Article

Macroecological Patterns of Resilience Inferred from a Multinational, Synchronized Experiment

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Abstract: The likelihood of an ecological system to undergo undesired regime shifts is expected to increase as climate change effects unfold. To understand how regional climate settings can affect resilience; *i.e.*, the ability of an ecosystem to tolerate disturbances without changing its original structure and processes, we used a synchronized mesocosm experiment (representative of shallow lakes) along a latitudinal gradient. We manipulated nutrient concentrations and water levels in a synchronized mesocosm experiment in different climate zones across Europe involving Sweden, Estonia, Germany, the Czech Republic, Turkey and Greece. We assessed attributes of zooplankton communities that might contribute to resilience under different ecological configurations. We assessed four indicator of relative ecological resilience (cross-scale, within-scale structures, aggregation length and gap size) of zooplankton communities, inferred from discontinuity analysis. Similar resilience attributes were found across experimental treatments and countries, except Greece, which experienced severe drought conditions during the experiment. These conditions apparently led to a lower relative resilience in the Greek mesocosms. Our results indicate that zooplankton community resilience in shallow lakes is marginally affected by water level and the studied nutrient range unless extreme drought occurs. In practice, this means that drought mitigation could be especially challenging in semi-arid countries in the future.

Keywords: climate change; eutrophication; ecological resilience; zooplankton communities; synchronized mesocosm experiment; discontinuity analysis

1. Introduction

Climate change is expected to globally alter temperature and precipitation patterns [1]. There is evidence that altered temperature and precipitation patterns resulting from climate change [1] can further enhance eutrophication in freshwaters [2] due to enhanced transport of nutrients from land to lakes and increased internal loading of nutrients [3–5]. Changes in precipitation can also influence eutrophication, for instance, through changing water levels in lakes that can subsequently prolonged water residence time and create optimum conditions to increase phosphorus loading from sediment [3,6–8]. Thus, water level change and eutrophication are two important drivers of ecosystem and community dynamics due to climate change.

Shallow lakes have proven to be useful models for understanding large, sudden and lasting changes in the structure and function of ecosystems [9–11]. For instance, cultural eutrophication can trigger a regime shift from a clear water to turbid water state in lakes, affecting negatively ecosystem services such as fisheries, recreation and fresh water supply [12,13]. In other words, regime shifts occur when the ecological resilience, *i.e.*, the ability of an ecosystem to tolerate disturbances without changing its original structure, functions and processes [14,15], of a system is exceeded. Once a regime shift has occurred, ecosystems reorganize in alternative states with new structures, functions and

processes [10,16]. Climate change is expected to erode the resilience of shallow lakes, potentially leading to regime shifts [17]. However, climate change impacts on ecosystems can vary regionally. For instance, the frequency and duration of droughts are predicted to increase in Mediterranean countries, while countries at more northern latitudes are expected to become wetter [1]. This highlights that the impact of eutrophication or water level may vary as a function of climatic conditions. Thus, studies are needed to account for regionally contingent effects of eutrophication and water level change on resilience.

Here, we investigate regional climatic effects on the resilience of shallow lakes on the basis of a synchronized, controlled mesocosm experiment, carried out in six European countries. Our experiment builds on a space-for-time substitution approach, which has been frequently used to investigate the response of ecosystems along broad environmental [18–20] and climatic gradients [21,22]. The experiment overcomes shortcomings identified for space-for-time substitutions [23,24], and was designed to allow for mechanistic insights regarding the predicted effects of climate change on shallow lakes [23,25]. It therefore allows revealing resilience patterns at a macroecological scale for which information in the literature is currently scant. Specifically, we simulated different ecological conditions of shallow lakes by manipulating water levels and nutrients, two important components of predicted climate change in lakes, in mesocosms across a latitudinal gradient in the countries of Sweden, Estonia, Germany, Czech Republic, Turkey and Greece. In the experiment, we measured abiotic and biotic changes in the mesocosms during one growing season and conducted a comparative assessment of patterns of ecological structure as a function of regional and local climatic conditions (northern boreal region: Sweden and Estonia, central continental: Germany and Czech Republic, and southern Mediterranean: Turkey and Greece) along the latitudinal gradient. The specific aim of this study was to assess attributes of ecological resilience [14] in zooplankton communities and investigate how climate change may affect the resilience of our simulated lake ecosystems (mesocosms). The tight coupling of zooplankton to environmental changes has long been recognized [26] and has been used as indicator of: eutrophication [27–29], acidification [30] and watershed disturbances related to agricultural practice [31]. Zooplanktons are larger than phytoplankton species, thus making species identification easier. They also respond faster to environmental changes than fish [26,32]. Zooplanktons are crucial components of aquatic ecosystems as they occupy an intermediate level in the foodweb of shallow lakes and have an important role in matter and energy flow between primary producers and fish [33]. Zooplanktons are therefore useful for testing how resilience characteristics in communities change as a function of eutrophication, water-level and regional climate effects.

An operational measure of resilience is needed to embrace the complex, multidimensional, hierarchical and nonlinear structures and processes in ecological systems [34,35]. The discontinuity hypothesis [36] builds the foundation of such an approach. It is based on the notion that species perceive and interact with their environment at scales that are relative to their body size, and persistence depends in part on how well a species' body size allows it to take advantage of the available resources at a specific scale. Animal body size distributions for a given ecosystem are reflected in groups of similar-sized species that exploit resources at the same range of scale [36]. That is, each body size group mirrors a specific scale of structure and resource availability in the ecosystems, so that the number of body size groups in a community indicates the number of scale domains present in the ecosystem [36,37].

It is now widely accepted that ecological communities and other complex systems are discontinuously structured [38,39]. Although with a few exceptions, their ultimate drivers are still not fully elucidated (e.g., Nash *et al.* [40]) and testing of the discontinuity hypothesis is useful for generating patterns that facilitate an interpretation of resilience [41]. By quantifying the number of scale domains present in a system the cross-scale aspect of resilience can be assessed [42,43]. There is also a within-scale aspect of resilience (*i.e.*, species redundancies at a single scale), and the combined within scale and across scale distribution of functions is posited to be a robust measure of the relative resilience of ecological systems [42,43]. It has been suggested that resilience increases with an increasing redundancy of species functions at a single scale, as well as how often these functions occur across scales [42]. Theoretically, structural attributes (*i.e.*, within and cross-scale structures) that contribute to resilience should persist over time and be replicated across space [42]. Similarly, species diversity might expand or contract due to immigration or local extinction, and habitat configuration might change, however the structural attributes should be negligibly affected unless the resilience of the system has been exceeded [42]. In addition to the two resilience indices (within and cross-scale) described by Peterson *et al.* [43], we also included two other indices; aggregation length and gap size. There is evidence that several ecological phenomena, like species invasions and extinctions, are non-random with regard to their location in body-size aggregations [44]. That is, species situated at the periphery of aggregation groups (*i.e.*, close to discontinuities) are more prone to extinction, and the likelihood of invasion is also higher close to discontinuities. Thus, quantifying aggregation lengths and gap sizes in addition to within- and cross-scale structure provides opportunities for characterizing the broader impacts of climate change on zooplankton community resilience (a conceptual overview of the discontinuity approach is shown in Supplementary Figure S1).

In this paper, we quantify four indicators of resilience of zooplankton communities (resilience of what; see Carpenter *et al.* [45]) to the experimental manipulations of nutrients and water levels across countries in different climatic settings (resilience to what). We infer resilience based on discontinuities in body size and expect that resilience attributes reflect conservative patterns [46,47]. We compare the results with patterns derived from biomass [48], which integrates fast and dynamic responses to changing environmental processes in the mesocosms [49,50]. Both approaches are expected to provide complementary information about resilience patterns in our synchronized cross-country experiment.

2. Experimental Section

2.1. Lake Selection

A thorough description of the experimental design can be found in Landkildehus *et al.* [51]. Briefly, one lake from each of the six participating countries (Sweden, Estonia, Germany, Czech Republic, Turkey, Greece) was selected based on water depth (<5 m), alkalinity (<4 meq/L), water color (<20 mg Pt/L), electrical conductivity (<500 mS/m) and nutrient concentration (<25 μg/L of total phosphorus (TP) to accommodate the experiment. These conditions reflect natural abiotic settings of shallow, nutrient-poor lakes across Europe, increasing the generality of the mesocosm study. The experiment ran simultaneously in the respective locations (Table 1) using standardized sampling

methods and lasted for approximately six months (May to beginning of November 2011), corresponding to the ice free period in the northern countries [51].

Table 1. Location of the selected lakes used for setting up the experiment.

Country	Lake	Coordinates	Altitude (m a.s.l.)
Sweden	Erken	59°49′59″N 18°33′55″E	11
Estonia	Võrtsjärv	58°12′17″N 26°06′16″E	35
Germany	Müggelsee	52°26′0″N 13°39′0″E	32
Czech Republic	Vodňany	49°09′14″N 14°10′11″E	395
Turkey	DSI Gölet	39°52′38″N 32°46′32″E	998
Greece	Lysimachia	38°33′40″N 21°22′10″E	16

2.2. Experimental Design

In each country, the experiment consisted of manipulation in four replicates of two nutrient levels (low, high) crossed with two water levels (shallow, deep), resulting in a total of 16 replicates. The enclosures were attached to floating pontoon bridges constructed from wooden boards and floating devices; pontoons were held in a fixed position by anchoring. The enclosures were randomly arranged in two rows each with eight mesocosms; the two rows were separated by a boardwalk to facilitate sampling. All mesocosms originated from the same manufacturer (Armaplast Polyester San. ve Tic. Ltd., Gebze, Turkey) and consisted of cylindrical fiberglass tanks (diameter 1.2 m and 4 mm thick), with two different heights of 1.2 and 2.2 m. The fiberglass material prevented exchange of water with the lakes, but allowed the tanks to share the same climatic conditions (temperature, precipitation and seasonality) as their hosting lakes. At the start of the experiment, the water depth was adjusted to 1 and 2 m in the shallow and deep water level treatments, respectively. Once the pontoon bridges were in place, a combination of sand and mud from a nearby mesotrophic lake was added as bottom substrate and equilibrated beforehand regarding TP fluxes between the water column and the sediment [51]. Subsequently, the mesocosms were filled with filtered nutrient poor water to reach 1020 and 2150 L, respectively corresponding to the shallow and deep water levels. Following water addition, suspended solids were left to settle for 96 h. Thereafter the mesocosms received inocula of plankton (phytoplankton and zooplankton) from five nearby lakes as a biotic inoculum, to enable the development of a diverse flora and fauna and to cover regional communities. Plankton inocula were collected by performing five vertical net hauls (plankton net with a mesh size of 50 μm and a diameter of 20 cm), over the entire water column from the five nearby lakes (from each respective countries) and pooled in 5 L barrels (Landkildehus *et al.* 2014). The contents of the barrels (5 L) from the five lakes were subsequently carefully mixed and subsamples of 1 L were added to each mesocosm [51]. From the same five lakes sediment was collected and sieved through a 10 mm sieve to avoid introducing fish eggs or large mussels. One liter

of this mix of sediments was added to each mesocosm. Eurasian water-milfoil (*Myriophyllum spicatum*), collected from the host lake, was planted in each mesocosm to establish submerged vegetation. Finally, all mesocosms were stocked with planktivorous fish. Three-spined stickleback (*Gasterosteus aculeatus*) was used in most countries, except Sweden where juvenile roach (*Rutilus rutilus*) was used due to ethical issues (legislation restricting translocation of specimens between habitats), and Greece where western mosquito fish (*Gambusia affinis*) was used due to limited availability of sticklebacks. Stocking was based on fish biomass (4–20 grams per enclosure).

The final step consisted of adjusting phosphorus concentrations to 25 µg TP/L and 200 µg TP/L, for low and high nutrient treatments simulating oligotrophic and hypertrophic conditions, respectively. Nitrogen was added to achieve a phosphorus to nitrogen ratio of 1:20 (by molecular weight). At the start of the experiment nutrient addition was only needed for the high nutrient treatments. To account for nutrients loss, monthly nutrient additions were necessary to maintain the two nutrient levels throughout the experiment. Nutrient dosing (see Supplementary Table S1) was determined from previous experiments [52,53].

2.3. Sampling

Zooplankton sampling of mesocosms was initiated directly after the addition of fish and macrophytes. Thereafter samples were taken at monthly intervals. Water samples representative of the water column, were taken with a Plexiglas® tube (length 60 cm with and internal diameter of 9.5 cm) sampler and pooled. A subsample of 5 L from the well mixed pooled sample was filtered using a plankton net (20 µm mesh size). The remaining water was poured back into each mesocosm. Zooplanktons were washed into a 50 mL bottle containing 2.5 mL Lugol's solution, for preservation. The temperature and water level of each enclosure were measured when zooplankton samples were taken. At the end of the experiment, an integrated sample, representing the whole experimental period, was prepared by mixing subsamples (25% of the original volume) from each of the monthly samples. From these compound samples, taxa were identified to the finest taxonomic unit possible (usually species) and body size (µm) and biomass (µg DW/L) were calculated from geometric shapes following a commonly agreed standardized protocol based on the work of Bottrell *et al.* [54], Culver *et al.* [55], Dumont *et al.* [56], McCauley [57], Michaloudi [58], Rosen [59], Ruttner-Kolisko [60] and Vuille [61].

2.4. Statistical Analyses

2.4.1. Measuring Resilience

We assessed the relative resilience of the zooplankton communities by determining discontinuities and within- and cross-scale resilience patterns in both body size [37,42] and biomass [48]. Prior to the analysis, we prepared a univariate data matrix for each mesocosm replicate and country, comprised of either the ascending log-transformed body size or biomass. We then carried out discontinuity analysis on these matrices using Bayesian Classification and Regression Trees (BCART), a method recommended by Stow *et al.* [37]. BCART identifies groups in the data by assessing within-group homogeneity [37] and has been found to be effective for identifying groups [62]. The outcome is portrayed as a branching tree, where the terminal nodes delineate groups of maximum homogeneity [37].

That is, groups of maximum homogeneity comprise aggregations of zooplankton individuals in terms of body size or biomass that are different from other homogeneity groups and presumably operate in distinct scaling regimes [36,42,48]. The number of homogeneity or aggregation groups identified in the analysis therefore allows assessing the cross-scale structure attribute of resilience (*i.e.*, the number of aggregation groups or scales present). The within-scale attribute of resilience can be assessed by evaluating the number of species present in each aggregation group (scale). In addition to the within- and cross-scale attribute of resilience we determined two additional metrics. First, we determined the length of each aggregation group measured as the difference between highest and lowest log-transformed body size and biomass of the species composing a specific group (aggregation body size/biomass length) (See the conceptual overview of discontinuity analysis Supplementary Figure S1). Second, we evaluated the distance in terms of body size and biomass separating aggregation/homogeneity groups of the BCART (*i.e.*, gap size or discontinuities sensu Allen *et al.* [42]).

The BCART software used in this study was developed by Chipman *et al.* [63] and is freely available at [64].

2.4.2. Statistical Comparisons

Cross-scale structure, within-scale structure (averaged for each replicate mesocosm), average aggregation length and average gap size were analyzed using a mixed model ANOVA, with "water depth", "nutrient level" and "climate" (three groups, northern boreal region: Sweden and Estonia, central continental: Germany and Czech Republic and southern Mediterranean: Turkey and Greece) as fixed factors, whereas "lake" (nested in climate) comprised a random factor. Log transformation was used in some cases to fulfil the assumptions of parametric tests. Interaction terms between water depth, nutrient level and climate were considered important for inferring climate change effects on zooplankton community resilience. Random effects were evaluated using restricted maximum likelihood, which is a robust method to compensate for the loss of replicates [65] that occurred in Germany during storm events.

These univariate ANOVA comparisons were complemented with multivariate analysis using non-metric multidimensional scaling (NMDS) to explore similarities of the overall resilience structure (combining cross-scale structure, within scale structure, aggregation length and gap size). This ordination method begins by scaling objects in full-dimensional space and reduces those dimensions to a few, while preserving the distance relationship among the objects [66]. Euclidean distance matrix was used on average values of our four metrics per replicate. Loss of some replicates did not allow us to use multivariate permutational ANOVAs and instead we used Analysis of Similarity (ANOSIM; 999 permutations) to test for significant differences between water depth, nutrient level and climate. This analysis is a non-parametric method to test for differences between groups (R = 0, no significant differences, R = 1 strong dissimilarity between groups). ANOSIM was used to supplement NMDS analysis. The mixed model and ANOSIM analyses were analyzed in R 3.0.2 statistical software package [67]. Given the differences in fish taxonomy and biomasses used across the experiment, we used the "envfit" function from the R vegan package (999 permutations) to assess whether fish had a likely impact on the NMDS representation of resilience characteristics found in our experiment.

3. Results and Discussion

3.1. Abiotic Variables: Water Level Change and Temperature

Water levels were more or less constant in Sweden, Estonia, Germany and Czech Republic, whereas substantial water loss due to evaporation occurred in Turkey and Greece (Figure 1). The magnitude of water loss was more pronounced in Greece (about 90% and 50% in shallow and deep enclosures, respectively) than in Turkey (approximately 50% and 25% in shallow and deep enclosures, respectively). Temperature followed the latitudinal gradient; lower temperatures in the northern boreal climate (Sweden and Estonia), intermediate in the central continental climate (Germany and Czech Republic) and higher in the southern Mediterranean (Turkey and Greece) (Figure 1 and daily average temperature is shown in Supplementary Figure S2).
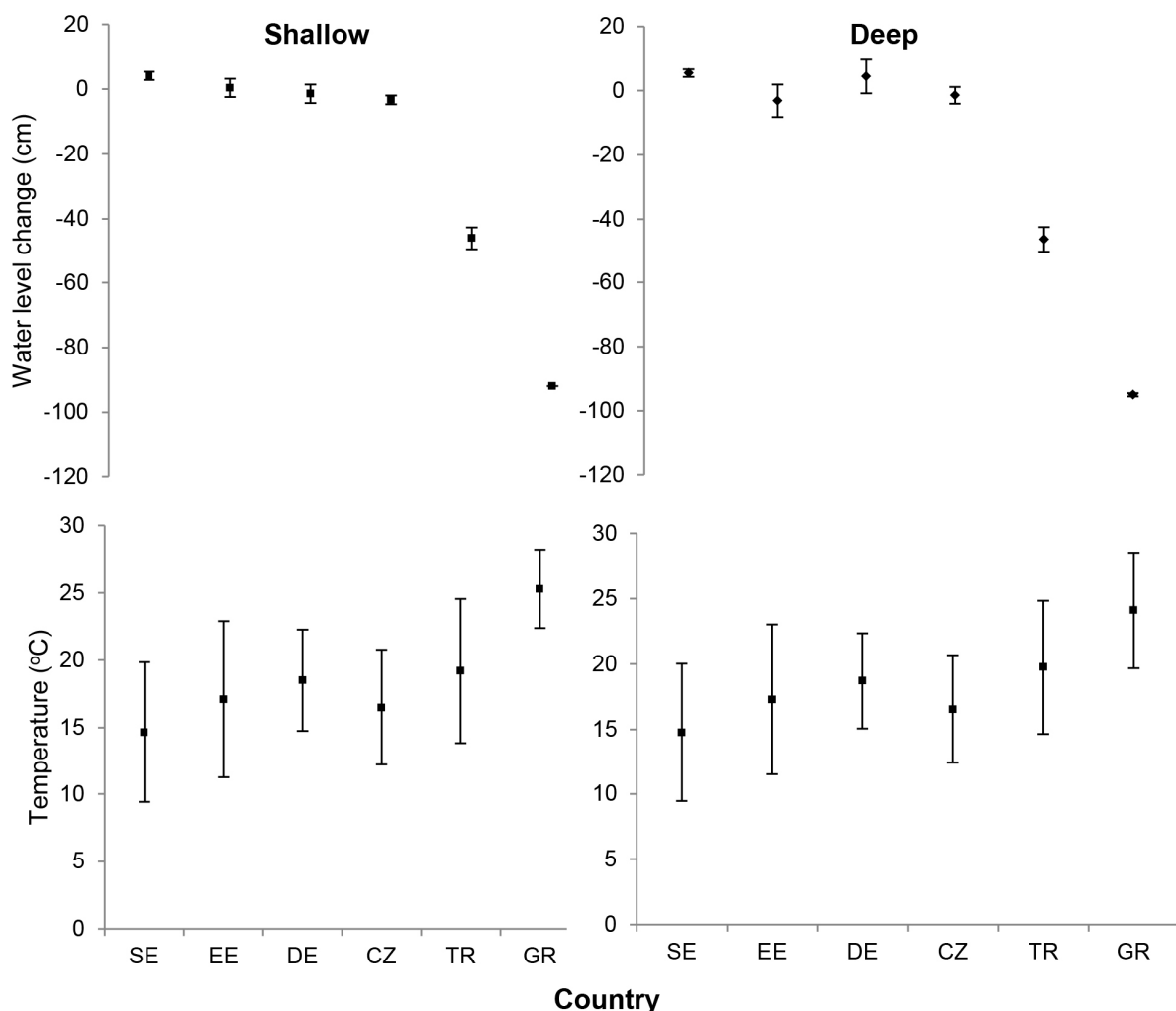
Figure 1. Comparison of water level change and temperature recorded from shallow and deep mesocosms. Shown are the overall patterns (mean ± standard deviations) for the different countries; SE, Sweden, EE, Estonia; DE, Germany; CZ, Czech Republic; GR, Greece; TR, Turkey.

3.2. Univariate Analyses

The zooplankton body size ranged between 47 and 2200 μm for Sweden, 42 and 1200 μm for Estonia, 10 and 2500 μm for Germany, 24 and 2100 μm for Czech Republic, 45 and 990 μm for Turkey, and 56 and 1200 μm for Greece. Zooplankton biomass in the enclosures, on the other hand ranged between: 37 and 460 μg DW/L for Sweden, 30 and 500 μg DW/L for Estonia, 34 and 1000 μg DW/L for Germany, 12 and 430 μg DW/L for Czech Republic, 11 and 720 μg DW/L for Turkey, and 11 and 1700 μg DW/L for Greece (see Supplementary Figure S3 for the distribution of zooplankton body size and biomass).

The discontinuity analysis performed on zooplankton body size and biomass gave comparable cross-scale structure with 4.53 average ± 0.81 SD (body size) and 5.33 ± 0.90 (biomass) aggregations groups (or scales) being present in the data. Within-scale structure, defined as the number of species present within each aggregation group of scales was 5.13 ± 1.40 (body size) and 4.46 ± 1.08 (biomass). Patterns of aggregation group length, in terms of the body size and biomass ranges of zooplankton individuals constituting these groups were 0.14 ± 0.03 and 0.44 ± 0.07, respectively. Patterns for gap size, *i.e.*, ranges of body size and biomass where no individuals were detected in the discontinuity analyses were 0.16 ± 0.08 and 0.45 ± 0.18, respectively (Figure 2). Overall, the number of scales (cross-scale structure), the number of species per scale, an aspect of within-scale redundancy, and gap size were similar across countries. Only Greece deviated from these patterns, showing larger gap sizes (on average 127% higher), lower cross-scale (on average 34% lower) and within-scale structures (on average 51% lower) relative to the other countries. Only aggregation length was similar across all treatments and countries (Figure 2).

The ANOVA model showed that none of the main effects (water depth, nutrient, and climate) were significant (complete ANOVA table in Supplementary Table S2). However, several interaction terms were significant, all of which involved climate, but the combination of effects varied with metric and approach (body size *vs.* biomass). For body size, water depth, nutrient and climate interaction influenced the number of scales ($F_{2, 59.33} = 3.87$, $p = 0.03$), the number of species per scale ($F_{2, 60.85} = 3.38$, $p = 0.04$) and aggregation length ($F_{2, 59.33} = 5.63$, $p = 0.006$), nutrient and climate interaction influenced the number of scales ($F_{2, 59.33} = 4.12$, $p = 0.02$) and the number of species per scale ($F_{2, 59.33} = 7.76$, $p = 0.001$), and the interaction between water depth and nutrient also influenced the number of scales ($F_{2, 59.33} = 3.27$, $p = 0.045$). For biomass, only the three-way interaction between water depth, nutrient and climate was significant for the number of species per scale ($F_{2, 59.76} = 4.76$, $p = 0.01$) and marginally significant for gap size ($F_{2, 59.76} = 2.91$, $p = 0.057$).
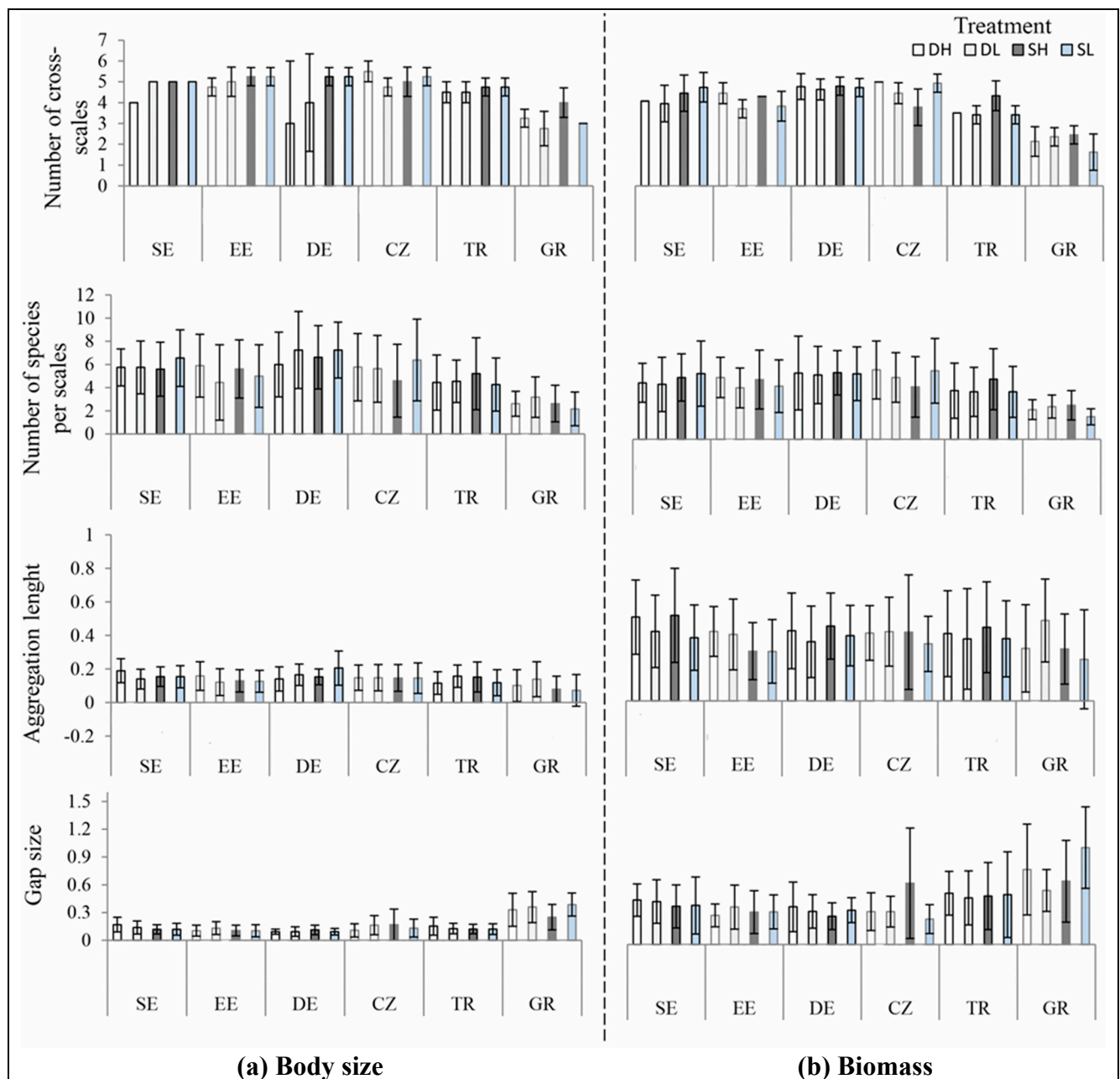
Figure 2. Comparison of cross scale (number of scales) and within scale (number of species per scale), aggregation length and gap size, *i.e.*, four attributes of resilience, derived from (**a**) zooplankton body size and (**b**) biomass. Shown are the overall patterns (mean ± standard deviations) for the different countries: SE, Sweden, EE, Estonia; DE, Germany; CZ, Czech Republic; GR, Greece; TR, Turkey.

3.3. Multivariate Ordinations

The NMDS analyses (Figure 3) supported the ANOVA model. Greece differed in zooplankton community resilience, based on the attributes within-scale and cross scale structure, aggregation length, and gap size from the other countries, independent of experimental manipulations. ANOSIM showed that the resilience structure in the water level (biomass: R = 0.01, p = 0.13, body size: R = 0.01, p = 0.15) and nutrient treatments (biomass: R < 0.01, p = 0.38, body size: R < 0.01, p = 0.31) was overall

very similar, whereas significant differences across climate (biomass: R = 0.28, *p* < 0.01, body size: R = 0.25, *p* < 0.01) were found.
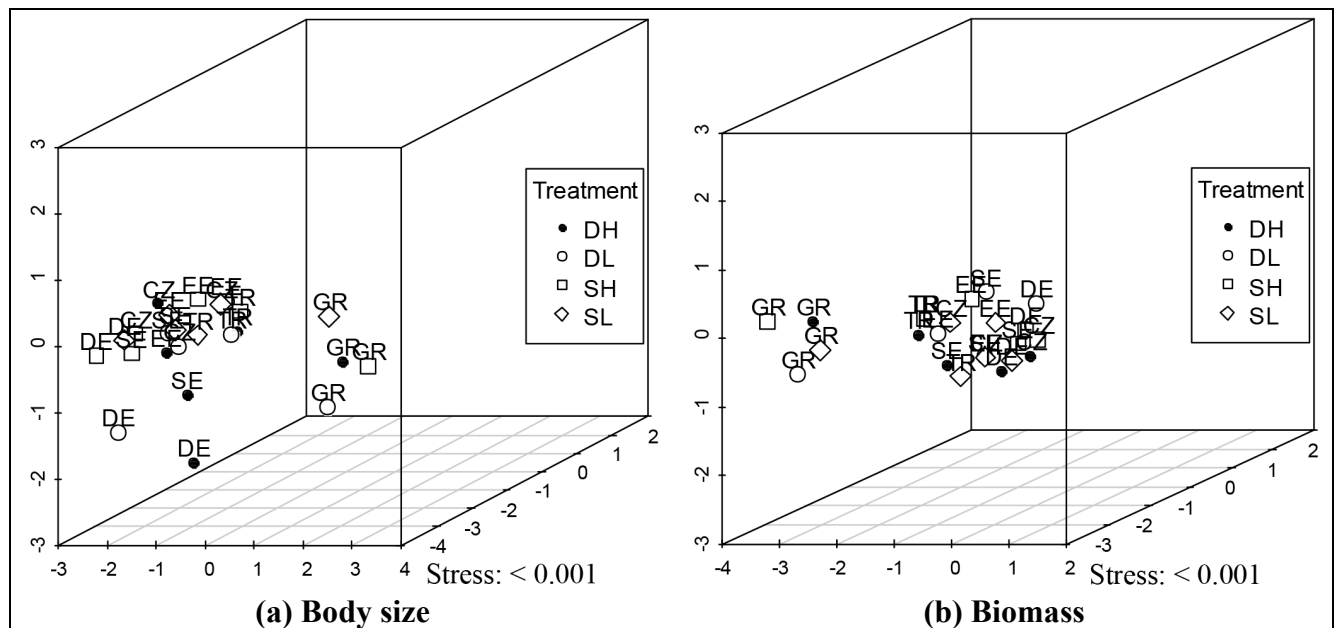
Figure 3. Non-metric multidimensional scaling (NMDS) ordination showing the overall resilience structure (combining the variables cross-scale structure, within-scale structure, aggregation length and gap size) across treatments and countries (abbreviations as in Figure 2).

The fish species used in the experiment were found to correlate with the overall resilience pattern derived from zooplankton body size ($R^2 = 0.64$, *p* < 0.01) and biomass ($R^2 = 0.75$, *p* < 0.001). However, the final fish biomass did not correlate with the overall pattern (body size: $R^2 = 0.23$, *p* = 0.09, biomass: $R^2 = 0.10$, *p* = 0.33).

3.4. Discussion

We assessed the resilience of zooplankton communities using within- and cross-scale patterns in zooplankton body size and biomass aggregations, which have been considered as proxies of the relative resilience of ecosystems [38,42,43]. We identified two additional measures (gap size and aggregation lengths). Research has shown that several ecological phenomena (e.g., invasions and species extinctions) are non-random with regard to the location of species in body mass groups [44,68]. These measures therefore provide additional information on how our experimental treatments affected body size and biomass aggregation patterns and thus the resilience of zooplankton assemblages. The four indicators of resilience were studied in mesocosms simulating two drivers that may have an important influence on the ecology of shallow lakes under climate change in the future: nutrient enrichment and water level change [3,6–8].

Synchronized multinational experiments hold a strong potential to study many profound and seemingly intractable ecological conundrums surrounding climate change impacts in ecosystems [21,69]. However, the scope and cost of such studies often require balancing study designs with available

financial resources, and our study was not exempt from such a trade-off. We aimed to strengthen inference from a spatial perspective by running the experiments in two countries located in similar geographical latitudes, which came at the cost of scrutinizing the temporal aspect of study. However, by analyzing a composite sample integrating monthly snapshots of ecological conditions in the mesocosms throughout an entire growing season, we believe that we have sufficiently characterized the broader systemic aspects in our mesocosms that have been considered necessary for assessing resilience using the discontinuity analysis. We are therefore confident that our results and inferences are not unduly influenced by sampling design.

Despite manipulating these factors, the resilience attributes inferred from our univariate and multivariate analyses were similar across treatments, highlighting conservative patterns and thus similar resilience attributes. Such conservatism despite different degrees of disturbance has also been found in other studies. For instance, Raffaelli *et al.* [47] exposed marine benthic communities to natural and anthropogenic disturbances to induce changes in trophic structure, species composition and community size. Substantial shifts in taxa were observed, whereas only minor changes in the benthic size spectrum occurred. This highlights that the robustness of resilience patterns is independent from the taxonomic composition of communities. Similarly, Havlicek and Carpenter [46] found that the body mass distributions of a wide range of species from a set of experimental lakes were conserved despite being subjected to nutrient manipulations. One notable exception in our study was the results from Greece, which consistently deviated from the other countries across all treatments. These differences were due to wider gaps and lower cross- and within- scale structures, which are in agreement with previous studies regarding the relationship between perturbation and animal body size aggregation structure [44] and suggest an overall weakened resilience in the Greek experiment. Contrary to all other sites, Greece faced the most severe drawdown conditions during the experiment, leading to a reduction in water level (about 90% and 50% in shallow and deep enclosures, respectively) due to evaporation losses. The other southern site (Turkey) faced a comparatively weak decline in water level in the mesocosms (approximately 50% and 25% in shallow and deep enclosures, respectively) probably due to the fact that the Turkish experiment was carried out at a higher altitude with less evaporation compared to the mesocosms in Greece. The effects of drought, unlike other types of disturbances, slowly increase in magnitude over time [70] and have been found to affect communities through increasing heat stress, decrease habitat availability, altering food web interactions and competition [71]. In addition, the differences in fish species and biomasses used can be expected to influence the patterns observed. Planktivorous fish are known to affect the resilience of aquatic ecosystems [9,50] and the combination of high temperature, as high temperature can stimulate feeding rates in fish [72,73], and drawdown conditions observed in Greece could have increased the predation pressure on zooplankton, thus impacting on the ecological resilience of zooplankton. This has some implications for climate change research, for instance the significance of indirect pathways mediated by changes in the functional response of some key organisms, which can ultimately affect ecological resilience of particular system is still not comprehensively explored [74].

Allen *et al.* [44] found that extinctions more likely affect species that are located at the periphery rather than at the center of body size aggregation groups. If the severe drawdown conditions during the Greek drought caused extinctions in zooplankton, it is also likely that these extinctions have occurred closer to the periphery. The increased gap size observed in the Greek zooplankton supports this

interpretation. In addition, the reduction of cross-scale structure with severe drought is in agreement with the results of a recent time series modeling study that found reduced cross-scale patterns during a prolonged drought relative to a wet period in a Mediterranean floodplain [34]. However, it is important to highlight the differences in time scale between this and the Mediterranean floodplain study to understand resilience from a more mechanistic perspective.

Recurring seasonal droughts form part of the natural disturbance regime of ecosystems and landscapes in Mediterranean areas [75]. It can therefore be expected, and it has been shown by Hershkovitz and Gasith [76], that communities in wet and dry periods of a year operate in a single broad basin of attraction. Because zooplankton resilience attributes were conservative across countries, except in Greece, our results suggest that the Greek zooplankton communities might have undergone a shift to an alternative community state as a result of the drawdown relative to zooplankton in the other countries. This is at odds with the expectation that communities operate in a single broad basin of attraction and also with the finding that the Turkish zooplankton did not undergo such a shift, despite having suffered drawdown. However, Angeler *et al.* [34] and Washington-Allen *et al.* [77] found that severe drought events over prolonged periods of time (*i.e.*, supra-seasonal droughts), a consequence of climate change [78,79] especially in arid countries [80], trigger nonlinear state shifts in hydrological functioning and biological communities. Such changes have also been documented in other studies [81–84]. Thus, non-linear abiotic and biotic changes triggered by climatic extreme events suggest that ecosystems can shift between alternative wet and dry states on supra-seasonal time scales. These state shifts should be discerned from the seasonally recurring wet-dry phases, part of which we have covered in our mesocosm experiment.

Our results have implication for the alternative states theory within the context of climate change. Our nutrient manipulations can be considered a spatial analogue of a regime shift from an oligotrophic to a eutrophic system (supplementary Figure S4; showing chlorophyll-a concentration across nutrient treatments) state described for shallow lakes [10,11]. The theory predicts that systems can undergo profound changes in structures, functions and feedbacks after a regime shift [16,85]. However, despite creating condition after a regime shift based on nutrients, we did not observed a major change in resilience characteristics. Thus, our zooplankton communities suggest that changing structures and functions after regime shifts must not be necessarily alter resilience characteristics. Both oligotrophic and eutrophic states of shallow lakes can be stable and resilient [10,11,86], and our study shows that for zooplankton similar within- and cross-scale patterns contribute to this resilience.

Climate change increases the frequency and magnitude of prolonged drought events at regional scales, especially in arid and semi-arid countries [78–80]. There is concern that eutrophication and water level changes will influence patterns of structure and processes in shallow lakes [3–5]. However, our results, together with findings from previous research [34,77], suggest that unless persistent dry spells caused by a state shift in meteorological and climatological settings on a regional scale, resilience attributes of shallow lakes may be otherwise little affected by changing water levels or trophic state conditions at least within our studied range. In practice, this means that drought mitigation and natural resource management might be especially challenging in arid and semi-arid countries in the future, because as our study suggests, these effects can be spatially contingent and difficult to predict [70,71,87].

4. Conclusions

Although our mechanistic understanding of resilience within a climate change context at macroecological scales is still in its infancy, our results suggest that the dynamic and hierarchical structures of ecological systems need to be explicitly accounted for when assessing the ability of ecosystems to withstand stress [88]. Experiments like ours hold the potential to assess the generalities of the patterns found for zooplankton in this study across other organism groups and the implications for ecosystem level resilience.

Supplementary Materials

Supplementary materials can be accessed at: http://www.mdpi.com/2071-1050/7/2/1142/s1.

Author Contributions

Erik Jeppesen and Martin Søndergaard designed the experiment. All authors performed the experiment. Didier L. Baho carried out the statistical analysis and wrote the paper together with David G. Angeler. Co-authors commented on the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

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