Preface: advances in the ecology of shallow lakes

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Introduction

The concept of ecosystems is one of the most important within ecology, and ecosystem ecology has become a significant paradigm (sensu Kuhn 1962) for studying ecological systems. However, this paradigm has undergone changes over the last decades with pronounced consequences for limnology. Underlying the old paradigm of ecosystem ecology is an over-emphasis on the steady state, a suggestion that ecological systems tend to be self-regulated and remain in balance. This old paradigm still influences limnology despite the many limitations associated with it, as discussed by O’Neill (2001) two decades ago. Several changes of the paradigm have been proposed to solve these limitations and reconcile the concept of ecosystems with our current understanding of ecological systems as adaptive, metastable systems that can and tend to operate far from equilibrium (O’Neill 2001).

Ecological systems vary over time in complex ways, and they are spatially heterogeneous at all
spatial scales, but the old paradigm focuses on studying the averaged or integrated properties of all interacting populations within a specified spatial area. The old paradigm considers a unit of space, usually a lake or a small watershed, and within these limits it identifies the significant dynamics that require explanation and the significant processes that will explain those dynamics. While it is recognized that every ecosystem is open to the exchange of organisms, energy, and matter with neighbouring ecosystems, the old paradigm assumes that the interactions and feedback loops necessary and sufficient to explain dynamics occur within the boundaries of the ecosystem. Another limitation of the old paradigm is that spatial heterogeneity within the ecosystem is often ignored by averaging the variables across sampling units in order to focus on the integrated properties of the lake. However, the dispersion of organisms and the flows of energy and matter across ecosystem boundaries are a system stability mechanism. Moreover, it is precisely the internal heterogeneity, or the heterogeneity of the larger spatial context, that maintains the entire range of populations required to uphold the stability of the system (Turner & Gardner, 2015).

In the new paradigm of ecosystem ecology, the spatial context needs to be included in the ecosystem definition and analyses. Landscape ecology focuses on the relationships between spatial patterns and ecological processes and considers spatial scales that extend well beyond the individual ecological system traditionally studied by ecologists (Turner & Gardner, 2015). From a landscape perspective, conceptual frameworks have been proposed to emphasize the importance of ecosystem boundaries, including their permeability and resistance to flows of energy, materials and organisms, dispersal of organisms influencing the gene flow and community assembly, subsidies of nutrients and energy from one habitat to another, and the challenges of managing systems to maintain biodiversity and ecosystem services at the landscape scale (Loreau et al. 2003; Leibold et al. 2004).

Shallow lakes are embedded in heterogeneous landscapes, and their density and surface area (size) are important determinants of landscape connectivity that influences metapopulation, metacommunity, and meta-ecosystem dynamics. They are also embedded in a mosaic of terrestrial systems and human influences. This fosters a view of land–water interactions that encompasses the integrated sets of lakes, streams, and wetlands that occur in a landscape. Understanding the implications of the dynamic landscape mosaic for ecosystem processes remains a frontier in both ecosystem and landscape ecology and is actualized also in the ongoing global change perspective. Despite the great advances in shallow lake ecology over the last decades, we do not yet sufficiently grasp all the consequences of regional processes for the structure and function of shallow lakes. There is great opportunity to integrate ecological theories that address both the role of local and spatial processes for population, community, and ecosystems dynamics in shallow lakes and to consider the implications for their management.

Here, we present contributions from the 10th International Shallow Lakes Conference that devoted special attention to landscape ecology and its importance to understand the structure and function of shallow lakes. Among these contributions, most have covered other important issues of shallow lakes ecology not directly related to landscape ecology, including the response of shallow lakes to global warming and eutrophication, the role of aquatic macrophytes and spatial heterogeneity in shallow lakes structure and dynamics, harmful algal blooms and lake restoration, the role of salinity, among other topics. Shallow lakes are important freshwater ecosystems worldwide as they contribute substantially to biodiversity and ecosystem services locally as well as at the landscape scale. We hope that this special issue will improve the understanding of these important ecosystems and also challenge shallow lakes ecologists to consider in their studies the relationships between spatial patterns and ecological processes at spatial scales that extend well beyond the individual lake.

The conference

The 10th International Shallow Lakes Conference was originally scheduled for June 2020 in the city of Natal, Brazil. However, due to the Covid 19 pandemic, the conference was postponed and instead held online from 1 to 5 March 2021. The new conference format mixed live-streamed and pre-recorded talks, which reduced the environmental footprint of the meeting while also lowering barriers to inclusiveness (Blackman, 2020). The reduced costs of attending the online conference democratized access to the
event and allowed participation of many students and professionals. Overall, the conference had 317 participants (188 professionals and 129 students) from 32 countries. A total of 9 plenary talks plus 190 oral communications distributed between 19 oral sessions were presented. The participants were invited to submit their work to the journal *Hydrobiologia*, which has published the proceedings of the International Shallow Lakes Conferences since its first edition (Nandini et al., 2019). *Hydrobiologia* has contributed the most to the advance of shallow lakes ecology as evidenced by any quick search in the Web of Science database using the keyword *Shallow Lakes*. Overall, 37 manuscripts were submitted for publication in this volume, of which 27 were accepted and are presented here. We thank the Editor in Chief, Dr. Koen Martens, and the Associate Editor in Chief, Dr. Sidinei Magela Thomaz, for offering us the opportunity to maintain the publication tradition with this special issue of *Hydrobiologia* on the proceedings of the 10th International Shallow Lakes Conference. We also thank Dr. Sidinei Magela Thomaz and the many reviewers who helped ensure the high quality of the articles published in this volume. Last, but not least, we thank the authors for submitting their work to this special issue on shallow lakes ecology.

The volume

In this section we provide a short summary of the papers published in the proceedings divided into topic areas.

Landscape perspectives

Lake depth affects the availability of light and nutrients to primary producers and is considered an important driver of lake productivity and the relative importance of benthic and pelagic primary production. In contrast, the effects of hydrologic connectivity on lake productivity are not so well understood. Cheruvelil et al. (2022) conducted a macroscale study of total phosphorus (TP) and chlorophyll *a* (CHLa) relationships in 2210 shallow and 4360 non-shallow lakes with distinct levels of hydrologic connectivity in the Upper Midwestern and Northeastern USA. Their results support the expectation that shallow and connected lakes tend to have higher levels of TP and/or CHLa compared to non-shallow and unconnected lakes. Further, they found that regional variation contributed to predictive models of TP and CHLa concentrations and that the slope of TP-CHLa relationships varied regionally. Important predictors of TP and CHLa included lake-specific watershed:lake area ratio, forested land use/cover, and baseflow. They also found that unconnected lakes were more difficult to predict than connected lakes and that region-specific predictors were overall unimportant.

Hydrologic connectivity is the main driving force influencing shallow lakes in river-floodplain systems. The dominant role of the flood pulse for the connectivity of floodplain habitats and the spread of propagules and success of non-native species (NNSs) in these systems is reviewed by Thomaz (2022). After the establishment of NNSs, floodplains may function as steppingstones for future invasions because propagule pulses enhance invasions in nearby landscapes. Moreover, the flood pulse changes environmental filters, with consequences for invasion success and for the coexistence of native and NNSs. Flooding represents a disturbance that enhances the success of some NNSs by reducing biotic resistance and changing resource availability but diminishes the success of others. On the other hand, drought enhances the invasion success of NNSs that colonize the aquatic-terrestrial transition zone. Therefore, impacts caused by river regulation and global changes alter the flood pulse, which in turn affects the invasion success in these ecosystems.

Two studies have investigated patterns of beta-diversity at a landscape scale. Simões et al. (2022) analyzed the difference in zooplankton beta diversity between shallow natural lakes (29) and artificial reservoirs (30) in Brazil during dry and wet seasons. Rotifer beta diversity did not differ between lakes and reservoirs, while copepod beta diversity was higher in reservoirs. Environmental filters were important during the dry period for both lakes and reservoirs, while copepod beta diversity was higher in reservoirs. Environmental filters were important during the dry period for both lakes and reservoirs, indicating that deterministic processes drove beta diversity during that season. CHLa was of key importance for zooplankton beta diversity in both lakes and reservoirs, while the spatial turnover of zooplankton communities depended on the biological characteristics of zooplankton groups and their responses to environmental filters. Understanding how local conditions and dispersal dynamics structure communities of passively dispersing aquatic invertebrates remains
uncertain, especially in arid areas. In these systems, dispersal is irregular, and successful colonization is subject to priority effects. Brown et al. (2022) compared rotifer species composition from desert rock pools, playas, and tanks. They found 132 species and high beta-dissimilarity among sites. Correlation between species richness and habitat area was significant, but weak, for all sites. They further found that hydroperiod was important for playas and tanks, but not rock pools, conductivity overall had a strong influence, and richness was greatest in habitats with the highest amounts of vegetation. The authors provide a conceptual model that highlights the distinctive nature of aquatic communities in arid areas compared to temperate regions.

Habitat complexity and aquatic macrophytes

Habitat complexity is affected by processes acting at different spatial scales, ranging from the landscape level to the local shallow lake ecosystem. At local scale, the pelagic, littoral, and benthic habitats are characterized by different degrees of structural complexity and a particular set of organisms and processes. Most shallow lakes can have high levels of within-lake spatial heterogeneity, depending on the presence, diversity, and density of aquatic macrophytes in the benthic and littoral habitats. Meerhoff & Gonzalez-Sagrario (2022) reviewed patterns and mechanisms by which habitat complexity affects biodiversity and the functioning of shallow lakes and pond ecosystems. Direct and indirect effects of changes in within-lake habitat complexity can either hinder or promote regime shifts in these systems. They also reviewed several anthropogenic pressures that decrease lake resilience through changes in habitat complexity and strategies for habitat complexity restoration. Overall, they emphasize the need for preserving and/or restoring habitat complexity as key challenges to account for ecosystem integrity, maintenance of local/regional biodiversity, and the provision of crucial ecosystem services.

Urban ecology is a new research field in limnology, and little is known about how urban waterbodies can help sustain biodiversity. Pinel-Alloul et al. (2022) studied urban waterbodies in the city of Montreal, Canada, aiming at evaluating if biodiversity and community structure of food-web components (phytoplankton, zooplankton, and macroinvertebrates) are valuable tools for assessing the ecological status of urban waterbodies and examine the driving factors. The authors showed that the urban waterbodies were important sources of biodiversity and revealed that food-web based biological indicators are reliable tools for the biomonitoring of urban waterbodies. They further found that food-web biodiversity and community structure were more influenced by habitat complexity than by trophic status and that the key determinants of variation were the differences in water regime, management of temporary and permanent waterbodies, habitat complexity depending on pond origin (artificial or natural), and macrophyte cover.

It is well-established that macrophytes play a key role in the structure and functioning of shallow lakes, thereby increasing habitat complexity and spatial heterogeneity. Information about the drivers of changes in macrophyte communities and traits is therefore needed, also for lake management purposes. Søndergaard et al. (2022) analyzed long-term monitoring data on submerged macrophytes and water chemistry from 666 shallow Danish lakes to elucidate how plant cover (COV), plant volume inhabited (PVI), and species richness related to physical, chemical, and environmental variables. Boosted regression tree (BRT) analyses revealed that CHLa, Secchi depth, and mean depth were the strongest predictors of COV and PVI. Macrophyte species richness was best predicted by lake area and alkalinity and CHLa by TP and TN, but plant cover and alkalinity had significant additional effects. The analyses revealed limited direct effects of nutrients on macrophyte abundance but an indirect hierarchical effect of nutrients mediated through CHLa, with additional interactive effects by plant cover itself, alkalinity, mean depth, and color. In another study on intraspecific variation of leaf traits, Vecchia & Bolpagni (2022) found that leaf area and fresh and dry weight of a rooted-leaved macrophyte increased with water depth and that the specific petiole area decreased with increasing conductivity. The authors conclude that including petioles in the assessment of leaf traits enhances the possibility of understanding the ecological/adaptive processes of nymphaeids.

Macrophytes also affect lake metabolism and greenhouse gases dynamics. There are several studies of carbon dioxide (CO₂) and methane (CH₄) fluxes in shallow lakes, showing strong variation depending on the dominant primary producers, but subtropical
systems are understudied. Colina et al. (2022) compared summer CO₂ and CH₄ fluxes (diffusion and ebullition) in littoral and pelagic zones of three subtropical shallow lakes with contrasting states (clear to turbid). Significant differences among the lakes only occurred for CH₄ fluxes. In the sediment-turbid lake, CH₄ concentrations were below the atmospheric equilibrium, implying CH₄ uptake. Differences between zones occurred in the clear-vegetated and phytoplankton-turbid lakes, with higher total CH₄ emissions in the littoral zone. CO₂ uptake occurred in the littoral of the phytoplankton-turbid lake (in summer) and in the pelagic of the clear-vegetated lake even in winter. The authors conclude that submerged macrophyte dominance may decrease carbon emissions to the atmosphere, also in the subtropics.

It is known that macrophytes can affect the interaction between macroinvertebrates and fish, with cascading effects on zooplankton in shallow lakes. Mamani et al. (2022) investigated how these predators interact to affect zooplankton, algal biomass, and water turbidity by conducting 15-day experiments in mesocosms that were divided into an open water zone and a macrophyte zone. They found significant effects of zooplanktivorous fish on the abundance of Cladocera and its aggregation in the macrophyte zone but no effects of Anisoptera on zooplankton abundance or distribution and no interactions between the predators for most variables studied. Macrophytes offered a refuge for zooplankton to fish predation, but antagonist interactions appeared when both predators were present, making the shelter effect from fish predation less strong. The authors conclude that the fauna of the littoral zone should be carefully considered when developing restoration plans of shallow eutrophic lakes. Nevertheless, regression models based on the combined dataset show higher cyanobacteria and total phytoplankton biomass at lower zooplankton to phytoplankton biomass ratio and at higher fish to zooplankton biomass ratio. Cyanobacteria biomass was dominated by non-bloom forming taxa and was inversely related to the biomass of calanoid copepods, suggesting that these herbivores may play an important role in controlling edible cyanobacteria in warm shallow lakes.

Trophic cascades are well documented in temperate lakes but may not be as pronounced in (sub)tropical lakes due to the higher degree of fish omnivory. Lacerot et al. (2022) analyzed fish communities along a climatic gradient and showed that the classical correlation between body size and relative trophic position disappears in warmer climates where large fish appear to be feeding systematically at the lowest trophic levels. This concurs with experimental findings demonstrating that omnivorous fish tend to include more plant and less animal matter in their diet at higher temperatures. Accordingly, the trophic diversity declined from cold to warm lakes and the trophic webs became more truncated towards warmer climates. This finding also concurs with results from a recent analysis of a global dataset of freshwater fish species, which revealed that larger tropical fish occupied a significantly lower trophic position than their temperate counterparts, suggesting that feeding at a lower trophic position may compensate for the higher energetic constraints of larger body size at warmer temperatures (Dantas et al., 2019).
Warmer temperatures may reduce nitrogen availability to primary producers due to accelerated denitrification and may also affect phytoplankton and periphyton biomass and composition. Pacheco et al. (2022) compared periphyton responses to N decline in 12 shallow lake mesocosms during one year at low N and high N under three temperature scenarios: ambient, A2 IPCC scenario, and A2 increased by 50%. They used two submerged macrophyte species and artificial imitations of these as substrates for periphyton growth. They found that nitrogen decline increased periphyton biomass and induced compositional changes irrespective of season, plant type, and temperature. Periphyton biomass was negatively associated with phytoplankton and positively with plant complexity. Warmer scenarios negatively affected periphyton only at high N loadings. Low N conditions were associated with lower periphyton taxonomic richness, lower biovolume of N2-fixing cyanobacteria, and an increased biovolume of large-sized chlorophytes and non-N2-fixing cyanobacteria. Their results suggest that low N conditions promoted periphyton due to a more efficient use of nutrients and improved light conditions resulting from lower phytoplankton biomass and contrasting effects of temperature.

Global climate change is also altering precipitation patterns worldwide with reported increases (or decreases) in both the frequency and intensity of daily rainfall in different regions. Warmer temperatures and intensified precipitation may increase the transport of terrestrial organic matter, varying in both quantity and quality, to freshwater ecosystems. Calderó-Pascual et al. (2022) conducted a mesocosm experiment in a Turkish shallow lake and found impacts of increased input of allochthonous dissolved organic matter (DOM) with different quality and seston elemental stoichiometry. These results demonstrate that accounting for the optical and stoichiometric properties of allochthonous DOM is crucial to improve the ability of explaining the effects of climate-driven flooding on freshwater ecosystems in response to the global climate change.

To elucidate the effect of a sudden increase in DOM input, Moura et al. (2022) conducted a field experiment on the role of fresh terrestrial DOM on the degree of heterotrophy. Detritus input resulted in increased net heterotrophy and respiration rates after two days and increased primary production after 21 days. Moreover, it also changed the zooplankton community to dominance of copepods and rotifers. Their results thus indicate that fresh terrestrial organic matter input to aquatic systems initially increases net heterotrophy via direct DOM bacterial mineralization and planktonic respiration, followed by a stimulation of primary production and net autotrophy due to the mineralization of the nutrients.

Neves and Santos (2022) aimed at identifying short-term effects of extreme rainfall events on abiotic and biological indicators of water quality in a coastal lagoon in Brazil. They found that heavy rain led to increased *Escherichia coli* (Escherich, 1885) density and decreased dissolved oxygen concentrations and phytoplankton abundance. Moreover, shifts in the relative contribution of phytoplankton groups were detected. The authors conclude that the predicted increase in rainfall intensity and frequency of extreme events in the future may lead to harsher and unpredictable changes in ecosystem functioning and lagoon conditions, impairing aquatic biodiversity and fisheries.

Climate warming may also affect the phenology of plankton. Free et al. (2022) used satellite data to examine the influence of climate on CHLa in a lake in Italy. The main parameters of importance were seasonality, interannual variation, lake level, water temperature, North Atlantic Oscillation index (NAO), and antecedent rainfall. No evidence was found for an earlier onset of the summer phytoplankton bloom related to the earlier onset of warmer temperatures. Instead, a curvilinear relationship between CHLa and the temperature length of season above 20°C was found with longer periods of warmer temperature, leading to blooms of shorter duration.

Climate change has led and will lead to prolonged droughts in semiarid regions and, consequently, lake and reservoir sediments have been more frequently exposed to the atmosphere. Pinheiro et al. (2022) experimentally evaluated the influence of rewetting on CO2 and CH4 fluxes from the drawdown area of a Brazilian semiarid reservoir with and without agricultural activity. They found that the CO2 and CH4 emissions were two and three times higher, respectively, in the sediment with agricultural activity, reflecting higher contents of organic carbon, organic matter, and nutrients. In the same semiarid region, Cardoso et al. (2022) investigated the effects of a prolonged drought on environmental heterogeneity (EH) and on phytoplankton and zooplankton α, β, and γ diversities.
between and within two shallow man-made lakes. In agreement with their hypothesis, the between-lake $\alpha$ and $\gamma$ diversities from phytoplankton and zooplankton were generally negatively related to EH, whereas the plankton $\beta$ diversity showed an opposite pattern at both within-lake and between-lake scales.

Non-native species introductions have increased in the last decades primarily due to anthropogenic causes such as climate change and globalization of trade. Macêdo et al. (2022) focused on a stress-tolerant cladoceran widely used in bioassays and aquaculture, which now is spreading in temporary and semi-temporary natural ponds outside its natural range. They characterized the variations in its climatic niche during its invasion, specifically examining to what extent the climatic responses of this species diverged from the characteristics for its native range, and they also made predictions for its potential distribution in current and future scenarios. They found that the environmental space occupied by this species in its native and introduced distribution areas shares more characteristics than randomly expected and that the introduced niche has a high degree of unfilling, meaning that new areas are expected to be colonized in the future.

Harmful algal blooms and lake restoration

Harmful algal blooms (HABs) are common in eutrophic freshwater ecosystems, and they promote poor water quality and toxin release. How bivalves affect HABs was studied by Marroni et al. (2022). They conducted laboratory experiments with a species of Diplodon (native to South America) feeding on a laboratory culture of Cryptomonas spp and a wild population of Microcystis aeruginosa (Kützing) complex (MAC) in various combinations. The results supported the hypothesis that the bivalve might favor the occurrence of MAC blooms by (1) not being able to consume it when it is forming scums, (2) actively consuming potential competitors, and (3) potentially boosts MAC growth by nutrient releasing.

Harmful algae are now spreading to new areas at high speed, in part due to the climate change. González-Madina et al. (2022) compared the demography of a rotifer species from saline ephemeral pools and a lake in Mexico. Population growth tests were conducted at three salinities ($10–15$ g l$^{-1}$) and two algal food concentrations. The authors found that (1) survivorship and growth rates increased with increasing food availability, (2) clones established from the ephemeral pools had higher growth rates than those from the permanent lake, (3) growth rates were lower in the lifetable experiments than in the population growth studies and (4) performance overall decreased with increasing salinity in the range studied.

Role of salinity

Salinity is a dominant environmental driver in both inland lakes in drylands and in coastal waters. NANDINI et al. (2022) compared the demography of a rotifer species from saline ephemeral pools and a lake in Mexico. Population growth tests were conducted at three salinities ($10–15$ g l$^{-1}$) and two algal food concentrations. The authors found that (1) survivorship and growth rates increased with increasing food availability, (2) clones established from the ephemeral pools had higher growth rates than those from the permanent lake, (3) growth rates were lower in the life-table experiments than in the population growth studies and (4) performance overall decreased with increasing salinity in the range studied.

Guimarães et al. (2022) explored the association between land use and fish species richness in 52 coastal lagoons in Southeast and South Brazil. In the Southeast, where most lagoons are subject to marine
influence, richness was negatively associated with agriculture and positively with urbanization; while in the South, dominated by freshwater lagoons, richness was negatively associated with urbanization and positively with agriculture. The results suggest that fish communities from freshwater coastal lagoons are more sensitive to land use than those from brackish lagoons. Differently from brackish lagoons, colonized by both freshwater and marine species, freshwater lagoons relied on neighboring lagoons as species donors. The authors conclude that the apparent resilience of the brackish lagoons should be regarded with caution since the increase in marine connections due to artificial sandbar openings may impair freshwater species with time. Shallow coastal habitats are regulated by fluctuating environmental conditions that cause shifts in fish communities.

Franco et al. (2022) studied how functional groups of habitat use and trophic strategy affected the fish composition and diversity in three coastal lagoons in Southeast Brazil. Despite the importance of other environmental factors (i.e., temperature and transparency), salinity was the key structuring factor in all the coastal lagoons. They found a great number of indicator species, typically of marine affinity in the lagoon with continuous and broad connection to the sea (euhaline conditions), while the lagoon with less contact to the sea was an important refuge for freshwater species. The authors stress the key role that coastal lagoons of varied water conditions have for supporting fish diversity at regional levels.

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