scale extrinsic driver not identified in these sediment records.

A second possibility is that this transition represents an intrinsic regime shift. The local environmental changes reconstructed from the variables used in this study indicate relatively stable environmental conditions across the time period. There was limited influence of only minor tidal disturbance events, and only gradually

increasing salinities reconstructed indicate smaller-scale responses to any larger-scale climate variability (e.g., Conroy et al. 2009). In addition, the dual relationship identified between disturbance indicator (Ti influx) and $\delta^{13}\text{C}$ is potential evidence of complex, nonlinear dynamics. Since theoretical modeling studies indicate that systems close to threshold transitions can experience amplified responses to small disturbance events (e.g., Scheffer et al. 2001), any one or a combination of these variables interacting across scales (e.g., Booth et al. 2012), could have combined to drive the local transition to microbial mat at the coring site.

Implications

Detection and understanding of regime shifts has become an increasing research focus within both paleoecology and ecology. There are numerous examples of abrupt changes from both aquatic (Kröpelin et al. 2008, Sayer et al. 2010) and terrestrial (Parker et al. 2002, Shuman et al. 2009) records, but uneven sampling resolution, age uncertainties, and obtaining independent environmental records can make the identification of regime shifts in paleoecological data a major challenge. As a result, these studies have remained largely qualitative in nature (but see Randsalu-Wendrup et al. 2012). One strength of our study, therefore, is the integration of a set of clear detection methods to investigate the timing, drivers, and ecological dynamics in response to changes observed in the local environment in such data sets to (1) identify periods of assemblage change; (2) test for a series of hypothetical relationships (i.e., linear through to threshold) between ecological response variable and environment; and (3) test for the relative importance of intrinsic and extrinsic dynamics in response to environmental perturbations.

By applying these techniques to our record from a Galápagos coastal lagoon, we were able to identify regime shifts in diatom assemblage and coastal wetland habitat types. While the transitions in the diatoms closely tracked the sequence of disturbance (RS1), recovery (RS2), and habitat shift (RS3) that have occurred over the past 2600 years, mangrove–microbial mat dynamics demonstrated a highly nonlinear relationship, with possible evidence of an intrinsic regime shift. The framework has broad implications for testing regime shifts in other systems. When used in combination with multiproxy data sets, it is possible to extract robust interpretations into the underlying dynamics of regime shifts in the paleoecological record.

ACKNOWLEDGMENTS

The authors thank Parc Nacional Galápagos for providing research permits, and the Fundacion Charles Darwin (FCD) for aiding the fieldwork logistical arrangements. Simon Haberle, Iona Flett, Jim Neale, Henk Heijnis, Iain Robertson, Emily Coffey, Benson Schliesser, and Salome Maldonado have aided in the sediment sampling in this study. Melanie Leng and the NERC Geoscience Laboratory, Keyworth, and the ICP facility at Royal Holloway, University of London helped analyze and interpret the stable isotope and geochemistry data.

We thank John Birks for providing useful comments on an earlier version of the manuscript and Richard Telford and Joseph Chipperfield for providing statistical advice.

This research was supported by a UK Natural Environment Research Council postgraduate studentship (A. W. R. Seddon) and grant NE/C510667/1 (K. J. Willis, C. A. Froyd), the British-Polish Young Scientists Program funded by the British Council and Polish Ministry for Science and Higher Education (A. W. R. Seddon), by the Polish National Science Centre in Cracow, grant number N 2012/04/A/ST10/00544 within the Maestro program (A. Witkowski) and by the Climate Change Consortium of Wales (C. A. Froyd). This publication is contribution 2095 of the Charles Darwin Foundation for the Galápagos Islands.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–E and the Supplement are available online: <http://dx.doi.org/10.1890/13-1974.1.sm>