



Changes in functional composition and diversity of waterbirds: The roles of water level and submerged macrophytes

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Abstract

1. Water level and submerged macrophytes are critical players for the functioning of shallow lake ecosystems; understanding how waterbird communities respond to changes in both can have important implications for conservation and management. Here, we evaluated the effects of changes in water level and submerged macrophyte status on wintering waterbird community size, functional group abundances, functional diversity (FD), and community assembly by using a dataset compiled over 50 years.
2. We built generalised linear models to evaluate the effects of water level and submerged macrophyte status on the above-listed attributes of the waterbird communities by using mid-winter waterbird censuses, water level measurements, and submerged macrophyte surveys, along with submerged macrophyte macrofossil records from two shallow lakes in Turkey. Using a relevant set of functional traits, we defined functional groups, calculated four FD measures, and simulated null distributions of the FD measures for assessing assembly rules.
3. We found that macrophyte-dominated years had significantly higher abundances of waterbirds in one of the study lakes, and had more diving herbivores and omnivores in both lakes, while diving/scooping fish-eating waterbird abundance was lower in macrophyte-dominated years. Community size in Lake Beyşehir exhibited a negative association with water level; surprisingly, however, none of the functional group abundances and FD indices were significantly related to water level.
4. In our study communities, standardised effect sizes of functional richness and functional dispersion—two indices that are particularly sensitive to community assembly processes—were mostly lower than those of randomly assembled communities, which implies functional clustering. Shifts to a scarce-macrophyte state were associated with increases in these two indices, possibly due to either changes in the relative strength of environmental filtering and limiting similarity in community assembly or sampling of transitional communities. Further studies covering a wider range of the trophic/macrophyte status spectrum are needed to be certain.
5. The results of this study indicate that shifts between abundant and scarce-macrophyte states can have significant effects on wintering waterbird abundances, FD and community assembly. The results also suggest that shallow lakes in

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macrophyte-dominated states can support more wintering waterbirds, especially diving omnivores, some of which are globally threatened.

KEYWORDS

community assembly, functional diversity, functional groups, shallow lakes, submerged plants

1 | INTRODUCTION

A variety of terrestrial and aquatic organisms depend on freshwater lakes to exist (Hoverman & Johnson, 2012). Among these organisms are waterbirds that have become the focus of conservation and management efforts in shallow lakes and wetlands due to their widespread and dramatic decline (Green et al., 2017; Ramirez, Rodriguez, Seoane, Figuerola, & Bustamante, 2018). Waterbirds of the Northern Hemisphere depend on the lakes in mid-latitudes as essential wintering habitats (Cramp, 1977; Weller & Batt, 1988). However, these vital ecosystems are being increasingly threatened by human activities and climate change, resulting in deterioration in ecosystem services and biodiversity loss (Dudgeon et al., 2006; Green et al., 2017; Nassauer, 2004).

Water level and submerged macrophytes are important components of shallow lake ecosystems of mid-latitudes, both of which are capable of influencing various biotic and abiotic factors, including the trophic status of the lakes (Beklioğlu, Altınayar, & Tan, 2001; Coops, Beklioğlu, & Crisman, 2003; Scheffer, Hosper, Meijer, Moss, & Jeppesen, 1993). Shallow lakes can exist in two alternative equilibria: clear-water state dominated by abundant submerged macrophytes and turbid-water or eutrophic state characterised by high nutrient concentrations and large amounts of phytoplankton (Scheffer et al., 1993). Water level can be an important player in shifts between these two states, whereas submerged macrophytes can help maintain them (Beklioğlu et al., 2001; Jeppesen, Sondergaard, Sondergaard, & Christofferson, 2012; Rip, Rawee, & de Jong, 2006). Waterbird communities are sensitive to changes in water level and submerged macrophytes since they can directly or indirectly affect the availability, diversity, accessibility, and amount of waterbird food sources and foraging habitats (Colwell & Taft, 2000; Diehl & Kornijów, 1998; Noordhuis, van der Molen, & van den Berg, 2002). Considering the fact that the widespread eutrophication problem and strong water level fluctuations in the Mediterranean are both expected to intensify due to climate change and growing land use and human needs (Beklioğlu, Meerhoff, Søndergaard, & Jeppesen, 2011; Coops et al., 2003), studying responses of waterbird communities to water level changes and eutrophication-caused submerged macrophyte loss becomes a necessity.

Understanding and quantifying the response of waterbird communities to habitat changes can be challenging, and functional approaches dealing with functional attributes of organisms can be particularly useful in examining the effects of habitat changes on the communities. This is because, when compared to taxonomic approaches, functional approaches more readily relate to how species

are affected by ecosystem alterations and how they affect ecosystems in return (Santillán et al., 2019; Villéger, Miranda, Hernández, & Mouillot, 2010). Functional traits are traits that moderate how species affect ecosystem processes and how they respond to changes in the ecosystem (Luck, Lavorel, McIntyre, & Lumb, 2012). Functional diversity (FD) quantifies the diversity and distribution of functional traits (Villéger, Mason, & Mouillot, 2008). As a result, it has the potential to reach beyond taxonomic measures and explain ecosystem functions, processes, and community assembly and reliability more effectively (Tilman et al., 1997). Functional groups are collections of species having a similar set of functional traits, affecting some of the same ecosystem processes, and responding to changes similarly (de Bello et al., 2010). They are defined to simplify ecological complexity while maintaining relevant ecological differences between groups of species, thus allowing us to assess functional consequences of ecosystem changes in communities (Reynolds & Cumming, 2016).

Community assembly can be influenced by processes operating at both local and metacommunity scales (Leibold et al., 2004). Species sorting metacommunity perspective is expected to apply at the metacommunity scale for organisms such as birds that are highly mobile, capable of quickly responding to environmental changes and have strong habitat associations (Li et al., 2019; Özkan, Svenning, & Jeppesen, 2013; Spasojevic, Copeland, & Suding, 2014). In this perspective, assemblies are determined chiefly by local interactions (Leibold et al., 2004), and at the local scale, communities can be shaped by stochastic processes, environmental filtering, limiting similarity, fitness equalising, priority effects, or any combination of these (Spasojevic & Suding, 2012). Using patterns in FD to detect signs of environmental filtering, limiting similarity or stochastic processes assumes that priority effects and fitness equalising are unimportant in assembly (Spasojevic & Suding, 2012), which may be true for wintering waterbird communities of large shallow lakes (Daniel, Gleason, Cottenie, & Rooney, 2019). Both environmental filtering and limiting similarity (and stochastic processes) have traceable functional outcomes, and by using a relevant set of functional traits and FD measures, one can attempt to reveal which ones are in action (Mason, de Bello, Mouillot, Pavoine, & Dray, 2013). Under the species sorting perspective, the relative importance of these two processes are expected to change along environmental gradients, with changing spatial-scales, and with the age of habitats (Daniel et al., 2019; Li et al., 2019; Spasojevic et al., 2014).

Here, we used long-term waterbird census data to assess the influence of water level and submerged macrophytes on the community size, functional structure, FD, and community assembly of wintering waterbirds in two shallow lakes in Turkey, Uluabat and

Beyşehir. We hypothesised that abundant-macrophyte conditions, which are associated with increased ecological value at shallow lakes (Beklioğlu et al., 2017), would attract more wintering waterbirds, primarily by offering greater amounts food for them. Having considered the importance of food supply and feeding ecology for waterbird distribution in winter (Dalby, Fox, Petersen, Delany, & Svenning, 2013), we expected changes in food availability, occurring with shifts between high-macrophyte and low-macrophyte conditions, to determine which functional groups will be favoured under each of these conditions. Regarding FD, we expected macrophyte-dominated years to have communities with higher FD due to the increased structural and ecological diversity created by submerged macrophytes (Elmberg, Nummi, Pöytä, & Sjöberg, 1993; Li et al., 2019). We also predicted the relative strengths of local community assembly processes to change along macrophyte status and water level spectrums, and environmental filtering to dominate due to the strong habitat dependence of waterbirds (Li et al., 2019). We expected increases in water level to decrease the abundances of non-diving functional groups and increase FD by offering a wider depth range.

2 | METHODS

2.1 | Study sites

Our study focused on two shallow lakes from Turkey. Lake Uluabat (40.1489°N, 28.6148°E) is a freshwater lake located in north-west Turkey (Figure 1), where climate is mild throughout the year

(Altınayar, 1998). The mean annual temperature in the lake's surrounding is around 15°C and mean winter temperature is 6°C (Altınayaçlı & Griffiths, 2001). The lake's elevation is around 7–8 m, its surface area is approximately 120 km², and its depth ranges between 2.5 and 5.5 m for the most part (Altınayar, 1998; Levi et al., 2016). The lake is fed primarily by Mustafakemalpaşa River, several small streams, and groundwater (Beklioğlu, Tan, & Altınayar, 2006; Levi et al., 2016). Most of the water loss regulated by an outflow stream that joins Susurluk River, which eventually enters the Sea of Marmara (Levi et al., 2016). There are 12 islands in the lake and some get flooded depending on the water level (Eken, İsfandiyaroğlu, & Bozdoğan, 2006). The main human activity in the lake is fishing (Magnin & Yazar, 1997). The lake's catchment is 9,629 km² in size and is dominated by agricultural areas (Beklioğlu et al., 2006; Levi et al., 2016). High amounts of agricultural fertilisers in the runoff, together with several domestic and industrial effluents, have led to high nutrient concentrations in the lake (>0.1 mg/L total phosphorus), and the lake's trophic status is eutrophic (Levi et al., 2016). Dense reedbeds cover half of the lake's shores, while, along the other half, their distribution is patchy (Magnin & Yazar, 1997). The lake also contains some nympeid vegetation, although they are limited in extent (Eken et al., 2006; Levi et al., 2016). Most of the macrophyte macrofossil specimens found in the sediment cores belonged to *Najas*, *Chara*, *Myriophyllum*, *Potamogeton*, and *Ceratophyllum* genera (Levi et al., 2016).

Lake Beyşehir (37.7724°N, 31.5212°E) is the largest freshwater lake in the entire Mediterranean Basin, with a surface area of approximately 650 km² (Bucak et al., 2018). The lake is located in the Mediterranean Region (Figure 1), where prevailing climate is semi-dry



FIGURE 1 Locations of the study lakes (white stars)

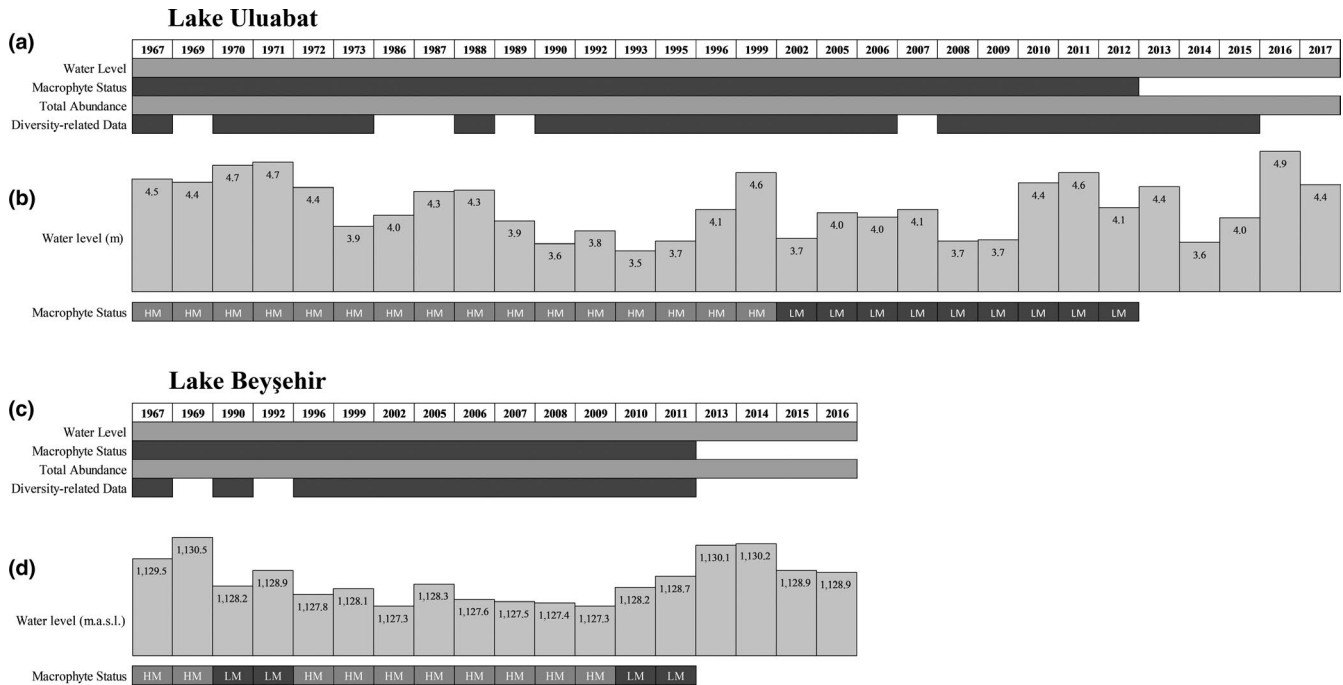


FIGURE 2 Availability of water level, macrophyte status, total abundance, and diversity-related (for functional group and functional diversity analyses) abundance data (a and c), and water level values and macrophyte status classification results (b and d) for Lake Uluabat (a and b) and Lake Beyşehir (c and d) for the study years

(Bucak et al., 2018). Mean annual temperature is 11°C, and mean winter temperature is 5.5°C around the lake (Bucak et al., 2018; Sari & İnan, 2011). The lake's average elevation is around 1,123 m, and it has an average depth of 5–6 m (Altınayar, Ertem, Aydoğan, & Akkaya, 1988; Bucak et al., 2018; Levi et al., 2016). Lake Beyşehir is fed mainly by rivers, streams emerging at the Anamas and Sultan mountains, freshwater springs, and precipitation (Bucak et al., 2018). Most of the water loss at the lake occurs via evaporation, controlled outflow for irrigation, and groundwater leakage into the Mediterranean Sea through karstic soil (Beklioglu et al., 2006; Levi et al., 2016). The lake lies within the boundaries of two national parks and two big provinces, and has been a first-degree Specially Protected Area since 1991 (Eken et al., 2006). There are 33 islands in Lake Beyşehir (Eken et al., 2006). Fishing is the main human activity in the lake (Eken et al., 2006). Its catchment encompasses 4,086 km², and approximately 80% of the catchment is made up of agricultural areas (Ciftci, Dursun, & Levend, 2010). Despite the heavy land use in its catchment, nutrient levels and phytoplankton biomass in the lake are low, and the lake's trophic status is oligo-mesotrophic with an average total phosphorus of 0.01–0.04 mg/L (Levi et al., 2016). Narrow reedbeds span a large portion of the shores, while dense reedbeds occur only at some parts of the lake (Magnin & Yazar, 1997). The lake also accommodates sparsely distributed patches of nymphaeid vegetation (Magnin & Yazar, 1997). Most of the submerged macrophyte macrofossils preserved in the sediment cores from the lake were from *Najas*, *Nitella*, *Chara*, *Potamogeton*, *Ranunculus*, and *Ceratophyllum* genera (Levi et al., 2016).

Both lakes host hundreds of thousands of migrating and wintering birds, and they are both Important Bird Areas, while Lake Uluabat is also a Ramsar Site (Eken et al., 2006).

2.2 | Mid-winter waterbird censuses

Mid-winter waterbird censuses (MWC) in Turkey are conducted between 15 January and 15 February as a part of International Waterbird Census of Wetlands International (DKMP, 2018). Dates of the censuses used in the current study ranged between 5 January and 9 February with >80% of them having been conducted in mid-January. The censuses were conducted by using point counts (Bibby, Burgess, Hill, & Mustoe, 2000) from a set of standard locations on land, and the whole lake surface was covered in a single day by multiple teams working simultaneously to minimise redundant count risk. Although MWC have been conducted in Turkey since 1967, there are many multiyear gaps during which no MWC were conducted, and some censuses were problematic, such as those reporting too many unidentified waterbirds. We excluded censuses reporting >50% unidentified individuals from diversity-related analyses (such as the ones regarding functional groups and FD), but included them in total abundance analyses. All waterbirds, except shorebirds, which were not counted in MWC in the past, were included in the study. Census years available for total abundance and diversity-related analyses are shown in Figure 2a,c. See Supporting Material S3 for information about how we dealt with the recent taxonomical split in the *Larus argentatus* complex.

2.3 | Water level and submerged macrophytes

We obtained water level data from the Directorate of Water Affairs of Turkey and from Middle East Technical University

Limnology Laboratory's database. To get a single water level measure that relates well to our study, we averaged monthly means for winter months of each census year and growth season months (March to August) of the preceding year. The resulting water level measure (hereafter water level) reflected both immediate water levels faced by wintering waterbirds and water levels under which most of the waterbird winter food sources grew and proliferated.

Published literature reporting submerged macrophyte coverage and diversity in the study lakes was used as the primary source to classify submerged macrophyte status of each study year (hereafter macrophyte status) into either low macrophyte (LM) or high macrophyte (HM). However, for most of the study years, such data were not available. For those years, we used sediment core data from Levi et al. (2016), which studied submerged macrophyte and cladoceran macrofossils and diatoms microfossils in relation to water level changes, to infer past macrophyte status. See Supporting Material S1 for the full list of published sources used in the classification and detailed information on how the classification was carried out by using the sediment core data.

Water level and results of the macrophyte status classification for the study years are given in Figure 2b,d. It was shown in a previous study that submerged macrophyte status of the study lakes can be linked to mean annual water level for some years (Beklioglu et al., 2006). To check whether this was the case with our data, we built binomial generalised linear models assessing the effect of water level measure used in the study on macrophyte status for both lakes. The models did not support any significant effect for either of the lakes, allowing us to include the variables simultaneously in the statistical models. This lack of association is plausible because macrophyte status and water level were defined differently here, and there are many factors other than water level that can potentially affect

submerged macrophyte coverage and diversity such as nutrient concentrations (Moss, 2013).

2.4 | Functional diversity

We chose 13 avian functional traits for FD calculations, and most of them were related to food acquisition and foraging habits, which relate well to the study and its aims because both submerged macrophytes and water level affect the food web structure, availability, and diversity of waterbird food sources (Table 1; Diehl & Kornijów, 1998; Ma, Cai, Li, & Chen, 2010; Noordhuis et al., 2002). Traits linked to resource use and capture are also deemed as drivers of ecosystem functioning and biodiversity relations and are associated with organisms' ability to respond to environmental changes (Luck et al., 2012).

Information related to the traits were obtained from Cramp (1977), del Hoyo, Elliott, Sargatal, and de Juana (2018), Kirwan et al. (2010), Wilman et al. (2014), and the sources listed in Supporting Material S2. We used winter diets of the species to score diet traits and mean values for body mass. We weighted the traits following Laliberté and Legendre (2010) and Seymour, Simmons, Joseph, and Slingsby (2015) to eliminate artificial overweighting. For example, we had seven traits related to spatial and temporal foraging habits, and we assigned 1/7 weight to each so that their cumulative effect has one unit weight.

We calculated Gower distances (Podani, 1999), which allows for use of categorical and numerical traits together, to build a distance matrix. We used the resulting distance matrix to calculate four FD indices that are uncoupled to each other and assess different facets of FD: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis). Functional richness is the volume of the multidimensional trait space occupied by species coexisting in a community (Villéger et al., 2008).

TABLE 1 Functional traits used in functional diversity calculations

Trait category	Trait	Data type	Units/classes
Resource quantity and energy consumption	Body mass	Continuous	Grams
	Migratory strategy	Binary	Long distance migrants, others
Food accessibility and foraging habits	Nocturnal	Binary	Yes, no
	Land	Binary	Yes, no
	Reeds	Binary	Yes, no
	Shallows: surface	Binary	Yes, no
	Shallows: water column and bottom	Binary	Yes, no
	Open water: surface	Binary	Yes, no
	Open water: water column	Binary	Yes, no
Diet	Open water: bottom	Binary	Yes, no
	Fish	Binary	Yes, no
	Invertebrates	Binary	Yes, no
	Plants	Binary	Yes, no

Functional evenness is a measure of evenness of species abundances in trait space occupied (Mason, Mouillot, Lee, Wilson, & Setälä, 2005). Functional divergence is a measure of the deviance of species from the mean distance of the community to its centroid (Villéger et al., 2008). Functional dispersion measures trait dispersion in a community; it is the average distance of individual species to the centroid of the whole community in trait space (Laliberté & Legendre, 2010). Calculations of the FD indices were carried out in R 3.5.0 (R Core Team, 2018) by using the *dbFD* function from the *FD* package (Laliberté, Legendre, Shipley, & Laliberté, 2014). The *dbFD* function conducts principal coordinates analysis (PCoA) to produce PCoA axes and uses them as traits (Laliberté et al., 2014). The number of PCoA axes used for the calculations was always high enough to ensure at least 92% representation. We allowed for weighting by relative abundances while calculating FDiv and FDis.

2.5 | Functional groups

The cumulative number of waterbird species included in this study was 50, and we classified them into 11 functional groups by using the functional traits given Table 1. Unweighted pair-group method with arithmetic mean was used to cluster the Gower distance matrix—built using the functional traits—and produce a cluster dendrogram. The resulting cluster dendrogram was examined visually to delimit the functional groups. The defined functional groups were as follows: diving herbivores, non-diving herbivores, diving omnivores, surface omnivores, reed-dwelling omnivores, generalist gulls, wading piscivores, surface piscivores, diving/scooping piscivores, surface invertebrate/small fish consumers, and diving invertebrate/small fish consumers. The cluster dendrogram and detailed descriptions of the functional groups are given in Supporting Material S2.

2.6 | Null models

We used null models to investigate mechanisms that shaped the functional structure of the communities and to eliminate any artefact in FD that may be caused by changing species richness (Flynn et al., 2009; Swenson, 2014). We simulated null distributions of FD measures for the observed species richness values and abundances to see if the observed FD values differ from those of randomly assembled communities. For a community with n species, the null model was created by sampling n species randomly from the regional pool—defined as cumulative list of wintering waterbird species from the corresponding lake—without replacement 999 times and calculating FD indices for these 999 *random* communities (Che et al., 2018; Seymour et al., 2015; Swenson, 2014). In this way, species richness and community size are kept the same for each community, while only the names of the species are shuffled (Che et al., 2018; Swenson, 2014). The simulated FD values were then combined with the observed values to calculate standardised effect sizes (SES) for each observation. Positive SES values indicate

functional overdispersion and may point to limiting similarity being the dominant factor in community assembly, whereas negative SES values indicate functional clustering and may point to environmental filtering being the dominant force in community assembly (de Arruda Almeida, Sebastián-González, dos Anjos, Green, & Botella, 2019). Standardised effect size values close to zero, by contrast, may indicate a neutrally assembled community or that the chosen functional traits are not important in community assembly (Mouchet, Villéger, Mason, & Mouillot, 2010). We also calculated p -values for each observation to see whether the observed values are significantly different from the expected values.

2.7 | Statistical analyses

We used generalised linear models (GLMs; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) to evaluate the effects of both water level (continuous; either in m above sea level or m) and macrophyte status (categorical with two levels; HM and LM) on total abundance, abundances of the functional groups, the four FD measures, and SES of the FD measures. Positive continuous response variables (e.g. FD metrics) were modelled with Gamma-distributed errors (log link), count responses (e.g. functional group abundances) were modelled with negative-binomial-distributed errors (log link), and standardised continuous responses (e.g. SES of the FD measures) were modelled with normally-distributed errors (identity link). We also pooled the data from the two study lakes to increase statistical power and to reach more general conclusions. Before pooling, we standardised the response variables and water level predictor to mean 0 and standard deviation 1 to make them comparable without bias and used these standardised values in our models. We included lake identity, which had two levels, as a fixed effect (Bolker et al., 2009) in these *pooled* models to evaluate and control for between-lakes variation.

To minimise possible biases due to relatively small sample sizes, we followed the guidelines set by Bolker et al. (2009) and allowed at least >10 observations per predictor variable in each model, meaning that some of the models were built with a single predictor (Lake Beyşehir models) while others were built with two (Lake Uluabat models) or three predictors (the pooled models, which also included a lake identity term—see above). GLMs and model selections were done in R 3.5.0. We used *glmmTMB* function from *glmmTMB* package to build the models (Brooks et al., 2017). Model selection was done by using corrected Akaike information criterion (AICc; Burnham & Anderson, 2002) which performs better with small sample sizes. Corrected Akaike information criterion scores were compared to that of the null models, and models whose AICc was not 2 units smaller than the null models' AICc were discarded. Models with $\Delta\text{AICc} < 2$ were considered as competitors to the best model (Burnham & Anderson, 2002). We assessed the significance of effects of predictors by checking whether 95% confidence intervals overlapped 0. We validated the models by visual inspection of the residuals and by plotting the residuals against the included and excluded predictors to check for patterns (Zuur et al., 2009). We tested

for violation of independence by using autocorrelation and partial autocorrelation plots (Brockwell, Davis, & Fienberg, 1991; Venables & Ripley, 2013). When autocorrelation/partial autocorrelation in residuals was significant, we used autocorrelation and partial autocorrelation patterns to define covariance structures in the models to eliminate it. To validate if the model predictions comply with the data, we used *simulateResiduals* function in *DHARMA* package in R 3.5.0 (Hartig, 2018) and fitted models to simulate 10,000 datasets for each model. A Kolmogorov–Smirnov test was then applied on the simulated residuals and the observed ones to test for uniformity. As a part of model validation, we also used *testDispersion* function from *DHARMA* package to perform a simulation-based test for over-/under-dispersion. Models whose residuals exhibited autocorrelation (that cannot be fixed by defining covariance structures), unbalanced distribution or patterns (that cannot be fixed by including higher degree predictors or simply other predictors), models whose predictions did not comply with the data, and models with significant over-/under-dispersion were discarded.

3 | RESULTS

3.1 | Total abundance and functional group abundances

At Lake Beyşehir, periods of low water level (Figure 3a; Table S2/1) and HM (Figure 3b; Table S2/2) were associated with significant increases in the total abundance of wintering waterbirds. The associations disappeared when the data was combined with Lake Uluabat's data for which no significant water level and macrophyte status effects were observed. It should be noted, however, that the pooled model with macrophyte status predictor supported a mostly positive but non-significant effect of HM status on total abundance, with 95% confidence intervals of the effect barely overlapping zero (negative binomial GLM with log link, estimate = 0.871, standard error = 0.450, $p = 0.053$, $n = 20$, $\Delta\text{AICc} = 2.19$).

Changes in percent representation of the functional groups at the study lakes in relation to macrophyte status over the study years are shown in Figures S2 and S3. Diving herbivores, diving omnivores and diving/scooping piscivores were the only functional groups whose abundances were related to changes in water level and macrophyte status. For the pooled dataset, HM status was positively associated with diving herbivore and diving omnivore abundances (Figure 4a; Table S2/3–4), and negatively associated with diving/scooping piscivore abundances (Figure 4a; Table S2/5). When the lakes were evaluated individually, for both lakes, HM years were positively related to diving herbivore abundances (Table S2/6–7). Both of the best models of diving omnivore abundance at Lake Uluabat included macrophyte status terms, and they both supported a positive effect of HM status (Table S2/8–9). At Lake Beyşehir, HM years were negatively related to diving/scooping piscivore abundances (Table S2/10). Water level was not associated with any of the functional groups' abundances.

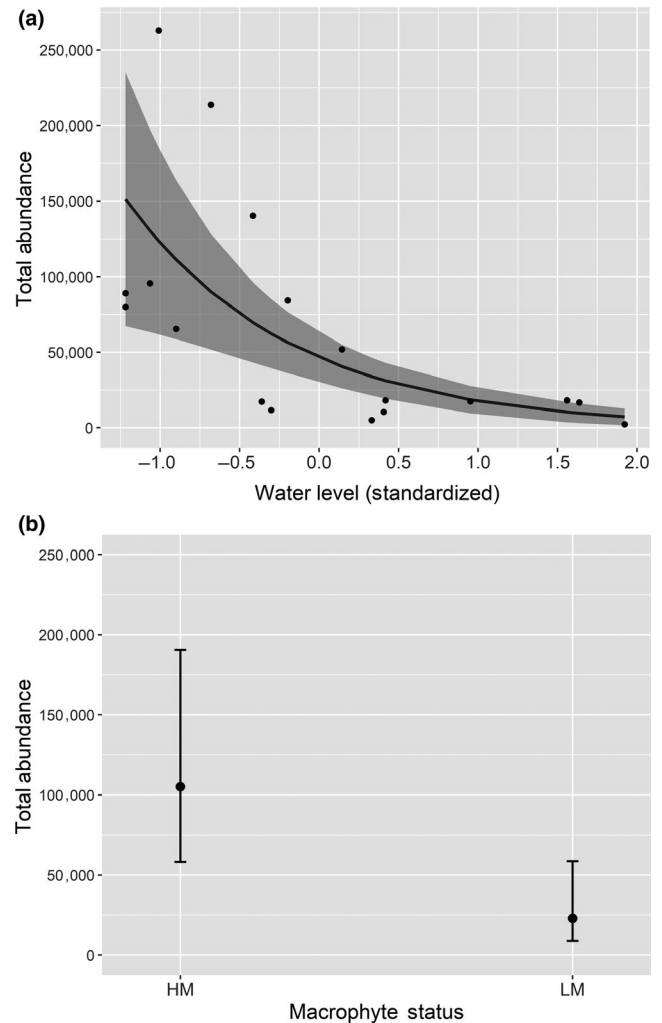


FIGURE 3 Predictions from generalised linear models assessing the influence of (a) water level ($n = 18$) and (b) macrophyte status (HM: high macrophyte; LM: low macrophyte; $n = 14$) on total abundance of wintering waterbird communities in Lake Beyşehir. (a) Dark line indicates predicted values; dots indicate observed values and light band indicates 95% confidence intervals. (b) Dots indicate predicted values and bars indicate 95% confidence intervals

3.2 | Functional diversity

FDis was the only FD measure for which significant effects were observed. For the pooled data and Lake Uluabat, increases in FDis were associated with LM status (Table S2/11–13).

In the pooled dataset, 87% of SESFRic were negative, and 26% of SESFRic were significantly lower than expected (Figure 5). Statistical models built for the pooled data and Lake Uluabat supported a positive effect of LM conditions on SESFRic (Figure 4b; Table S2/14–16). It was found that 85% of SESFDis in the pooled dataset were negative, and 8% of SESFDis were significantly lower than expected (Figure 3). Based on GLMs built for the pooled dataset and Lake Uluabat, LM years were associated with higher SESFDis (Figure 4b; Table S2/17–18). 59% of SESFEve were negative in the pooled dataset, and 8% of SESFEve were significantly lower than expected by chance (Figure 5). Neither macrophyte

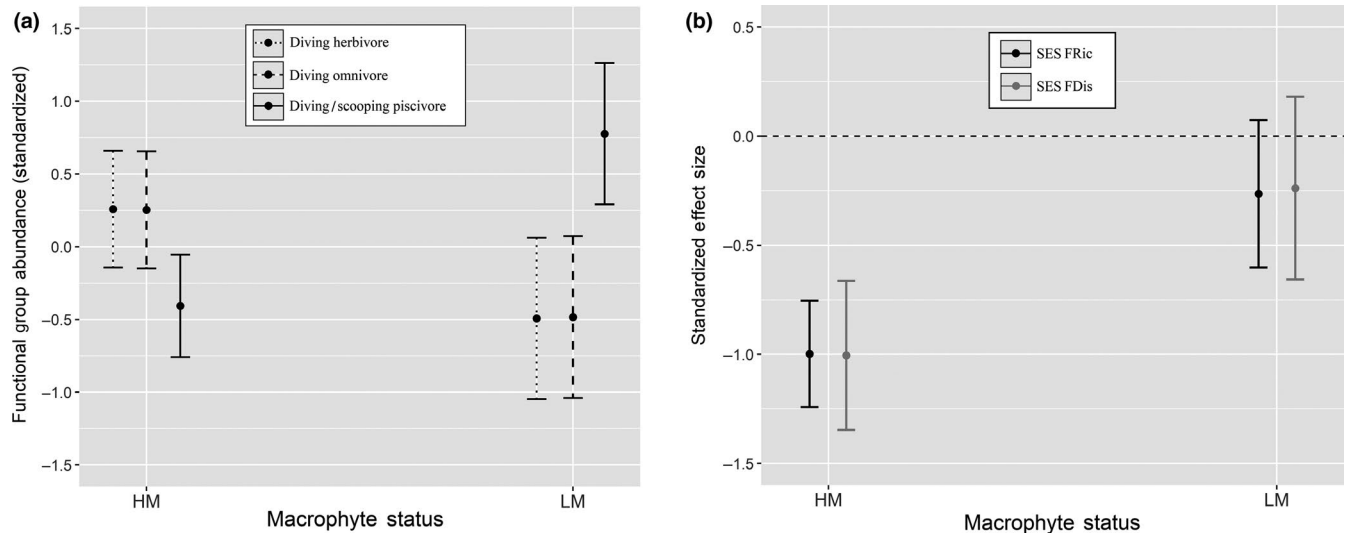


FIGURE 4 Predictions from generalised linear models assessing the influence of macrophyte status (HM: high macrophyte; LM: low macrophyte): (a) on the pooled standardised abundances of diving herbivore (dotted bars), diving omnivore (dashed bars) and diving or scooping piscivore (solid bars) functional groups ($n = 32$ for each); and (b) on the pooled standardised effect sizes (SES) of observed functional richness (FRic; black bars) and functional dispersion (FDis; gray bars; $n = 32$ for each), and (b). Points indicate mean predicted values and bars indicate 95% confidence intervals

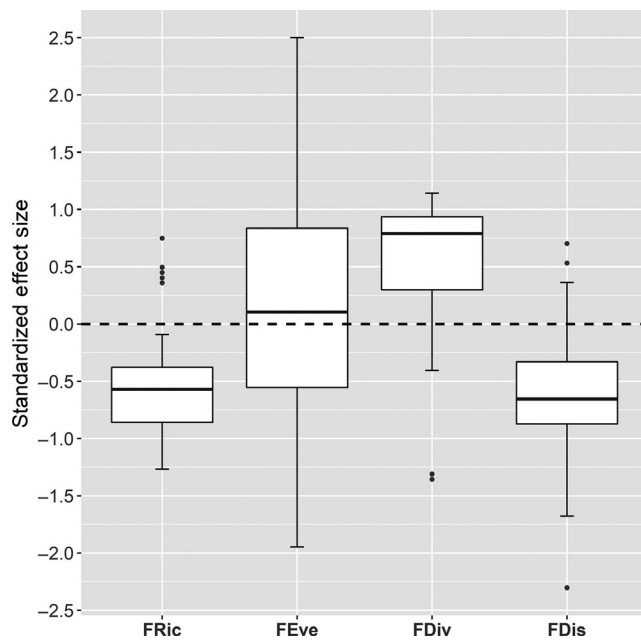


FIGURE 5 Standardised effect sizes of the observed functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis) for the pooled dataset ($n = 39$ for each)

status nor water level were significantly related to SESFEve in our models. In total, 87% of FDiv observation in the pooled dataset had positive SES (Figure 5), but none was significantly different from null expectations. Based on the statistical models, SESFDiv was not related to the water level and macrophyte status. Our models did not support any significant water level effect on FD indices and their SES.

4 | DISCUSSION

Our results provide support for our hypothesis that shallow lakes in macrophyte-dominated states can attract more wintering waterbirds. Abundances of some functional groups changed in accordance with changes in their food sources as we expected. Contrary to our expectations, water level had significant influence only on total abundance in one of the study lakes. The effect of submerged macrophytes on FD was opposite to what was expected: FD of low-macrophyte years was higher than that of HM years. Our null assembly simulations showed that environmental filtering may be the dominant assembly force, and relative contributions of assembly processes may change as shallow lakes switch between macrophyte-dominated and scarce-macrophyte conditions.

4.1 | Total abundance and functional group abundances

We found that submerged macrophyte status can be highly influential in shaping total abundance and functional group abundances of wintering waterbird communities of the study lakes. In Lake Beyşehir, HM years were associated with greater wintering waterbird abundances, which was primarily due to increases in diving herbivore and diving omnivore abundances. In Lake Uluabat, the findings were similar, although non-significant. These results corroborated with our predictions and with previous literature reporting an increase in number of non-breeding waterbirds in lakes with increased macrophyte coverage and diversity (Beklioğlu et al., 2006; Froneman, Mangnall, Little, & Crowe, 2001; Milberg, Gezelius, Blindow, Nilsson, & Tyrberg, 2002). Increases in diving herbivore

and omnivore abundances in HM years can be explained by the importance of submerged macrophytes' vegetative tissue and seeds as food sources for these functional groups in winter (Cramp, 1977; Noordhuis et al., 2002), the submerged macrophytes' ability to provide suitable habitat and shelter for aquatic macroinvertebrates (Diehl & Kornijów, 1998; Pardue & Webb, 1985; Tománková, Harrod, Fox, & Reid, 2014), and the suppressing effect of submerged macrophytes on benthivorous fish (Bekliöglu et al., 2001, 2006) that compete with diving omnivore waterbirds over benthic macroinvertebrate prey (Maceda-Veiga, López, & Green, 2017). As we expected, unlike diving herbivores and omnivores, the abundances of diving/scooping piscivores were higher in LM years, and this could be due to the increase in benthivorous fish biomass. It has been shown that scarce-macrophyte conditions in the study lakes can increase benthivorous/planktivorous fish biomass (Altınayar, 1998; Altınayar et al., 1988; Bekliöglu et al., 2001). Submerged macrophytes can also provide physical shelter for fish against predation by dive-chasing piscivore waterbirds (Paillisson, Carpentier, Le Gentil, & Marion, 2004). Consequently, LM years may be able to support more diving/scooping piscivores by offering a greater and more accessible fish biomass.

Water level was found to be related only to total abundance at Lake Beyşehir. This can be because decreasing water level may: (1) increase the extent of foraging habitat for non-diving waterbirds such as dabbling ducks and waders (Ma et al., 2010; Perry & Deller, 1996); (2) increase feeding efficiency and decrease energy expenditure for many waterbirds as it is harder to seize prey and more energy is consumed per prey item in deeper water (Guillemain, Martin, & Fritz, 2002; Ma et al., 2010; Nolet, Bevan, Klaassen, Langevoord, & Van Der Heijden, 2002); and (3) promote submerged macrophyte growth and bring about all the positive effects of submerged macrophytes. Although no significant association between the water level measure and submerged macrophyte status were observed for our study years, the water level predictor in the best model of submerged macrophyte status of Lake Beyşehir, water level predictor had a non-significant but mostly negative effect estimate (binomial GLM with logit link, Estimate = -3.175, SE = 1.889, $p = 0.093$, $n = 14$). Since our binary macrophyte status classification force-converts continuous variables, macrophyte coverage and diversity, into a single discrete variable, it most probably has failed to capture some information.

Abundances of functional groups other than diving omnivores, diving herbivores and diving/scooping piscivores were not related to the two predictors used in the study. See Supporting Material S6 for a short discussion on possible underlying reasons for the observed lack of association.

4.2 | Functional diversity

Contrary to our expectations, in Lake Uluabat and the pooled dataset, it was LM years that had communities with significantly higher FDis. Functional richness, which is inherently linked to species richness

(Villéger et al., 2008), did not exhibit any significant patterns when tested for effects of water level and submerged macrophytes. This may be because of the evident turnover of species from different functional groups taking place after state shifts. When shallow lakes start shifting from HM to LM conditions, the trophic structure of the lakes changes, which can gradually invite previously unfavoured species (e.g. diving/scooping piscivores) while some other species are lost (e.g. diving omnivores). The resulting species turnover can balance the loss and keep the convex hull volume unchanged as it switches position in trait space.

Although FRic and FDis can have some considerable power in detecting trait convergence/divergence (Aiba et al., 2013), they have low power in detecting community assembly mechanisms (Mason et al., 2005). Two complementary measures, SESFRic and SESFDis, which are sensitive to assembly processes on species occurrence and abundance, respectively, are suggested indices for detecting assembly mechanisms (Mason et al., 2013). SESFRic in the pooled dataset were mostly negative and 26% of them were significantly lower than that expected by a neutral assembly. Similar to SESFRic, SESFDis were also overwhelmingly negative. Negative values of SESFRic and SESFDis may be because of environmental filtering, which was the assembly process we predicted to dominate waterbirds assembly in winter. Environmental filtering would result in negative SESFRic and SESFDis values by allowing only a set of species with certain functional traits to persist and by forcing most of the biomass into a small trait space (Liu, Swenson, Zhang, & Ma, 2013; Mason et al., 2005). These findings were also in concordance with some of the previous studies on waterbirds that reported functionally clustered waterbirds communities (the western populations in Che et al., 2018; summer season in Che et al., 2019; Li et al., 2019). For organisms like waterbirds, which have high-dispersal capabilities and can respond to changes in the environment quickly, priority effects (Chase, 2003) and stochastic processes (Hubbell, 2001) are less likely to be dominant players in community assembly (Daniel et al., 2019; Fukami, 2015; Li et al., 2019). One may argue that highly mobile taxa such as birds should rely on larger landscapes and should be exposed to filtering at the landscape scale (Rooney, Bayley, Creed, & Wilson, 2012). However, most waterbirds depend strongly on wetlands and have strong habitat associations, which means that environmental filtering can also be a strong force in community assembly at local scale (Li et al., 2019), especially during times of the year when environmental stress is high such as winter in our study region (summer season in Che et al., 2018). Furthermore, in permanent and large lakes such as our study lakes, environmental filtering is expected to be more prominent in community assembly as compared to smaller and temporary wetlands, where stochastic events and priority effect are expected to be major determinants of assembly (Daniel et al., 2019; Li et al., 2019). However, it should also be noted that there have been other studies reporting neutrally assembled waterbird communities (spring and autumn populations in Che et al., 2019; populations of temporary wetlands in Daniel et al., 2019; de Arruda Almeida et al., 2019) and functionally over-dispersed waterbird communities (the eastern populations in

Che et al., 2018; winter populations in Che et al., 2019). Overall, various factors including climate, wetland age, wetland size, season of the year, population densities, and trophic states of wetlands seem to be capable of influencing waterbird community assembly.

Unlike SESFRic and SESFDIs, SESFDiv in the pooled dataset were mostly positive (Figure 3). Although FDiv index is not very good at detecting community assembly processes (Mason et al., 2013), higher than expected values of FDiv can indicate high niche differentiation and/or high dissimilarity of the most abundant species (Mouchet et al., 2010). In other words, although the community is forced into a smaller-than-expected trait space, most of the biomass lies in the species located near the peripheries of the occupied trait space. This might be because of limiting similarity playing its part after the initial filtering forces the biomass into a smaller-than-expected trait space (Mason et al., 2005).

The models of SESFRic and SESFDIs supported positive effects of LM status for the pooled dataset and Lake Uluabat. Although the SESFRic and SESFDIs were still mostly on the negative side, meaning that they were still lower than those of randomly assembled communities, as the lakes shifted to LM status, SESFRic and SESFDIs started to approach zero. We offer three explanations for this. First, as we hypothesised, the observed patterns can be the result of changes in relative importance of community assembly processes (Spasojevic et al., 2014). It is known that multiple assembly processes can act simultaneously to yield a complex assembly pattern or a neutral outcome, and their relative importance can change along environmental gradients (Mason et al., 2013; Spasojevic et al., 2014; Spasojevic & Suding, 2012). This means that the higher SESFRic and SESFDIs values observed for LM conditions can be explained by an increased prevalence of competitive interactions under nutrient-enriched LM conditions. In ecosystems with high nutrients levels or productivity, competition can become a dominant process (Döbert, Webber, Sugau, Dickinson, & Didham, 2017; Santillán et al., 2019; Spasojevic & Suding, 2012). This would cause both species occurrence and abundance to show signs of limiting similarity, as seen in our case with a gradually increasing SESFRic and SESFDIs. The observed patterns can also be the result of a weakening in environmental filtering. A weaker filtering process is expected to cause the exact same effects listed above, and the nature of the available data make it practically impossible to tell whether either one of the two or both are responsible for the observed pattern. Second, as suggested by Döbert et al. (2017), the reason for observing higher FD values in communities of degraded habitats (LM years in our case) may actually be that they are in fact transitional communities. This can be plausible because habitat change can be a gradual process and while present niches are gradually disappearing, new niches can form or previously smaller niches can grow. Consequently, some previously present species may decline in abundance while new individuals from functionally dissimilar species may start settling in, which can gradually increase FDIs, SESFDIs, and SESFRic. This may well be what we are observing in LM years, although we cannot be certain since our samples probably cover only a portion of the trophic spectrum or macrophyte status spectrum.

It seems practically impossible for the current study to conclusively answer whether the major cause for increased SESFRic and SESFDIs under LM conditions is the changes in relative strength of the community assembly processes (the first explanation) or an ecological transition (the second explanation). However, it is almost certain that studying waterbird communities over a wider range of the trophic/macrophyte status spectrum would give more insight because, depending on the assembly processes operating at local and metacommunity level, we might be seeing only a portion of the relationship between the predictors and FD (Spasojevic et al., 2014), meaning that the relationships might actually be hump-shaped as well as linear. It should also be noted that FD values and detection of community assembly processes depend strongly on the set of functional traits used (Pakeman, 2014), and we believe that we have chosen a relevant collection of functional traits for the study, but inclusion of different functional traits may yield different patterns.

4.3 | On the lack of significant relationships with water level

Contrary to our expectations, water level predictor had a significant effect estimate in only a single model. Changes in open water area and submerged macrophyte coverage can be controlled by changes in water level in shallow lakes, and changes in these confounding factors may have more direct effects on waterbird communities than water level itself (Beklioğlu et al., 2006; Ma et al., 2010). Consequently, studying waterbird communities in relation to solely water level can be very difficult in natural ecosystems and may require experimental manipulations. We advise researchers intending to investigate the effect of water level on waterbirds to be wary of the factors that are linked to water level and design their studies accordingly.

5 | CONCLUSION

To the best of our knowledge, our study was the first to investigate the FD and community assembly of waterbird communities in relation to the submerged macrophyte status of shallow lakes. We used paleolimnological data and published literature to reconstruct past submerged macrophyte status of two shallow lakes, together with water level data, and found that macrophyte-dominated clear-water years can support more wintering waterbirds, especially diving omnivores, some of which are globally threatened such as the white-headed duck (*Oxyura leucocephala*) and the common pochard (*Aythya ferina*) (IUCN, 2019). Widespread loss of submerged macrophytes due to eutrophication can cause significant declines in the food sources of herbivorous and omnivorous waterbirds, thereby decreasing the carrying capacity of shallow lakes for these waterbirds in winter. Hence, we suggest that policy makers and local managers increase their efforts on having shallow lakes in a clear-water state in important waterbird wintering grounds, like the Mediterranean,

where the eutrophication problem is expected to worsen due to human actions and climate change (Beklioğlu et al., 2011). Our results indicate that both the FD of waterbird communities and the relative importance of environmental filtering and limiting similarity in community assembly may change when shallow lakes switch between abundant and scarce-macrophyte conditions. Studies covering a wider range of the trophic/macrophyte status spectrum are needed to eliminate possible artefacts caused by the sampling of transitional communities and to have a better understanding of how different facets of FD and community assembly processes change along the trophic/macrophyte status spectrum at shallow lakes. We also suggest that future studies aiming to evaluate the effect of water level on waterbird communities of shallow lakes should be designed by taking the possible confounding effects of other factors into careful consideration.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data used in the study are available at <https://figshare.com/s/1e3b281a0afdaf2c624a>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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