Climatic Change
DOI 10.1007/s10584-014-1077-4

Downscaling the non-stationary effect of climate forcing on local-scale dynamics: the importance of environmental filters

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Received: 19 September 2013 / Accepted: 2 February 2014

Abstract Large-scale climatic variability exerts a strong influence on local-scale environmental patterns and processes. However, disentangling the effects of global climate forcing from observed patterns in local processes requires robust understanding of the underlying patterns of temporal variability and consideration of the specific setting in which these processes take place. Here, we examine the influence of intermediate-scale environmental factors in modulating the effects of the North Atlantic Oscillation (NAO) on long-term water level dynamics in natural lakes. Lakes are ideal systems to study these relationships because of their acute sensitivity to environmental change and their linkages with multi-scale processes through the hydrological cycle. Using a novel combination of analytical tools, we show that the coupling between the NAO and water level dynamics is markedly nonstationary (i.e., time-frequency variant) and strongly lake-specific, filtered through the particular weather and environmental settings of lakes and their catchments. We conclude that to fully understand the nonstationary interplay between climate and ecology, we need first to disentangle the intermediate links between climate and different embedded environmental factors related to the process of interest. This knowledge should enhance significantly our ability to produce adequate long-term water resource management strategies, to preserve biological diversity and to achieve sustainable development under a globally changing climate.

Electronic supplementary material The online version of this article (doi:10.1007/s10584-014-1077-4) contains supplementary material, which is available to authorized users.

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Published online: 22 February 2014

1 Introduction

Large-scale climate fluctuations influence ecological patterns and processes by modifying local weather conditions, such as temperature, precipitation and wind, over large geographic areas through atmospheric teleconnections (Stenseth et al. 2002). Global climate indices related to prominent atmospheric modes, such as the North Atlantic Oscillation or the Pacific Decadal Oscillation, have thus long been used as proxies for the effect of climate forcing on terrestrial and aquatic ecosystems (Stenseth et al. 2003). By integrating information on a variety of weather parameters across time and space, these large-scale climatic indices often convey more ecologically meaningful information than isolated weather descriptors (Hurrell and Deser 2009). Indeed, high spatial coherence in ecological responses to global climate variability (as described by these indices) over remarkably large areas is well documented (Blenckner et al. 2007).

Projecting the effects of large-scale climate forcing on processes occurring at much finer spatial resolutions is a complex task (Stenseth et al. 2003), requiring consideration of factors that reflect conditions across intermediate scales (Levin 1992; Turner 2010). The ultimate expression of external climate forcing on local scale processes can be regulated strongly by geographical, orographic and site-specific factors, including biotic and abiotic components, even within regions where high spatial climatic coherency can be expected (Straile et al. 2003; Blenckner et al. 2007). Traceability of the effect of global climate forcing on local environmental processes is also hindered by the issue of nonstationarity (Stenseth et al. 2003). Stationarity, implying constancy in the statistical properties (i.e., mean and variance) of a time series over time, is a key mathematical assumption underlying most traditional approaches to time series analysis (Wei 2006). However, this is rarely, if ever, attained in natural time series (Rao et al. 2003). When the distribution of variance at different frequencies is nonstationary, the local behaviour of a process becomes key to describing the true signal (Torrence and Compo 1998) and understand its ecological implications (Matthews and Gonzalez 2007). Consequently, inferences from stationary models are likely to provide a poor representation of the underlying environmental processes and can lead to strongly biased interpretations of their ecological effects (Mumby et al. 2011). Further, these errors are likely to be exacerbated because of on-going (Schär et al. 2004) and predicted (Meehl et al. 2007) changing trends in climate variability and the complex influence of environmental variability on all levels of ecological hierarchy from organisms to ecosystems (Ruokolainen et al. 2009; García Molinos and Donohue 2010; O'Connor and Donohue 2013). Studying the relationship between these two factors is therefore necessary to fully understand the interplay between climate and ecology.

Lakes are ideal systems to study these processes because of their acute sensitivity to environmental change and their linkages with multi-scale processes through the hydrological cycle (Williamson et al. 2009). The ultimate effect of climate forcing on individual lake processes is likely to be modulated by different environmental filters, which may include geographic, orographic and site-specific factors, including biotic and abiotic components (Straile et al. 2003; Blenckner et al. 2007). Natural water level fluctuations in lakes, encompassing cyclical seasonal components superimposed on long-term trends and stochastic variability, comprise one of the most important physical processes affecting whole lake ecosystems (Zohary and Ostrovsky 2011). These are subject to frequent temporal shifts and changes linked to the nonlinear, stochastic or transient effects of external factors such as global climate forcing (Pasquini et al. 2008) and human activities (Zhang et al. 2006).

Here, we use a novel combination of complementary analytical tools to examine the long-term (30 year) monthly water level series of natural lakes in Ireland in order to (i) investigate the existence of links between long-term (inter-annual to inter-decadal) cycles of water level fluctuations and the North Atlantic Oscillation, the key large-scale climate driver in the region, and (ii) test whether those links are moderated by landscape-scale environmental filters. Importantly, our analyses enable us to trace patterns in the time-frequency domain and test our hypotheses under nonstationary conditions. Understanding these links is crucial to management and conservation because the functioning of whole lake ecosystems is influenced strongly by the natural fluctuations in water levels occurring at different temporal scales (Hofmann et al. 2008).

2 Methodology

2.1 Data

We examined monthly mean water level data from 30 years of continuous time-series (April 1979 to March 2009) from 18 natural lakes in Ireland (Appendix A). The monthly series of the PC-based version of the Hurrell North Atlantic Oscillation (NAO) Index (Hurrell 1995) was used as a proxy for external climate forcing. The North Atlantic Oscillation comprises the most important mode of climate variability operating in the North Atlantic, exerting a strong influence on the weather conditions over most of Europe (Hurrell and van Loon 1997). The PC-based NAO index, which defines the time series of the leading empirical orthogonal function of sea level pressure anomalies over the Atlantic sector, gives improved representation of the full spatial patterns of the NAO compared with the more traditional station-based NAO index of tracking seasonal movements of the Icelandic low and Azores high, while also being less prone to the interference of small-scale transient meteorological phenomena (Hurrell and Deser 2009).

Twenty explanatory variables, comprising measures of conditions across six different categories; precipitation, temperature, catchment and lake morphology, landscape position, land use and degree of anthropogenization (Table 1), were used to investigate the influence of environmental filters in downscaling the effects of the NAO on water level fluctuations. All variables within each of the lakes and their respective catchments (i.e. the area upstream the lake outlet) were GIS-derived from a variety of data sources (Appendix A).

2.2 Data analyses

Our analysis comprised the following steps (Appendix B):

i. Find the local correlation in time-frequency space between the NAO and the water levels for each lake using wavelet coherency analysis. Wavelet analysis is well suited for the analysis of nonstationary, aperiodic and transient time series because it performs a time-scale decomposition of a signal revealing how the periodic components of a time series change over time (Cazelles et al. 2008b). Signal decomposition is performed using the wavelet transform, which decomposes a signal over specific wavelet functions that adapt their form to the frequency of the signal as they are translated over time allowing for a good localization in time and frequency. Wavelet coherency is a generalization of wavelet analysis that measures the cross-correlation between two time series as a function of frequency (Cazelles et al. 2008a). Graphical representation of the wavelet coherency is done through the coherency spectrum which allows us to track the temporal evolution of the dominant modes of correlation between the signals as a surface plot expressing the

Table 1 Environmental variables used to explore the nonstationary patterns of covariation between the North Atlantic Oscillation index and lake water levels with their respective mean and range (n=18 lakes)

Variable (Acronym)	Description	Mean	Range
Precipitation			
Annual precipitation (Prec)	Mean total annual precipitation (mm year^{-1})	1401.8	1026.9–2258.7
Precipitation variability (CV_Prec)	Coefficient of variation in total annual precipitation	0.16	0.11–0.31
Temperature			
Annual temperature (Temp)	Mean annual temperature (ºC)	9.02	8.2–9.72
Temperature variability (CV_Temp)	Coefficient of variation in mean annual temperature	0.06	0.048–0.071
Evapotranspiration (Evap)	Annual evapotranspiration (mm year^{-1}) (Allen et al. 1998)	489.8	473–525.5
Morphology			
Catchment area (CA)	Lake catchment area (km^2)	130.8	3.2–566.9
Surface area (SA)	Lake surface area (ha)	308.4	23.2–1381.1
Shore length (SL)	Lake shore length (km)	19.2	2.6–69.8
Shoreline development ratio (SDR)	Ratio of lake shore length to the perimeter of a circle of equal area to that of the lake	3.2	1.5–7.7
Landscape position			
Lake order (LO)	Landscape position as connections to streams (Martin and Soranno, 2006)	3.5	1–5
Drainage density (DD)	Density of tributary network in catchment (km km^{-2})	1	0.3–2.3
Catchment slope (CS)	Mean catchment slope (%)	5.6	2.8–10.7
Land use			
Runoff coefficient (C)	Catchment-weighted mean runoff coefficient (Viessman and Lewis 2003) based on mean CORINE land cover categories and soil permeability classes (Cecchi et al. 2007)	0.79	0.6–0.97
Artificial use (Ar)	Proportion of artificial land use (CORINE Level 1 Class 1)	0.45	0–2.21
Agricultural use (Ag)	Proportion of agriculture (CORINE Level 1 Class 2)	52.9	0–97.1
Forest use (For)	Proportion of natural vegetation (CORINE Level 1 Class 3)	15.7	0–54.4
Wetlands use (Wet)	Proportion of wetlands (CORINE Level 1 Class 4)	24.6	0–79.6
Anthropogenic			
Abstraction ratio (AR)	Annual volume abstracted from a lake to annual run-off calculated by the rational method (Viessman and Lewis 2003)	0.04	0–0.32
Mean population (Pop)	Mean catchment human population density based on electoral division censuses between 1979 and 2011 (n=8; inhabitants km^{-2})	20.1	1.8–43.8
Population growth rate (Pop_rate)	Regression slope of population density over time based on electoral division censuses between 1979 and 2011	0.06	−0.11–0.27

strength of the correlation between the time series across time and scale (e.g. Fig. 2). We used the continuous Morlet wavelet, an established wavelet function that has the practical advantage of allowing interpretation of the wavelet scale in terms of the Fourier period (Torrence and Compo 1998). Statistical significance of the patterns exhibited by the wavelet coherency spectrum was assessed by comparison of the observed spectra with 10^3 bootstrapped surrogate series (i.e., series generated randomly with equal mean and variance) at an α-level of 0.05.

ii. Comparison of NAO-water level coherency patterns among lakes. One of the main limitations of wavelet analysis is that there is not a straightforward extension of the bivariate case onto multivariate analysis, making it difficult to look for common time-frequency patterns underlying the spectra of multiple time series simultaneously (Cazelles et al. 2008a). Rouyer et al. (2008b) proposed a solution based on the Maximum Covariance Analysis (MCA) criterion (Appendix B). Essentially, the method consists of a singular value decomposition performed on the covariance matrix between each pair of spectra by which a given number of axes of the MCA are extracted accounting for a specified proportion of the total covariance (99 % in our analysis). The common frequency-time patterns between the two spectra are thus extracted in decreasing order of importance and this information is used to estimate the distances between each pair of spectra with which a dissimilarity matrix is finally generated suitable for traditional ordination methods (Rouyer et al. 2008a).

iii. Use the coherency dissimilarity matrix to test the importance of different environmental filters in moderating patterns of covariation between water levels and the NAO. For this purpose, we use distance-based linear modeling (DISTLM; Legrende and Anderson 1999; McArdle and Anderson 2001) which offered the necessary flexibility of allowing choice of any distance measure (Anderson and Gorley 2007). Given the relatively small sample size (n=18), we used the first principal component (PC1) of the standardized variables within each environmental category ($|r|_{\text{within-category}}>0.5$) to reduce the number of predictors (Table 2). The PC1s captured a high proportion (73.6±5.6 %; mean ± SD, n=6) of the total variability in the data within each category, and may, therefore, be considered good descriptors of the original variables. The resulting six synthetic variables (Table 2) were subsequently used as predictors in the linear models. Because the purpose of our analysis was exploratory (i.e., we did not intend to find an optimal model for prediction but rather to explore the relationships between predictor and response variables), estimates of the relative importance of each predictor variable were assessed jointly using marginal permutation tests (Anderson and Gorley 2007), indicating their significance and the proportion of total variance explained when considered alone, and their Akaike weights ($w_+(j)$; Appendix C). Where the Akaike weight of a model provides an unbiased measure of its likelihood, representing the relative strength of evidence for the model given the data and the set of competing models, the Akaike weight of a variable can be interpreted as the evidence of the importance of that variable relative to all the others given the set of models considered (Burnham and Anderson 2002). All permutation tests were based on 9,999 permutations of the residuals under a reduced model (Anderson and Ter Braak 2003).

All water level time series were normalised before analysis to enable comparisons among lakes. Given the dominance of the annual seasonal cycle on the local wavelet power spectra, we used deseasonalised series to aid interpretation of the power existing at lower frequencies. Removal of the seasonal component was done by subtracting the monthly historical means from monthly data series. Wavelet computations were run using R (R Development Core Team

Table 2 First principal components used in the distance-based redundancy models with their constituent environmental variables, with their absolute loadings in parentheses, and the proportion of total variance explained by each first component. See Table 1 for key to variable abbreviations

PC1	Variables	Variance explained (%)
Precipitation	Prec (0.71); CV_Prec (0.71)	80.6
Temperature	CV_Temp (0.63); Evap (0.6); Temp (0.5)	73.9
Morphology	SL (0.56); CA (0.5); SDR (0.48); SA (0.46)	75.6
Landscape position	DD (0.62); LO (0.56); CS (0.56)	76.7
Land use	Ag (0.52); Wet (0.48); C (0.46); Ar (0.46); For (0.34)	69.5
Anthropogenic	Pop_rate (0.69); Pop (0.65); AR (0.32)	64.9

2011). Distance-based redundancy analysis was done using the DISTLM and dbRDA routines in PERMANOVA+ (Anderson and Gorley 2007) for PRIMER 6.1.11 (PRIMER-E Ltd., Plymouth, UK).

3 Results

All deseasonalised water level series presented strong overall similarities in global power (i.e., time-averaged distribution of variance across scales) with statistically significant dominant modes of inter-annual fluctuation associated mainly with the 6–8 year (83 % of lakes), the 2–4 year (61 %) and the 4–6 year (33 %) period bands (Fig. 1; Appendix D). Significant near-decadal and inter-decadal fluctuations were also present though less common. Despite overall similarities in global power, all lakes had different significant nonstationary patterns of local

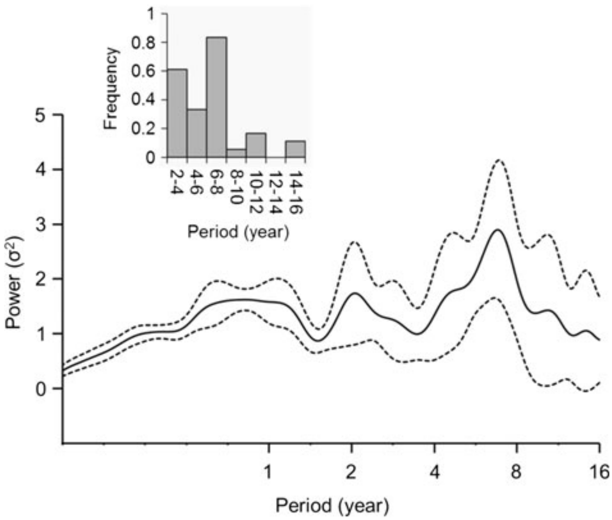

Fig. 1 Mean (± S.D.; n=18) global power spectrum for all lake series. The global spectrum is a time-averaged one-dimensional representation of the overall power (i.e., variance) associated with each periodicity in the series and is therefore comparable to the classical Fourier spectrum. The inner insert provides the proportion of statistically significant (P<0.05) periodicities found in the study lakes based on the individual global spectra for the lakes (Appendix D)

correlation between the NAO index and water level fluctuations (Fig. 2). Over time, the 1980s appear as the most similar decade among the lakes with high coherency distributed broadly over a wide frequency range but concentrated in particular on the 2–8 year period band (Fig. 2). However, coherency patterns appeared to diverge among lakes from the late 1980s. While high coherency was still persistent at near-decadal to inter-decadal periodicities (>8 years), at intermediate inter-annual frequencies (2–8 year period band), signals displayed strong intermittent transient behaviour with frequent periodicity shifts over time towards higher or lower periodicities (Fig. 2).

No single model of the coherency-based dissimilarity matrix based on the suite of first principal components (as proxies for the environmental variables) emerged as clearly superior (Appendix C). From the full set of 63 models, the subset of competitive models ($\Delta_i \leq 4$; $n=39$) accounted for an overall Akaike weight of 0.9 indicating a 90 % chance that the best model was contained within this subset. Within these models, the multi-inference Akaike weights for the predictor variables ranged between a maximum of 0.45 for the PC1 representing local precipitation patterns (mean and variation) and a minimum of 0.24 for the principal component accounting for catchment and lake hydromorphology (Table 3). Land use related variables were similar in importance with precipitation whereas landscape position, anthropogenic and temperature descriptors ranked at intermediate positions. These results were consistent with those of the marginal permutation tests (Table 3), where only the principal components related to morphology and temperature did not account for a significant proportion of the overall variation in coherency-based dissimilarities among lakes when considered alone, though the latter was bordering on statistical significance and had similar relative importance to other significant PCs. The ordination plot based on the first two axes from the distance-based linear model including all significant predictor variables offered a reasonably good representation of the fitted model (accounting for 62.6 % of the variation) and accounted for 28.4 % of total among-lake variation in coherency dissimilarities (Fig. 3). The distribution of lakes in the plot followed a distinctive general gradient along the first axis from lakes experiencing more stable and drier weather with densely populated catchments, simpler hydrological networks and a less flashy profile on one side (with negative scores on the first RDA axis), towards lakes characterized by more variable and wetter weather, sparsely populated catchments, high hydrological responsiveness and more complex hydrological connectivity grouped on the other (Fig. 3). Wetlands, comprising mainly peat blankets, dominated the land use cover of the most responsive catchments, while agriculture was the major land use category for those lakes at the other extreme of the gradient (Fig. 3).

4 Discussion

Our study lakes showed complex and varied nonstationary patterns of significant local covariation between the North Atlantic Oscillation and water level fluctuations. Despite general similarities among lakes, patterns of covariation were lake-specific and appeared to be dependent on the particular meteorological, morphological, hydrological and anthropological characteristics of lakes and their catchments. With the exception of precipitation, all environmental filters shared similar weights in describing the observed variability of coherency patterns among lakes. This suggests strongly that this among-lake variability emerged as a result of multiple intermediate embedded processes, such as the interception and routing of water through the catchment or the use of water resources that moderated, over and across spatial and temporal scales, the effect of large-scale climate forcing on local water level fluctuations. Global water security for human use and biodiversity conservation is one of the

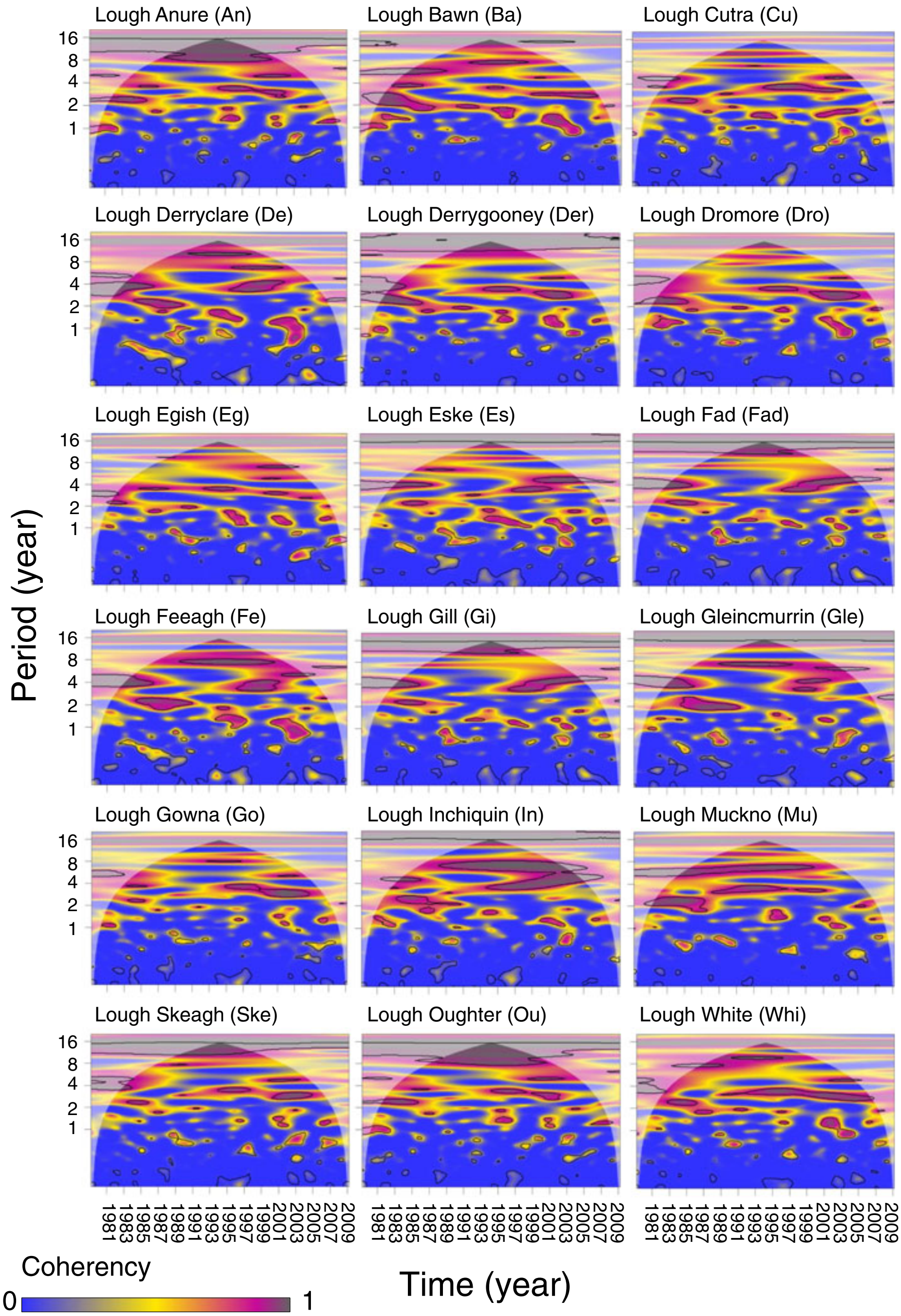

Fig. 2 Lake coherency spectra illustrating local covariation between the North Atlantic Oscillation index and water level fluctuations in the normalized and deseasonalized lake series. The coherency spectrum is presented as a heat plot of periodicities against time. Colour scales from low (*dark blue*) to high coherency (*magenta*). *Solid black lines* enclose statistically significant ($P \leq 0.05$) coherence regions based on 10^3 bootstrapped surrogate series. *Shaded regions* represent the cone of influence, where the signal can be distorted by the edge effects produced by zero padding

Table 3 Relative importance of each first principal component (PC1) in explaining the coherency-based dissimilarities between the NAO index and lake water levels assessed jointly by their multi-inference Akaike weights $w_{+}(j)$ computed from all the models (n_i) containing each variable within the selected subset of models (i.e., $\Delta_i \leq 4$; n=39), and marginal tests (9,999 permutations) indicating the proportion of variance explained by each PC in isolation. Significant values ($P \leq 0.05$) indicated in bold

PC1	n_i	$w_{+}(j)$	SS(trace)	Pseudo-$F_{16,2}$	P	Variance (%)
Precipitation	16	0.45	1.72	3.42	**≤0.0001**	17.6
Land use	16	0.44	1.68	3.33	**≤0.0001**	17.21
Temperature	15	0.32	0.85	1.52	0.059	8.15
Landscape position	15	0.31	1.12	2.07	**0.0074**	11.44
Anthropogenic	14	0.3	0.8	1.42	**0.041**	8.68
Morphology	14	0.24	0.63	1.11	0.3	6.46

major challenges of our time (Vörösmarty et al. 2010). These multi-factor interactions across spatial and temporal scales are therefore of great importance not only for the long-term planning of water resource management (Ford et al. 2011), but also because

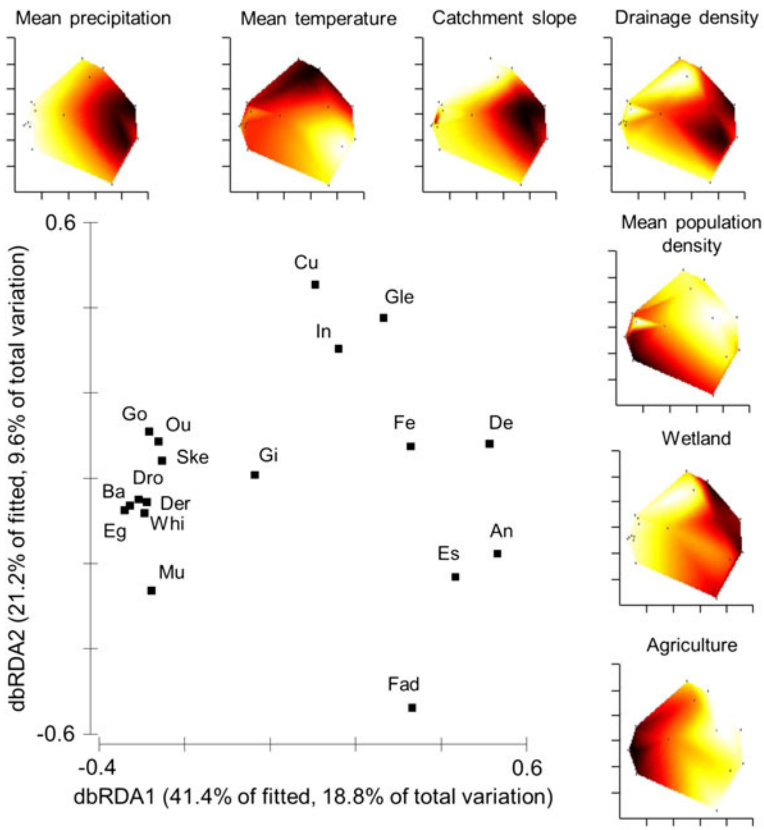

Fig. 3 Ordination plot displaying the first two axes from the distance-based linear model of observed coherency-based dissimilarities among lakes on selected environmental principal components. To aid interpretation, bicubic interpolated surface plots (with the same axes as the ordination plot) are provided for selected environmental variables within the region defined by the lake coordinates

inter-annual variations in water levels can be extremely important to biodiversity (Riis and Hawes 2002).

The dominant climatic influence that the North Atlantic Drift exerts on Ireland throughout the year confers a regime characterized by mild winters and cool summers lacking the extremes typical of other countries at similar latitudes. In contrast, Ireland is characterized by a moderate precipitation regime with high interannual variability, resulting in strong year-to-year fluctuations in the water balance (Daultrey 1996). This situation can have important consequences for lake water levels, in particular when wet-dry winters synchronize with the corresponding phases of the NAO (Kiely 1999). In the North Atlantic region, the NAO represents the foremost atmospheric mode of climate variability, exerting a strong influence on weather patterns over most of Europe throughout the year (Hurrell and Deser 2009). Positive values of the index are associated with stronger than average surface westerlies at mid-latitudes resulting in milder, wetter winters over north-west Europe. The geographical location of Ireland, on the Atlantic coastline of Europe between the NAO high and low centers of pressure, favors a strong fingerprint of the NAO on the climate of the island. Warmer temperatures, increased cloudiness and decreased radiation, stronger wind speeds, and higher precipitation and river discharge patterns have all been associated with high NAO phases; an effect typically stronger over the northern and western half of the country (Kiely 1999; Jennings et al. 2000).

Though the NAO drives important inter-annual and inter-decadal variability alternated with more stable periods (Hurrell and Deser 2009), it has its main spectral peaks at periodicities within the 2–4 and 6–10 year bands (Polonskii et al. 2004). These are in good agreement with the inter-annual periodicities observed in our water level series and correspond well with the observed significant coherency regions between the water level and the NAO. Interestingly, common patterns of variation between the NAO index and the water level series among the lakes diverged noticeably since the late 1980s when clear periodicity shifts in significant coherency developed in all lakes. This period of time matches a well-documented climate regime shift associated with a strong change in the North Atlantic Oscillation towards an almost uninterrupted lock in its positive phase ever since (Hurrell and Deser 2009). This strong climate shift has been associated with simultaneous and spatially coherent regime shifts in physical and biological processes in aquatic ecosystems across Europe (Blenckner et al. 2007). Though a strong correlation between the NAO and the hydrology, physicochemical properties, and ecology of European lakes has been suggested previously (Straile et al. 2003), our study is the first to provide evidence of the role of different intermediate-scale environmental filters in shaping those correlations across frequencies and over time. In Ireland, the main storm tracks pass to the northwest of the island from the Atlantic, producing a northwest to southeast decreasing gradient of precipitation. This variability in precipitation, which relate both to its mean and variance, is enhanced further during active phases of the NAO involving stronger (positive) or weaker (negative) westerlies over Ireland (Murphy and Washington 2001). Our results are highly consistent with this pattern; the lakes are distributed neatly along the first axis of the ordination plot from the distance-based linear model following a positive gradient towards a wetter and more variable precipitation regime. Given the intimate relationship between climate variability and the water cycle, the observed leading role of precipitation in explaining among-lake dissimilarities in patterns of covariance between the NAO and water level fluctuations highlights the importance of considering the differential effect of large-scale climate forcing on local weather parameters when applying global climate indices (Stenseth et al. 2003), even within relatively restricted geographical settings.

In spite of the key role of local- and regional-scale weather (precipitation) features, we found that several other non-climatic variables also accounted for a significant proportion of the dissimilarities among lakes in covariance patterns between the NAO index and water levels. This suggests strongly that the time-frequency interplay between global climate phenomena and natural processes is moderated significantly by local-scale environmental features in addition to regional climate variability (Blenckner 2005). Differences among our study lakes were driven mainly by factors describing the hydrological complexity and responsiveness of their catchments such as drainage density, catchment slope and land use. Catchments with steeper slopes and higher drainage density indicate a tendency towards prevalence of surface water over groundwater contributions and hence a flashy storm response. The dominant control exerted by catchment morphology on water flow paths is therefore linked directly to the hydrologic response of the catchment (Beven et al. 1988). The hydrological position of lakes within landscapes can also be an important factor filtering the effects of external climate forcing on lake dynamics (Umbanhowar et al. 2011). Lakes in small flashy upland catchments tend to be more vulnerable to climate change because of their relative sensitivity to shifts in precipitation and evaporation. Further, land use in these catchments was dominated strongly by peat formations. Runoff production in catchments dominated by peat blankets tends to be very flashy in nature with a rapid flow response even under low base flow conditions (Holden and Burt 2003). This high responsiveness to precipitation results from the combined effect of shallow water tables and low subsurface hydraulic conductivity with saturation-excess overland flow and near surface runoff as the dominant flow processes (Holden et al. 2007). As a result, lag times between rainfall peaks and discharge peaks in these catchments are typically of just a few hours and relatively insensitive to the spatial scale considered. Moreover, concentrated on the northwest quarter of the island, the lakes with these types of catchment are exposed to more variable and intense precipitation fuelled by the NAO. Given that the quantity, timing and variability of water inputs to a lake are all dependent on the complex interactions between the weather and the biophysical environment as water flows through the hydrologic cycle, this particular combination of hydrological behaviour and local weather conditions appear to be the key drivers behind the observed differences in covariation patterns between these peatland lakes and the other lakes in our study.

Our results suggest that anthropogenic pressures, as defined by the presence of water abstraction activities from lakes and the human population density of their catchments, play a significant role in modifying the influence of the NAO on lake water levels. Human development can alter catchment runoff and modify stream flow patterns through land transformation and use leading typically to increased flashiness and decreased groundwater recharge (Seth and Peters 2001). Nonetheless, the principal human pressure on water level regimes is thought to be water abstraction; reportedly the second most important anthropogenic disturbance of lakes in Ireland after diffuse nutrient pollution (Shilland et al. 2009). However, our abstraction data accounts only for water sourced directly from the lakes (i.e. it does not include water extracted from streams and wells within catchments). The significance of catchment human population density in explaining dissimilarities in patterns of covariance between water level fluctuations and NAO oscillations may therefore reflect a link between higher water demands in more densely populated catchments (Vörösmarty and Sahagian 2000). Further, human population metrics may also capture better temporal trends in demand as they go further back in time than abstraction records. Evaluating the ultimate effect of water abstraction is, however, difficult because of the poor temporal resolution of the data; a common problem encountered when studying the effects of abstraction on lake water level regimes (Becht and Harper 2002). A more meaningful analysis of effects of water abstraction will thus require the use of high resolution abstraction volume data from lakes and their catchments in the context of the overall water balance and the development of lake-specific hydrologic models. Because water withdrawal can potentially exacerbate the effects of external climate forcing (Meyer et al. 1999), this is clearly an urgent requirement for future research.

In conclusion, we found that the existing nonstationary coupling between the NAO and water level dynamics in natural lakes is modulated by different interacting factors operating at intermediate scales, such as the local weather and environmental conditions, which ultimately regulate the expression of the large scale climate driver on the local process. Consideration of multiple processes operating at different temporal and spatial scales is often necessary to appreciate fully how climate variability influences environmental and ecological processes (Straile et al. 2003). In face of increasing climate uncertainty (Meehl et al. 2007) and the apparent intensification of the global water cycle (Huntington 2006), a better understanding of the mechanisms by which these factors interact to produce spatial and temporal coherence in ecological responses to global climate variability is needed urgently to improve adaptive management strategies to a changing climate.

Acknowledgments We thank sincerely Tristan Rouyer for kindly providing the R-libraries that constituted the core of the wavelet analyses in this study. We acknowledge the E-OBS dataset from the EU-FP6 project ENSEMBLES (http://ensembles-eu.metoffice.com) and the data providers in the ECA&D project (http://www.ecad.eu). This work was part-financed by the European Union's INTERREG IVA Cross-border Programme managed by the Special EU Programmes Body under the project "Development of targeted ecological modelling tools for lake management; DOLMANT" (Ref. No: 002862).

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