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Influence of climatic conditions and hazelnut farming on the temporal trends and spatial distribution of waterbirds at wintering grounds

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Abstract

Waterbird distribution in Mediterranean wetlands during winter is shaped by habitat conditions, climate, food availability, and human activities. We analysed International Waterbird Census data collected between 2009 and 2025 at a volcanic lake in central Italy that has been heavily impacted by intensive hazelnut cultivation. Our aim was to assess spatio-temporal trends of long-distance migratory waterbirds and to evaluate the influence of large-scale climate, measured using the North Atlantic Oscillation (NAO), local climatic conditions, and hazelnut farming along the lake shores. Temporal trends were analysed using Generalized Additive Models (GAMs), while spatial patterns were assessed with Generalized Linear Mixed Models (GLMMs) assuming a negative binomial error distribution. Analyses were conducted at both the species level and by grouping species into taxonomic and trophic categories. In total, 74,207 individuals belonging to 28 species were recorded. Seven species exhibited significant declines, particularly among dabbling and diving ducks, as well as herbivorous and omnivorous birds. These declines may be linked to nutrient enrichment associated with hazelnut farming, which degrades aquatic vegetation and reduces food availability. Although most waterbirds were evenly distributed across the lake, both overall and within most taxonomic and trophic groups, invertivores were predominantly recorded along shores adjacent to hazelnut orchards. This spatial pattern may reflect the presence of patches of aquatic vegetation in nutrient-enriched areas, which in turn provide suitable habitats

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for aquatic invertebrates. We found no significant relationship between waterbird abundance and either large-scale or local climatic conditions, suggesting that habitat degradation may play a more important role than climate in shaping wintering waterbird distributions. Our findings highlight the importance of local environmental conditions, particularly land-use practices, in Mediterranean wetlands and encourage replication of this study across other sites to assess the generality of the observed effects of hazelnut cultivation.

Keywords: Intensive farming, waterfowls, volcanic lake, nutrient enrichment, wetland

INTRODUCTION

Mediterranean wetlands are critical habitats for waterbirds during winter, providing essential resources for feeding and roosting (Gilissen et al. 2002, Rendón et al. 2008, van Roomen et al. 2012, Pavón-Jordán et al. 2020). A key factor influencing the distribution of waterbirds is habitat availability and quality, which are determined by the extent of wetland areas, water levels, and vegetation cover (Guillemain et al. 2002, Taft & Haig 2006, Schummer et al. 2010, Adam et al. 2015, Li et al. 2019). Generally, sites with extensive water surfaces and abundant macrophytes and invertebrates are highly suitable for waterbirds because of their greater carrying capacity and improved protection from predators (Guadagnin et al. 2005, Ma et al. 2010, Adam et al. 2015, Zhou et al. 2020). However, habitat degradation caused by drainage, pollution, and water management practices often reduces carrying capacity, leading to population declines (Duncan et al. 1999, Zou et al. 2017, Xu et al. 2019). For example, the winter distribution of the Mallard (*Anas platyrhynchos*) and the Northern Shoveler (*Spatula clypeata*) is strongly related to seasonal variations in water conditions and management practices (Kirby & Mitchell 1993, Briggs et al. 2012, Herbert et al. 2018). Environmental changes in the surroundings of wetlands also play a crucial role in shaping waterbird distributions, as suitable feeding areas for many species may be located several kilometres from roosting sites (Jorde et al. 1983, Duncan et al. 1999, Beatty et al. 2014). For instance, in western France, the decline of the Northen Pintail (*Anas acuta*) over recent decades has been attributed to a substantial reduction in grasslands surrounding key wetlands (Duncan et al. 1999). Because waterbirds are highly responsive to habitat changes, they are widely regarded as effective indicators of wetland ecosystem quality (Stolen et al. 2004, Fernández et al. 2005, Amat & Green 2010, Zhang & Ma 2011).

Climate conditions are another pivotal factor influencing the wintering behaviour of waterbirds. Wintering waterbirds are highly sensitive to temperature variations and precipitation patterns, which affect wetland conditions and food availability (Gilissen et al. 2002, Guillemain et al. 2002, Maclean et al. 2008, Adam et al. 2015, Musilová et al. 2018, Pavón-Jordán et al. 2020). Although temperature alone does not fully explain distribution patterns (Dalby et al. 2013), freezing conditions, snow, and ice substantially reduce foraging opportunities and food availability (Jorde et al. 1983, Schummer et al. 2010), often forcing birds to move to areas with more suitable conditions. Birds may move locally to "cold weather refuge sites", where the selective pressures of winter harshness are reduced and unfrozen water bodies are available, such as running waters, urban areas, and freshwater reservoirs (Guillemain et al. 2002, Adam et al. 2015, Musilová et al. 2015). Alternatively, they may move longer distances to warmer regions where food is more abundant (Sauter et al. 2010, Caizergues et al. 2016, Giunchi et al. 2019, Kämpfer et al. 2023). For example, during colder winters, many species breeding in central Europe migrate southward within the Mediterranean Basin to avoid freezing conditions and exploit more temperate wetlands (Olivero et al. 1998, Rendón et al. 2008, Gaget et al. 2020). Conversely, mild winters promote broader distributions across northern and central Europe (Gilissen et al. 2002, Nilsson 2008, Lehikoinen et al. 2013, Musilová et al. 2018).

Food availability further shapes waterbird distributions and habitat use (Rendón et al. 2008, Ma et al. 2010, Musilová et al. 2022). Diving species, such as cormorants and pochards, which feed primarily on fish and aquatic invertebrates (Cramp & Simmons 1977, del Hoyo et al. 1992), preferentially select fish ponds and deeper waters (Rendón et al. 2008, Musilová et al. 2018). Waders require mudflats rich in benthic prey (Cramp 1983, del Hoyo et al. 1996), whereas herbivorous or granivorous species such as dabbling ducks and coots (Cramp & Simmons 1977, del Hoyo et al. 1992, Kear 2005) concentrate in marshes rich in submerged and emergent vegetation (Rendón et al. 2008, Zhou et al. 2020). Finally, human activities exert significant pressure on waterbird populations. Wetland reclamation, hunting, and disturbance from tourism or recreational activities disrupt habitat use (Ebbinge 1991, Madsen 1995, Schlacher et al. 2013, Scarton 2018). Conversely, well-managed protected areas and conservation actions, such as wetland restoration and hunting regulation, can mitigate these impacts and support waterbird populations (Ma et al. 2010, Zhou et al. 2020, Battisti et al. 2023). Although substantial evidence exists on the effects of individual factors on the wintering ecology of waterbirds, the combined influence of multiple drivers on the spatio-temporal distribution of wintering waterbirds in the Mediterranean Basin remains poorly understood, as most studies have been conducted in Central Europe (Adam et al. 2015, Musilová et al. 2018).

Relying on a long-term dataset of waterbirds wintering at a lake in central Italy that has been severely impacted by hazelnut orchards, we assessed (i) temporal trends in long-distance migratory waterbirds, (ii) whether these trends are influenced by climatic conditions in northern Europe, and (iii) whether the spatial distribution of waterbirds is affected by hazelnut farming along the lake shores. We hypothesized a decline in wintering waterbirds due to the reduction of suitable habitats in the study area caused by intensive agriculture. Indeed, between the 1950s and 1990s, traditional extensive cereal crops in the area were replaced by modern intensive hazelnut orchards, which require bare soil to optimise mechanical harvesting (Leone et al. 2003, Leone et al. 2008). This transition has contributed to increased nutrient loading in the lake, particularly phosphates and nitrates (Leone & Marini 1993, Dyer 1995, Leone et al. 2008, Garnier et al. 2010), mainly via runoff (Dyer 1995, Leone et al. 2003, Costantini et al. 2007, Recanatesi et al. 2013, Petroselli et al. 2014). Excessive nutrient enrichment and agrochemical pollution are likely to have negative impacts on aquatic vegetation (Forsberg 1964, Blindow 1992, Tamisier & Dehorter 1999, Van den Berg et al. 1999, Moss 2007, Kolada 2010). In our study area, this is reflected in the decline of key habitats for waterbirds: reedbeds decreased by 52% between 1960 and 2005, while *Chara* beds declined by 36% from 1971 to 2007, with further reductions ongoing (Azzella & Scarfò 2010). Additionally, given recent climate changes in Europe, with milder winters in northern and central regions (EEA 2024), we predicted a decline in wintering waterbirds in our study area associated with climatic conditions. Evidence suggests that climate change has shifted the winter distribution of waterbirds towards the northern part of their range (Nilsson 2005, Lehikoinen et al. 2013, Musilová et al. 2018, Pavón-Jordán et al. 2020). Finally, although we predicted an overall decline due to intensive agricultural practices, we expected waterbirds to be more abundant near hazelnut orchards than in other parts of the lake, because the lake is classified as meso-eutrophic (Margaritora et al. 2003) and nutrient enrichment may increase overall food availability (Sosiak 2002, Tessier et al. 2008, O'Hare et al. 2010, Schad et al. 2020).

MATERIALS AND METHODS

Study area

The study area was the Lake Vico, a caldera lake in central Italy (12.173 °E, 42.315° N; Fig. 1). It covers 1217 ha at an altitude of 507 m a.s.l. and is surrounded by the Vicani Hills (Mt. Fogliano 965 m a.s.l., Mt. Venere 851 m a.s.l.). The lake basin and its slopes are characterized by deciduous broadleaved forests (50.5%), mainly Turkey oak (*Quercus cerris*), beech (*Fagus sylvatica*), and chestnut (*Castanea sativa*). Hazelnut orchards represent the second most extensive habitat type (37.6%); reedbeds (2.5%), meadows (2.3%), other agricultural areas (5.1%), and anthropized areas (2.0%) also occur within the caldera. The climate at Lake Vico is typically temperate, with mild summers (mean 18-28 °C) and cool winters (mean 0-8 °C). The presence of the lake and its location within a volcanic caldera influence the local microclimate, making the area more humid than the surrounding regions. Annual rainfall (1200-1500 mm) is distributed throughout the year, with peaks in autumn and spring. Since 1982, the lake has been protected as the Lake Vico Natural Reserve; it is also designed as a Special Area of Conservation (SAC) under the Habitat Directive 92/43/EEC and as a Special Protection Area (SPA) under the Birds Directive 2009/147/EC.

Data collection

Count data were obtained from the International Waterbird Census (IWC), conducted once per year in January between 2009 and 2025 by volunteer and professional ornithologists, including two of the authors (GT, FS). The suitability of IWC data for analysing spatio-temporal trends of wintering waterbirds, including in relation to habitat and climate change, has been demonstrated in previous studies (Lehikoinen et al. 2013, Musilová et al. 2018, Pavón-Jordán et al. 2020). Counts were carried out from vantage points that allowed observers to scan the entire lake; therefore, they were treated

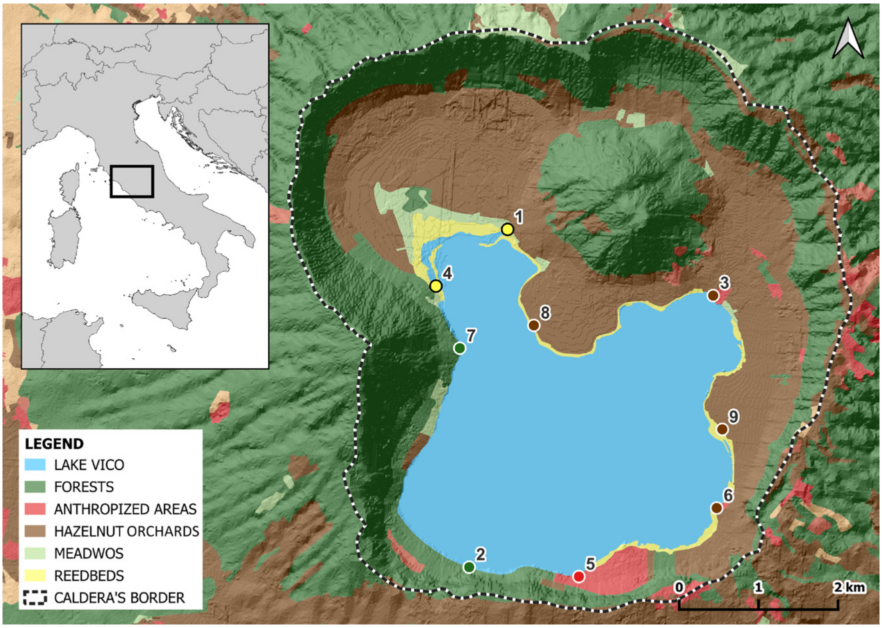

Fig. 1 Lake Vico, in central Italy. The nine sampling sites are shown; they were classified relying on the main environmental characteristics of the shores: anthropized areas (5), hazelnut orchards (3, 6, 8, 9), meadows and reedbeds (1, 4) and forests (2, 7).

as exact counts rather than estimates. The vantage points were grouped into nine sampling sites (Fig. 1). Based on the dominant habitat along the shoreline, sites were classified as anthropized areas (one site), hazelnut orchards (four sites), meadows and reedbeds (two sites), and forests (two sites). Target species were migratory species wintering in the Mediterranean Basin, belonging to the following families: Podicipedidae, Phalacrocoracidae, Ardeidae, Anatidae, Rallidae, Charadriidae, Scolopacidae, and Laridae. We also included the Marsh Harrier (*Circus aeruginosus*) as it is a key predator of waterbirds, particularly ducks and coots (Cramp 1980). Birds were counted in the morning (07:00-09:00) under favourable weather conditions (i.e. no strong wind or heavy rain), using binoculars and 20-60× spotting scopes.

Data analysis

For each species, we analysed spatio-temporal patterns of wintering individuals by fitting two sets of models. First, we investigated temporal trends in the total number of birds counted during the winters of 2009–2025 by comparing six Generalized Additive Models (GAMs) (Zuur et al. 2007, Wood 2017): a null model, a model including year as the predictor, and four models including year plus one of the following additional predictors: the North Atlantic Oscillation (NAO) index, air temperature (°C), air pressure (hPA), and precipitation (mm). The NAO index represents the difference in atmospheric pressure between Iceland and Azores Islands and is commonly used as proxy for large-scale climatic conditions particularly in studies of migratory waterfowl (Lehikoinen et al. 2006, Podhrázský et al. 2017, Pavón-Jordán et al. 2019, Thurber et al. 2020). Positive NAO values (NAO+) are associated with cool summers and mild, wet winters in Central Europe, whereas negative values (NAO-) indicate cold, dry winters and increased rainfalls (Bolle 2003, Wallace & Hobbs 2006). NAO data were averaged over the autumn-winter period (November-January) preceding the count and are freely available from the National Oceanic and Atmospheric Administration (NOAA) National Weather Service (https://www.cpc.ncep.noaa.gov/). Air temperature, air pressure, and precipitation were averaged over the same period and were used to represent local climatic conditions. These data were obtained from the ERA5 reanalysis product (Hersbach et al. 2023), available through the Copernicus Climate Change Service (C3S) Climate Data Store (CDS) (https://cds.climate.copernicus.eu/).

Given the small sample size (N = 17), the maximum basis dimension of the temporal smoother (*k*) was restricted to 3. To account for temporal autocorrelation between consecutive samples, we included a first-order autoregressive correlation structure (Zuur et al. 2009). For non-linear smooth terms, inference on temporal changes was based on the first derivatives of the smooth functions (Pedersen et al. 2019, Simpson 2024). First derivatives and their standard errors were estimated along the time series, and significance was assessed by examining whether 95% confidence intervals overlapped zero. Periods during which confidence intervals did not include zero were interpreted as significant increasing or decreasing trends.

We then analysed the spatial distribution of each species within the lake during the winters 2014-2025 by comparing three Generalized Linear Mixed Models (GLMMs) with a negative binomial error distribution (Zuur et al. 2009): (1) a null model, (2) a model including habitat as a fixed effect, and (3) a model including the interaction between habitat and year. Habitat was treated as a categorical variable with four levels (anthropized area, hazelnut orchard, reedbed, and forest). To account for potential non-independence among repeated observations from the same site, we fitted hierarchical negative binomial models including site as a random effect. Only species recorded in at least five years were included in the analyses (Gaget et al. 2020). In addition, we examined spatio-temporal variation in wintering birds by grouping species into five taxonomic groups (grebes, herons, dabbling ducks, diving ducks, and gulls) and four functional groups based on diet (herbivores, invertivores, piscivores, and omnivores; Storchová and Hořák 2018), respectively (Electronic Supplementary Material, ESM, Tab. S1).

The relative importance of covariates was assessed using an information-theoretic approach, comparing models based on the second-order Akaike's Information Criterion (AICc) (Burnham & Anderson 2002). Models with an AICc at least two units lower than competing models were considered better supported (Burnham & Anderson 2002). Autocorrelation in model residuals was evaluated using the autocorrelation function (ACF) (Zuur et al. 2009), and potential zero inflation in GLMMs was assessed by comparing observed and expected numbers of zeros using simulation-based residual diagnostics (Gelman & Hill 2006). The variance explained by each model was quantified using deviance explained (D^2) for GAMs and the coefficient of determination (R^2, marginal and conditional) for GLMMs (Zuur et al. 2007, Nakagawa & Schielzeth 2013). All statistical analyses were performed with R 4.2.2 (R Core Team 2022) using the packages *mgcv* (Wood 2023), *gratia* (Simpson 2025), *MuMIn* (Bartoń 2018), and *DHARMa* (Hartig 2024).

RESULTS

Temporal trends

In total, we counted 74,207 individuals belonging to 28 species (ESM, Tab. S1). We had sufficient observations to build robust models for 20 of the 28 recorded species (ESM, Tab. S2, Fig. S1). For 15 species, the null model provided the best fit, indicating the absence of a significant temporal trend. For the remaining species, the best-fitting model included year as a predictor (ESM, Tab. S2), revealing a decline in seven species (Mallard, Eur-

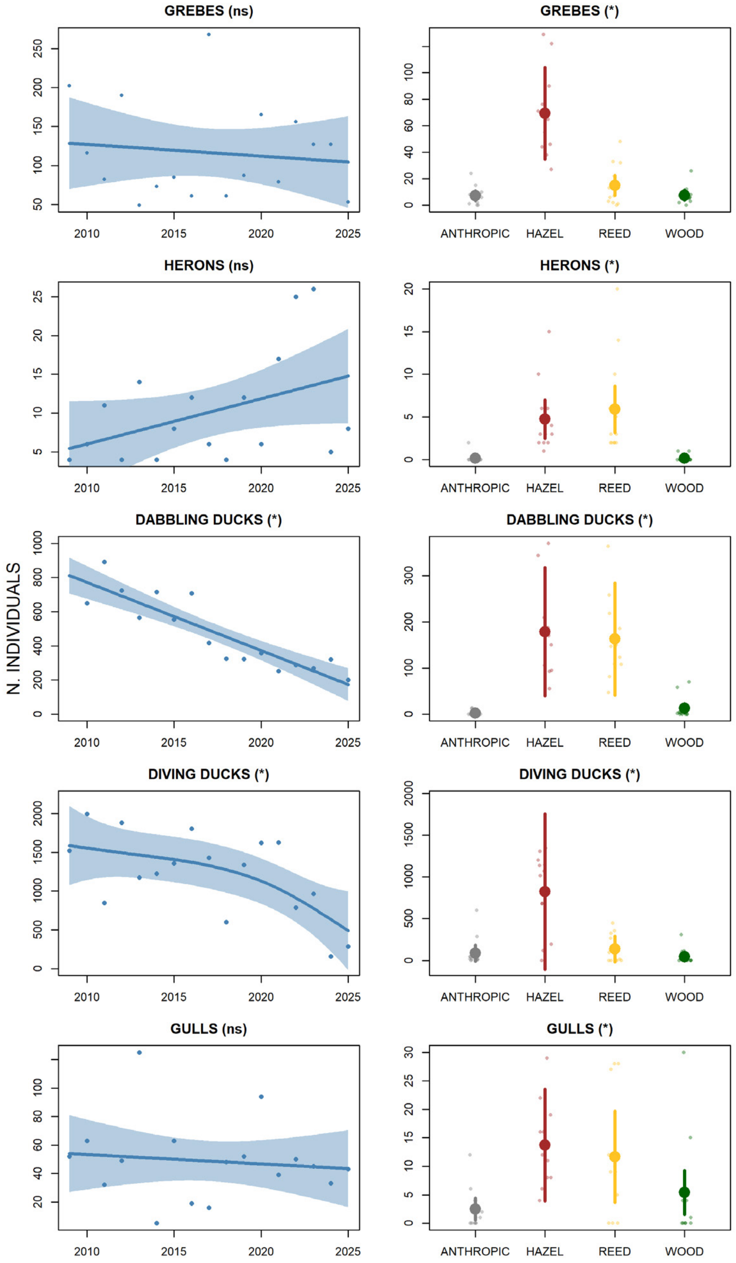

Fig. 2 Temporal trends (period 2009-2025, left panels) and spatial distribution (period 2014-2024, right panels) of waterbirds at Lake Vico, in relation to their taxonomic group (ns = not significant trend/distribution; * = significant trend/distribution)

asian Teal, Gadwall, Eurasian Wigeon, Common Pochard, Eurasian Coot, and Marsh Harrier) and temporal fluctuations in the Water Rail. Counts of dabbling and diving ducks showed a significant decline over the study period (Tab. 1). In contrast, herons exhibited an increasing trend, although this was not statistically significant (Fig. 2). With respect to diet, herbivorous and omnivorous species declined over time, whereas invertivores and piscivores did not show significant temporal changes in numbers (Tab. 2; Fig. 3). In all cases, neither large-scale climatic conditions in northern Europe, as estimated using the NAO Index, nor local climatic variables had a significant effect on temporal trends of wintering waterbirds in the study area (Tab. 1-2, and ESM, Tab. S2).

Spatial distributions

We had sufficient data to model the spatial distribution of 15 species (ESM, Tab. S3, Fig. S1). Habitat had a significant effect for only two species, the Grey Heron and the Eurasian Teal, both of which were more frequently recorded near meadows and reedbeds. For all other species, the null model was the best-fitting model, indicating an even distribution of individuals among sampling sites (ESM, Tab. S3). Among taxonomic groups, only herons were more abundant near meadows and reedbeds, whereas all other groups of wintering aquatic birds were evenly distributed across the lake (Tab. 1; Fig. 2). Similarly, among trophic guilds, invertivores were the only group showing a non-random spatial distribution, being predominantly associated with areas adjacent to hazelnut orchards (Tab. 2; Fig. 3).

DISCUSSION

Our results show a marked decline in both dabbling and diving duck populations, particularly Mallard, Eurasian Teal, Gadwall, Eurasian Wigeon, and Common Pochard. Similarly, the population of the Eurasian Coot exhibited a strong decline. These trends contrast with recent national counts, which report moderate to strong increases in most of these species, with the exception of the Eurasian Coot, whose decline is consistent with national trends (Zenatello et al. 2021). Regional trends also indicate increasing populations (Brunelli et al. 2009), suggesting that a local factor acting specifically at our study site may be responsible for the observed declines.

One plausible explanation is the substantial increase in nutrient loading in Lake Vico, particularly phosphates and nitrates, associated with intensive hazelnut cultivation (Leone & Marini 1993, Dyer 1995, Leone et al. 2008, Garnier et al. 2010). Excessive nutrient inputs are known to negatively affect aquatic vegetation (Blindow 1992, Van den Berg et al. 1999, Moss 2007, Kolada 2010). Consistently, both reedbeds and *Chara* beds have declined at Lake Vico since the 1960s (Azzella & Scarfò 2010), likely contributing to the observed decline in herbivorous and omnivorous waterbirds (Fox et al. 2025). In addition, the decline of

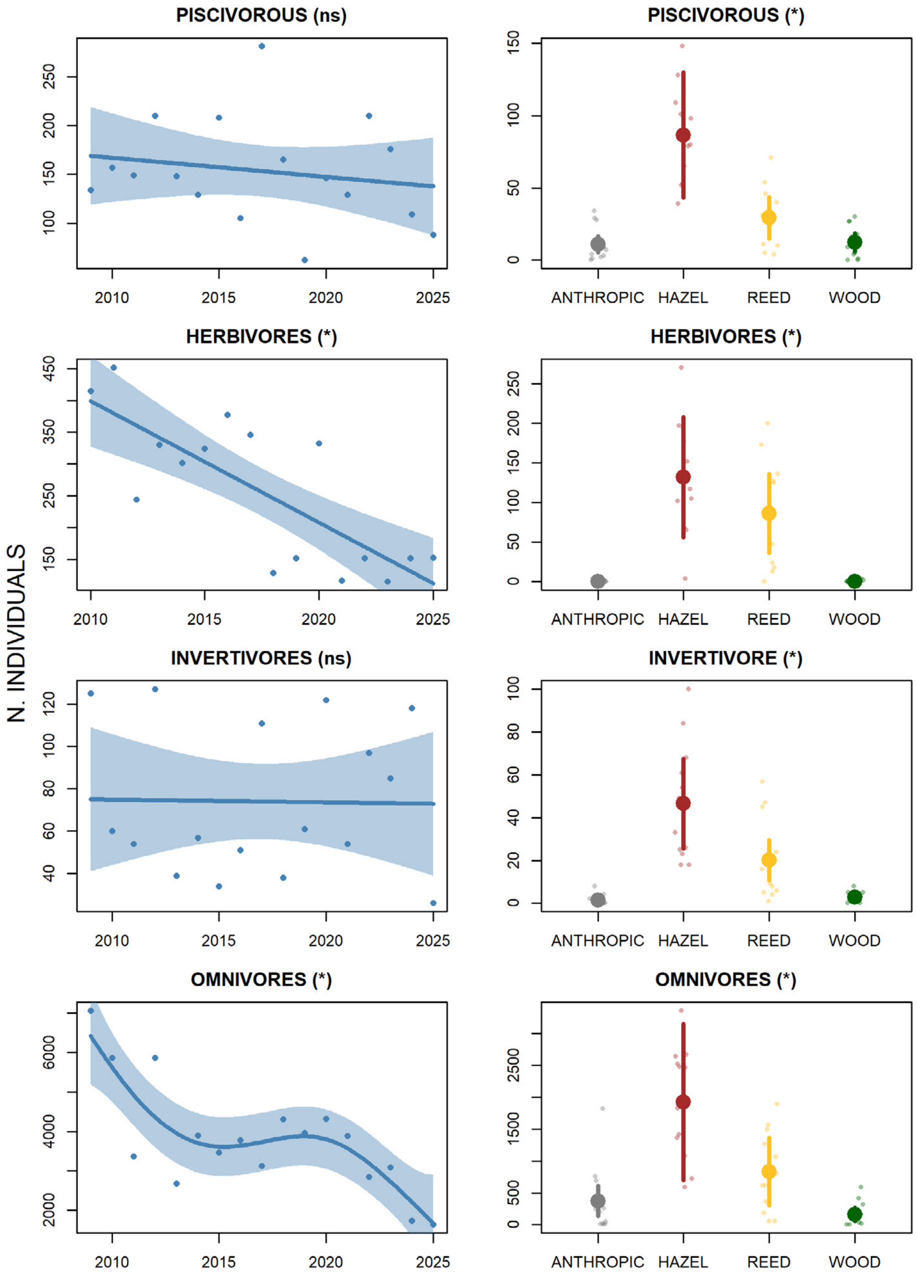

Fig. 3 Temporal trends (period 2009-2025, left panels) and spatial distribution (period 2014-2024, right panels) of waterbirds at Lake Vico, in relation to their trophic guild (ns = not significant trend/ distribution; * = significant trend/distribution).

waterbirds at Lake Vico may be partially related to poisoning associated with algal blooms. The lake is naturally vulnerable to eutrophication due to its geological, geomorphological, and hydrological characteristics (Leone & Marini 1993). Consequently, excessive nutrient inputs from agricultural activities may promote recurrent cyanobacterial blooms (e.g. *Planktothrix rubescens*, *Limnothrix redekei*, *Pseudanabaena* spp.), which have occurred regularly in the study area, particularly during autumn and winter (Mazza et al. 2008, Bruno et al. 2012, Manganelli et al. 2016, Messineo et al. 2024). Many cyanobacteria produce biologically active compounds, including microcystins (Skulberg et al. 1984, Messineo et al. 2024), which can negatively affect wildlife, especially aquatic birds (Skulberg et al. 1984, Matsunaga et al. 1999, Mancini et al. 2010, Messineo et al. 2024). Although no cases of poisoned birds were recorded during our study, further research is required to properly assess this potential mechanism.

One of the aims of this study was to investigate the spatial distribution of wintering waterbirds and to assess whether it was influenced by hazelnut farming along the lake shores. At the species level, only Grey Heron and Eurasian Teal showed a non-random spatial distribution, being more frequently recorded near meadows and reedbeds, a pattern observed also by herons as taxonomic group. All other taxonomic groups and trophic guilds, were evenly distributed across the lake. An exception was represented by invertivores, which were mainly associated with shores adjacent to hazelnut orchards. Although we hypothesised that the overall decline of wintering waterbirds at Lake Vico is linked to intensive hazelnut farming, the current association of non-declining invertivores with hazelnut orchards may paradoxically result from this same agricultural practice. While the lake is classified as meso-eutrophic (Margaritora et al. 2003), nutrient enrichment caused by intensive agriculture may have increased food availability in nearby waters (Sosiak 2002, O'Hare et al. 2010, Schad et al. 2020). Fertilized aquatic systems often support submerged macrophytes, which in turn provide suitable habitats for aquatic invertebrates (Tessier et al. 2008, Schad et al. 2020). Consequently, invertivorous species may concentrate their foraging activity along these nutrient-enriched shores. In contrast, this pattern was weaker or absent along shores adjacent to woodlands, reedbeds, and anthropized areas, where nutrient inputs are lower and food availability is likely more limited.

We also observed a decline in wintering Marsh Harriers, which is likely linked to the steady reduction in ducks and coots, their main prey (Ferguson-Lees & Christie 2001). Marsh Harriers are known to increase their foraging activity in wetlands with higher abundances of dabbling ducks (Fritz et al. 2000). Moreover, the reduction of reedbeds at Lake Vico may have further contributed to the decline of this species, as reedbeds constitute important roosting habitats (Ferguson-Lees & Christie 2001).

Despite recent climate change in Europe, characterised by milder winters in northern and central regions (EEA 2024), we found no relationship between wintering waterbird abundance and the North Atlantic Oscillation (NAO) index, nor with local climatic conditions. At the scale of individual wetlands, waterbird abundance may be more strongly influenced by local temperature anomalies than by large-scale climatic indices (Pavón-Jordán et al. 2020). Moreover, the strongest effects of winter temperature anomalies on waterbird abundance are typically observed in north-eastern Europe, whereas such patterns are weaker or absent in central and southwestern Europe (Pavón-Jordán et al. 2020).

Despite providing evidence consistent with a decline in waterbirds potentially associated with intensive hazelnut farming, this study has some limitations. First, we did not directly test the effects of agrochemical pollution on waterbirds. Disentangling the relative contributions of habitat modification, agrochemical contamination, and climatic variability is inherently challenging, particularly in complex wetland ecosystems. Second, our analyses were constrained by the available datasets. We did not include direct measurements of aquatic environmental variables, such as nutrient concentrations, water temperature, pH, dissolved oxygen, or aquatic vegetation cover. Incorporating such data would allow a more mechanistic understanding of the observed temporal declines and spatial patterns in waterbird assemblages. Third, we did not compare population trends at Lake Vico with those of nearby wetlands and water bodies within the same region. Such comparisons could provide insights into local movements of birds among neighbouring sites and help clarify whether observed declines reflect local redistribution or true population decreases. Finally, although International Waterbird Census (IWC) data are widely used to investigate large-scale temporal trends in waterbird populations, reliance on a single annual count at the local scale may introduce uncertainty. Stochastic or exceptional events occurring on the day of the census (e.g. disturbance or adverse weather shortly before counts) could temporarily displace birds to nearby sites, potentially biasing local abundance estimates.

In conclusion, we documented a significant decline in dabbling and diving ducks, Eurasian Coots, and herbivorous and omnivorous waterbirds wintering at a volcanic lake in central Italy. This decline is likely driven by increased nutrient loading, particularly nitrates and phosphates, originating from intensive hazelnut orchards surrounding the lake. Nutrient enrichment negatively affects aquatic vegetation, ultimately reducing food availability for waterbirds that depend on these resources. The decline in wintering ducks may also explain the marked decrease in Marsh Harriers, which rely heavily on these species as prey. In contrast, invertivorous species were primarily associated with shores adjacent to hazelnut orchards, possibly due to increased invertebrate availability in nutrient-enriched areas. Finally, no relationship was detected between wintering waterbird abundance and either large-scale or local climatic conditions. Replicating this study across additional wetlands would help determine whether the observed effects of hazelnut cultivation are site-specific or more widespread.

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DECLARATIONS

Competing interests

The authors declare no competing interests.

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Data accessibility

The datasets generated during and/or analyzed during the current study are available from the corresponding author on a reasonable request.

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Tables

Table 1. GAMs used to explore temporal trends in taxonomic groups of wintering aquatic birds at Lake Vico (central Italy) in 2009-2025, in relation to the year, air temperature (TEMP; °C), air pressure (PRESS; hPA), precipitation (PREC; mm), and NAO index. For each model, degrees of freedom (df), AICc and their difference with the lowest (ΔAICc), and Akaike's weights (Σw_i) are shown; models are sorted by AICc. Summary of the first derivatives of the smooth term is reported. Values represent averages across periods with significantly negative, positive, or non-significant trends, based on 95% confidence intervals of the derivatives. A derivative was considered significant when its confidence interval did not overlap zero. If the best model was a GAM, effective degrees of freedom (EDF), F-test and its significance (P) are shown, as well as deviance explained D^2 and the mean and maximum autocorrelation values (ACF).

Taxonomic group	**Model**	**df**	**AICc**	ΔAICc	$\Sigma \boldsymbol{w}_i$
Grebes	Null	2	192.2	0.00	0.681
	YEAR	3	195.0	2.73	0.174
	PREC + YEAR	4	197.7	5.46	0.045
	TEMP + YEAR	4	198.2	5.93	0.035
	NAO + YEAR	4	198.3	6.06	0.033
	PRESS + YEAR	4	198.4	6.13	0.032
	Not significant trend Intercept = 116.53 ± 14.96				
Herons	Null	2	117.8	0.00	0.346
	YEAR	3	118.1	0.34	0.291
	PREC + YEAR	4	119.6	1.80	0.141
	NAO + YEAR	4	120.4	2.65	0.092
	TEMP + YEAR	4	121.0	3.22	0.069
	PRESS + YEAR	4	121.3	3.46	0.061
	Not significant trend Intercept = 10.12 ± 1.69				
Dabbling ducks	YEAR	3	239.1	0.00	0.526
	NAO + YEAR	4	241.4	2.32	0.165
	PRESS + YEAR	4	241.5	2.38	0.160
	TEMP + YEAR	4	242.9	3.84	0.077

Taxonomic group	Model	df	AICc	ΔAICc	Σw_i
	PREC + YEAR	4	243.1	3.97	0.072
	Null	2	254.0	14.88	0.000
	Decreasing trend Intercept = 550.18 ± 52.33 s(YEAR) | 2009-2019 | Derivative: mean = -82.534, SE = 19.19, LCI = -120.15, UCI = -44.92 s(YEAR) | 2020-2025 | Derivative: mean = -15.169, SE = 24.53, LCI = -63.24, UCI = 32.91 EDF = 1.798, F = 15.92, P < 0.001 D^2 = 71.3%; ACF: mean = 0.104, max = 0.320				
Diving ducks	YEAR	3	262.1	0.00	0.325
	NAO + YEAR	4	262.3	0.20	0.295
	TEMP + YEAR	4	263.1	1.07	0.190
	PRESS + YEAR	4	264.4	2.36	0.100
	Null	2	265.9	3.80	0.049
	PREC + YEAR	4	266.2	4.12	0.041
	Decreasing trend Intercept = 1213.6 ± 104.3 s(YEAR) | 2009-2015 | Derivative: mean = -89.644, SE = 34.98, LCI = -158.21, UCI = -21.08 s(YEAR) | 2016-2025 | Derivative: mean = -24.826, SE = 40.41, LCI = -104.02, UCI = 54.37 EDF = 1.560, F = 6.459, P = 0.024 D^2 = 42.3%; ACF: mean = 0.124, max = 0.243				
Gulls	Null	2	165.8	0.00	0.553
	PREC + YEAR	4	167.8	2.07	0.196
	YEAR	3	168.5	2.75	0.140
	PRESS + YEAR	4	170.2	4.42	0.061
	TEMP + YEAR	4	171.9	6.17	0.025
	NAO + YEAR	4	172.0	6.22	0.025
	Not significant trend Intercept = 48.71 ± 6.87				

Table 2. GAMs used to explore temporal trends in trophic guilds of wintering aquatic birds at Lake Vico (central Italy) in 2009-2025, in relation to the year, air temperature (TEMP; °C), air pressure (PRESS; hPA), precipitation (PREC; mm), and NAO index. For each model, degrees of freedom (df), AICc and their difference with the lowest (ΔAICc), and Akaike's weights (Σw_i) are shown; models are sorted by AICc. Summary of the first derivatives of the smooth term is reported. Values represent averages across periods with significantly negative, positive, or non-significant trends, based on 95% confidence intervals of the derivatives. A derivative was considered significant when its confidence interval did not overlap zero. If the best model was a GAM, effective degrees of freedom (EDF), F-test and its significance (P) are shown, as well as deviance explained D^2 and the mean and maximum autocorrelation values (ACF).

Trophic guild	**Model**	**df**	**AICc**	ΔAICc	$\Sigma \boldsymbol{w}_i$
Herbivores	YEAR	3	189.4	0.00	0.504
	PRESS + YEAR	4	191.7	2.26	0.163
	TEMP + YEAR	4	192.2	2.76	0.127
	NAO + YEAR	4	192.2	2.82	0.123
	PREC + YEAR	4	193.0	3.62	0.082
	Null	2	201.5	12.07	0.001
	Decreasing trend				
	Intercept = 255.69 ± 18.73				
	s(YEAR) | 2009-2025 | Derivative: mean = -19.096, SE = 4.06, LCI = -27.06, UCI = -11.13				
	EDF = 1, F = 22.08, P < 0.001				
	D^2 = 61.2%; ACF: mean = 0.110, max = 0.360				
Invertivores	Null	1	173.4	0.00	0.720
	YEAR	3	176.3	2.98	0.162
	PREC + YEAR	4	179.3	5.91	0.038
	TEMP + YEAR	4	179.6	6.20	0.033
	PRESS + YEAR	4	179.8	6.44	0.029
	NAO + YEAR	4	180.6	7.25	0.019
	Not significant trend				
	Intercept = 74.06 ± 8.59				
Piscivorous	Null	1	187.1	0.00	0.643
	YEAR	3	189.5	2.39	0.194
	NAO + YEAR	4	192.2	5.17	0.049
	PREC + YEAR	4	192.5	5.40	0.043

Trophic guild	**Model**	**df**	**AICc**	ΔAICc	Σw_i
	TEMP + YEAR	4	192.8	5.72	0.037
	PRESS + YEAR	4	192.9	5.86	0.034
	Not significant trend				
	Intercept = 153.29 ± 12.85				
Omnivores	YEAR	3	289.8	0.00	0.550
	NAO + YEAR	3	292.8	2.96	0.125
	PRESS + YEAR	4	292.8	2.97	0.124
	PREC + YEAR	4	293.3	3.45	0.098
	TEMP + YEAR	4	293.3	3.48	0.096
	Null	2	298.8	9.01	0.006
	Decreasing trend				
	Intercept = 3816.7 ± 249.6				
	s(YEAR) | 2009-2025 | Derivative: mean = -199.77, SE = 50.95, LCI = -299.63, UCI = --99.91				
	EDF = 1, F = 15.38, P = 0.001				
	D^2 = 50.6%; ACF: mean = 0.163, max = 0.319				

Table 3. GLMMs used to explore the spatial distribution in taxonomic groups of wintering aquatic birds at Lake Vico (central Italy) in 2014-2025. For each model, degrees of freedom (df), AICc and their difference with the lowest (ΔAICc), and Akaike's weights (Σw_i) are shown. Models are sorted by AICc; the best model is in bold. Summary of the best model is shown (estimates, standard error (SE), lower (LCI) and upper (UCI) 95% confidence intervals); variance and standard deviation (SD) of the random effect is shown. Additionally, zero-inflation test, conditional (R^2c) and marginal (R^2_m) coefficient of determination, and the mean and maximum autocorrelation values (ACF) are shown.

Taxonomic group	**Model**	**df**	**AICc**	ΔAICc	$\Sigma \boldsymbol{w}_i$
Grebes	**Null**	**3**	718.4	0.00	0.639
	HABITAT	**6**	720.1	1.71	0.272
	HABITAT × YEAR	**7**	722.4	3.93	0.090
	Intercept = 2.195 ± 0.290				
	Random effect | Site (9 levels): Variance = 0.607, SD = 0.779				
	Zero-inflation test, P = 0.376				
Herons	**HABITAT**	**6**	**284.8**	**0.00**	**0.683**
	HABITAT × YEAR	7	286.9	2.14	0.250
	Null	3	288.8	3.98	0.066
	Intercept = -1.876 ± 1.005				
	Hazelnut orchard | Estimate = 1.809, SE = 1.075, LCI = -0.299, UCI = 3.916				
	Reedbed | Estimate = 2.892, SE = 1.125, LCI = 0.688, UCI = 5.096				
	Woodland | Estimate = -0.779, SE = 1.338, LCI = -3.402, UCI = 1.844				
	The reference level for habitat is "Anthropized area"				
	Random effect | Site (9 levels): Variance = 0.388, SD = 0.623				
	Zero-inflation test, P = 0.608				
	R^2_c = 0.70, R^2_m = 0.57; ACF: mean = 0.065, max = 0.140				
Dabbling ducks	**Null**	**3**	**738.5**	**0.00**	**0.790**
	HABITAT	7	742.3	3.73	0.122
	HABITAT × YEAR	6	742.9	4.38	0.088
	Intercept = 2.105 ± 0.862				
	Random effect | Site (9 levels): Variance = 6.178, SD = 2.486				
	Zero-inflation test, P = 0.336				

Taxonomic group	**Model**	**df**	**AICc**	ΔAICc	Σ***w**$_i$*
Diving ducks	**Null**	**3**	**943.8**	**0.00**	**0.811**
	HABITAT	6	947.5	3.66	0.130
	HABITAT × YEAR	7	949.1	5.27	0.058
	Intercept = 4.025 ± 0.638 Random effect | Site (9 levels): Variance = 3.103, SD = 1.761 Zero-inflation test, P = 0.424				
Gulls	**Null**	**3**	**503.0**	**0.00**	**0.898**
	HABITAT	6	508.2	5.24	0.066
	HABITAT × YEAR	7	509.4	6.42	0.036
	Intercept = 1.028 ± 0.437 Random effect | Site (9 levels): Variance = 1.429, SD = 1.195 Zero-inflation test, P = 0.952				

Table 3. GLMMs used to explore the spatial distribution in trophic guild of wintering aquatic birds at Lake Vico (central Italy) in 2014-2025. For each model, degrees of freedom (df), AICc and their difference with the lowest (ΔAICc), and Akaike's weights (Σw_i) are shown. Models are sorted by AICc; the best model is in bold. Summary of the best model is shown (estimates, standard error (SE), lower (LCI) and upper (UCI) 95% confidence intervals); variance and standard deviation (SD) of the random effect is shown. Additionally, zero-inflation test, conditional (R^2c) and marginal (R^2_m) coefficient of determination, and the mean and maximum autocorrelation values (ACF) are shown.

Trophic guild	**Model**	**df**	**AICc**	ΔAICc	Σw_i
Herbivores	**Null**	**3**	**513.1**	**0.00**	**0.651**
	HABITAT	7	514.3	1.24	0.199
	HABITAT × YEAR	6	515.3	2.20	0.150
	Intercept = 0.620 ± 0.947				
	Random effect | Site (9 levels): Variance = 7.354, SD = 2.712				
	Zero-inflation test, P = 0.464				
Invertivores	**HABITAT**	**6**	**606.1**	**0.00**	**0.620**
	HABITAT × YEAR	7	608.3	2.13	0.214
	Null	3	608.8	2.62	0.167
	Intercept = 0.430 ± 0.682				
	Hazelnut orchard | Estimate = 1.798, SE = 0.758, LCI = 0.312, UCI = 3.283				
	Reedbed | Estimate = 1.834, SE = 0.822, LCI = 0.223, UCI = 3.445				
	Woodland | Estimate = -0.140, SE = 0.840, LCI = -1.786, UCI = 1.506				
	The reference level for habitat is "Anthropized area"				
	Random effect | Site (9 levels): Variance = 0.266, SD = 0.516				
	Zero-inflation test, P = 0.752				
	R^2_c = 0.51, R^2_m = 0.39; ACF: mean = 0.053, max = 0.128				
Piscivorous	**Null**	**3**	**793.3**	**0.00**	**0.900**
	HABITAT	6	798.7	5.35	0.062
	HABITAT × YEAR	7	799.7	6.35	0.038
	Intercept = 2.482 ± 0.342				
	Random effect | Site (9 levels): Variance = 0.948, SD = 0.973				
	Zero-inflation test, P = 0.280				

Trophic guild	**Model**	**df**	**AICc**	ΔAICc	**Σw_i**
Omnivores	**Null**	**3**	**1344.1**	**0.00**	**0.885**
	HABITAT	6	1348.9	4.82	0.079
	HABITAT × YEAR	7	1350.5	6.41	0.036
	Intercept = 5.333 ± 0.522				
	Random effect | Site (9 levels): Variance = 2.232, SD = 1.494				
	Zero-inflation test, P = 0.400				

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