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Long-Term Changes (1993-2022) in Wintering Waders of the Largest Mediterranean Coastal Lagoon: Dominance Patterns, Habitat Shifts and Weak Thermal Signals

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Abstract

Coastal lagoons are key wintering habitats for waders, yet long-term changes in their community structure remain poorly understood in Mediterranean systems. We analysed a 30-year dataset (1993–2022, excluding 2021) of wintering waders in the Venice Lagoon to assess trends in abundance, community structure, thermal composition and spatial patterns. Total abundance increased significantly (+3.5% yr^{-1}), while species richness ranged between 12–21 species per winter. Community structure changed markedly, with increasing dominance of a few species, particularly Dunlin, leading to reduced evenness. Species-level analyses showed a prevalence of increasing trends: nine of the 19 species analysed increased significantly, one declined, one was stable and eight showed uncertain trends. The Community Temperature Index (CTI) increased significantly ($p = 0.001$), suggesting a shift towards species with higher thermal affinities, but this pattern was not robust to the exclusion of Dunlin *C. alpina*, indicating dominance-driven dynamics. Spatial analyses revealed a strong increase in the open lagoon ($p < 0.001$) and a decline in fish farms ($p = 0.008$), indicating a shift towards natural tidal habitats. Overall, the assemblage is increasing but structurally simplified, highlighting the need to integrate species- and community-level approaches when interpreting ecological indicators.

Keywords: community thermal index; fish farms; long-term monitoring; managed wetland; tidal flats; Venice lagoon

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1. Introduction

Coastal lagoons are key wintering habitats for waterbirds, particularly waders, which depend on shallow tidal habitats, exposed mudflats and transitional environments to meet their energetic requirements during the non-breeding season [1–3]. In the Mediterranean region, these systems play a crucial role within migratory flyways, functioning both as wintering grounds and as stopover sites linking breeding areas in northern Europe and Asia with southern wintering quarters [4,5]. The Venice Lagoon is the largest lagoon system in the Mediterranean basin, covering approximately 550 km^2 and hosting a highly heterogeneous mosaic of habitats, including tidal flats, salt marshes, shallow subtidal areas and managed fish farms [6]. This environmental diversity supports large and diverse assemblages of wintering waterbirds and makes the lagoon a site of international importance along the African–Eurasian flyway [7,8].

Over recent decades, coastal lagoons have undergone substantial environmental changes driven by both anthropogenic and natural factors. In the Venice Lagoon, these include dredging activities, alterations in sediment dynamics and hydrodynamics, and large-scale infrastructural interventions

[9,10]. At broader spatial scales, climate change and the associated sea level rise are increasingly affecting waterbird populations, with documented shifts in wintering distributions and abundance patterns across Europe [11,12].

Long-term monitoring datasets are essential to understand how these drivers interact in shaping community dynamics. Multi-decadal time series allow the evaluation not only of changes in total abundance, but also of shifts in community structure, species dominance and functional composition [13,14]. In many systems, community-level responses to environmental change are not evenly distributed across species but are instead driven by a limited number of dominant *taxa*, leading to increased unevenness without necessarily affecting species richness [13,15].

At the same time, synthetic indicators such as the Community Temperature Index (CTI) have become widely used to quantify climate-driven changes in species assemblages by integrating species-specific thermal affinities [12,16]. CTI has been successfully applied to European bird communities, including waterbirds, revealing consistent warming signals over recent decades [12,17]. However, recent studies have emphasized that community-weighted indices may be strongly influenced by dominant species, potentially biasing their interpretation if species-specific contributions are not explicitly accounted for [18,19].

Waders are particularly suitable for investigating these processes, as their ecology is tightly linked to habitat availability, tidal dynamics and benthic prey distribution. Their high mobility makes them sensitive to both local environmental conditions and large-scale climatic variability [1,3]. In Mediterranean coastal lagoons, environmental drivers such as sediment dynamics, hydrodynamic processes and tidal exposure strongly influence habitat configuration and benthic productivity, which in turn shape waterbird assemblages. These local processes interact with broader climatic drivers, leading to complex and multi-scale patterns of community reorganization [20–22].

Despite the importance of the Venice Lagoon and the ecosystem services it provides [23], no studies have explicitly addressed long-term changes in wintering wader assemblages at the community level, combining abundance trends, diversity metrics and climate-related indicators. In particular, the combined role of dominance structure, functional composition and thermal shifts remains unexplored.

The present study addresses this gap by analysing a 30-year dataset (1993–2022) of waders from the International Waterbird Census (IWC) made in the Venice Lagoon. Specifically, we aim to:

- describe changes in wader community structure, including diversity, evenness and dominance;
- quantify long-term trends in total abundance and species-specific populations;
- assess temporal trends in the Community Temperature Index (CTI), including sensitivity to dominant species;
- investigate differences among functional groups, with particular focus on trophic guilds.

2. Materials and Methods

The Venice Lagoon is the largest coastal lagoon in the Mediterranean Sea, covering approximately 550 km² along the northern Adriatic coast of Italy (45°25′ N, 12°18′ E; Figure 1). It extends for 50 km from the Piave River in the north to the Brenta River in the south and is separated from the Adriatic Sea by two barrier islands and two narrow peninsulas. The lagoon is connected to the sea through three inlets (Lido, Malamocco and Chioggia), which regulate tidal exchange and the hydrodynamic regime [9]. Tidal amplitude can reach up to 1 m, the highest in the Mediterranean [24], generating vast intertidal areas that represent key foraging habitats for waders and other waterbirds.

The climate is temperate sub-continental, with by marine influence. Mean annual air temperature is between 10 and 14 °C, with mild winters and warm summers; annual precipitation ranges between 800 and 1100 mm [25]. The Venice Lagoon is a highly heterogeneous system, comprising a mosaic of deep channels, shallow open waters, tidal flats (*velme* in Italian), salt marshes (*barene*), fish farms (*valli da pesca*) and reclaimed areas. This environmental heterogeneity supports a diverse waterbird community, with habitat use strongly influenced by tidal dynamics, water depth and food availability. In particular, waders are closely associated with intertidal habitats, where sediment characteristics and tidal exposure determine the availability of benthic prey.

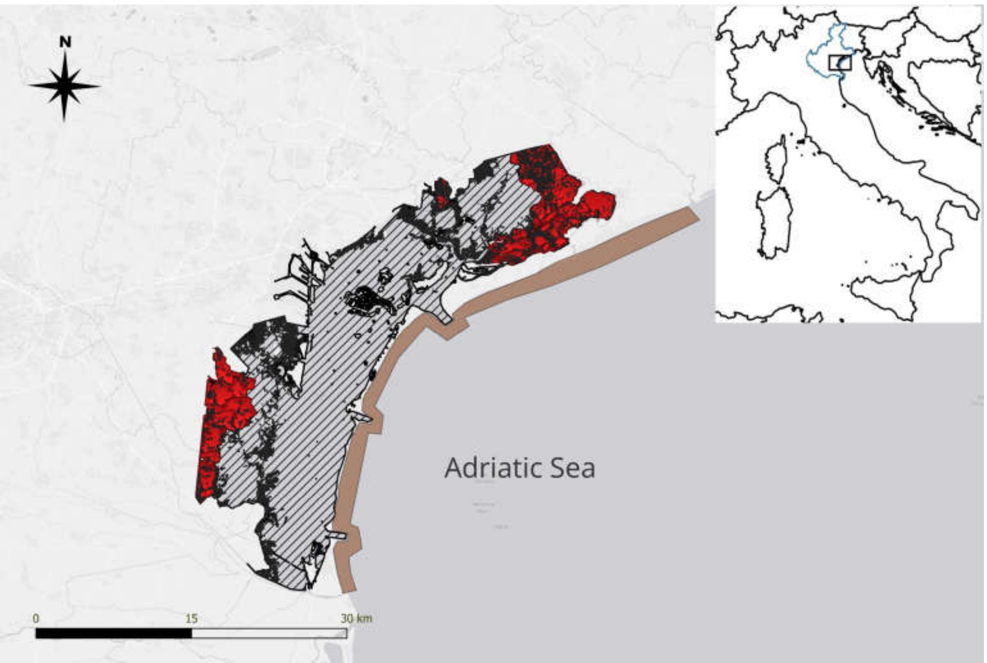

Figure 1. IWC macrozones used in this paper: (1) red, fish farms; (2) dashed black, open lagoon; (3) brown, littoral strip including marine waters < 1 km from the coastline. Minor wetlands are not reported for reasons of clarity.

For analytical purposes, during the IWC surveys (see below) the lagoon was subdivided into four major macro-areas reflecting differences in hydrology, management regime and ecological function (Figure 1):

(1) Fish farms. Approximately 20 privately owned fish farms, covering 9,600 ha, are located along the lagoon margins [26]. These are hydraulically regulated systems, largely disconnected from natural tidal exchange and where water levels are actively managed. During winter, site managers often provide supplementary food (e.g., rice, grain, millet) to attract and maintain high densities of waterbirds, particularly game species. These areas therefore offer stable, shallow habitats with high food availability and relatively low disturbance, supporting very high densities of wintering waterbirds. However, they generally play a secondary role for waders, which are less dependent on artificial food provisioning and more closely linked to natural foraging habitats.

(2) Open lagoon. This includes all areas directly connected to tidal exchange with the Adriatic Sea and comprises deep channels, shallow waters, tidal flats (approximately 4,000 ha), natural salt marshes (approximately 3,600 ha) and artificial salt marshes created from dredged sediments (approximately 1,400 ha [27]). These habitats represent the core wintering environment for waders, providing extensive foraging grounds associated with intertidal exposure and benthic productivity. The availability and spatial distribution of tidal flats are therefore key drivers of wader abundance and distribution. Each winter, in the open lagoon between ten and twenty traditional roosts (located on artificial saltmarshes and natural saltmarshes) are used by waders during high tides.

(3) Coastal littoral zone. This macro-area includes sandy beaches and nearshore marine waters, defined as those within approximately 1 km from the coastline. One coastal infrastructure (a breakwater) provides an additional roosting site for waterbirds, including waders, during high-tide periods [28]. Nevertheless, the coastal zone supports low densities compared to the open lagoon.

(4) Minor wetlands. This category includes small and heterogeneous habitats such as treatment wetlands, freshwater ponds within industrial areas, drainage basins and reclaimed lands. Although limited in extent, these sites can locally support certain wader species, especially those less strictly dependent on intertidal environments, and may function as supplementary feeding or resting areas.

2.1. Climate Data

Winter temperature trends were assessed using mean seasonal air temperature calculated for each winter between 1992/93 and 2021/22. Following standard practice [17], winter temperature was defined as the average of the mean monthly temperatures for November, December and January. Data were obtained from the meteorological station of Tessera Airport, located at the edge of the Venice Lagoon.

2.2. Waterbird Counts

Wintering waterbird data were collected within the framework of the International Waterbird Census (IWC), implemented in the Venice Lagoon by Associazione Faunisti Veneti through the national monitoring scheme coordinated by ISPRA, the Italian Institute for Environmental Protection and Research [7,29]. Counts have been conducted annually since 1993 in mid-January by trained volunteers, following standardized protocols that ensure comparability across years and sites. The entire lagoon was surveyed over three consecutive days and divided into approximately 50 survey units, each covered by teams of two to three observers using a combination of ground-based and boat-based surveys. All fish farms were surveyed on the same day during non-hunting periods, while open lagoon counts were conducted in a single day during high or rising tides to maximize detection of roosting birds. The coastal strip was surveyed on foot. No surveys were conducted in 2021 due to COVID-19 restrictions; therefore, the dataset includes 29 annual counts between 1993 and 2022, with 28 species recorded in at least one winter.

Waterbird count data derived from large-scale monitoring schemes such as the International Waterbird Census (IWC) are inherently affected by multiple sources of uncertainty, particularly in complex coastal systems such as lagoons. In these environments, counts involve large and spatially dispersed aggregations, making accurate enumeration challenging. Potential sources of bias include imperfect detectability, variation in observer experience, differences in survey conditions (e.g., visibility, weather, water level) and estimation errors in large flocks. Detectability may also vary among habitats and species. Although detailed metadata on observer identity and effort were not systematically archived for the entire study period, the survey design, spatial coverage and counting protocols remained consistent over time, as coordinated within the national IWC framework. This consistency supports the use of the dataset for long-term trend analyses despite the inherent limitations discussed above. Standardized protocols, repeated coverage of the same count units and coordinated surveys are designed to minimize variability and ensure temporal consistency, although they do not fully eliminate all sources of error. Nevertheless, we acknowledge that inaccuracies in absolute counts may occur, particularly for highly gregarious species such as waders or under suboptimal survey conditions. Despite these limitations, the consistency of methods through time makes IWC data well suited for detecting medium- to long-term changes in waterbird populations [30].

2.3. Data Aggregation and Community Metrics

Analyses were conducted at three levels: (i) lagoon-wide totals, obtained by summing counts across all macro-areas; (ii) macro-area totals, including fish farms, open lagoon, coastal littoral zone and minor wetlands; and (iii) species- and guild-level datasets. Species were assigned to three eco-functional guilds based on foraging behaviour and habitat use, following established classifications for shorebirds [1,31] (see Supplementary Material S1). The first group, “Probing benthic feeders”, includes species that extract invertebrates from soft sediments using tactile foraging, typically in intertidal mudflats. The second group, “Surface/visual feeders”, comprises species that capture prey at or near the sediment surface, relying primarily on visual detection. The third group includes “Non benthic and generalist feeders”, which exploit prey in shallow water or show flexible and opportunistic feeding strategies across different microhabitats. This classification reflects major ecological differences in feeding strategy and habitat dependence among waders, particularly in relation to sediment characteristics, water depth and tidal exposure, and provides a functional framework for interpreting patterns of abundance and community change.

Community structure was described using species richness and the Shannon diversity index. Interannual similarity between consecutive winters was quantified using the Jaccard index (presence–absence) and the Bray–Curtis index (abundance-based) [32].

2.4. Trend Analysis

Trends were estimated using TRIM v. 3.54 (Trends and Indices for Monitoring data) [33], based on log-linear Poisson regression models specifically developed for time-series count data with missing values. Standard TRIM settings were applied, including correction for overdispersion and serial correlation. Species recorded in fewer than 10 winters were excluded from trend analyses, resulting in a subset of 19 species. Trends were estimated for both the full period (1993–2022) and the most recent decade (2012–2022), always excluding 2021, to assess temporal consistency. The absence of data for 2021 was handled within the TRIM framework, which explicitly accounts for missing values in the time series. Given the length of the dataset and the magnitude of observed trends, the absence of a single year is unlikely to substantially influence the results. For each analytical unit (total abundance, macro-areas, species and guilds), we estimated (i) annual indices relative to a reference year, (ii) overall log-linear trends and (iii) trend classifications according to standard TRIM categories (strong increase, moderate increase, stable, uncertain, moderate decline, steep decline).

2.5. Species Temperature Index (STI) and Community Temperature Index (CTI)

Species thermal affinities were quantified using the Species Temperature Index (STI), defined as the mean January temperature across the non-breeding distribution of each species. STI values (see Table S1) were derived from published datasets based on the intersection of species distribution maps with long-term climatic data (baseline 1950–2000: [16,34,35]). From the overall pool of 28 species, two were excluded due to the lack of available STI values. The Community Temperature Index (CTI) was calculated annually as the abundance-weighted mean of STI values as follows:

$$CTI_y = \frac{\sum_{i=1}^{S} (N_{i,y} \cdot STI_i)}{\sum_{i=1}^{S} N_{i,y}}$$

where $N_{i,y}$ is the abundance of species *i* in year *y*, STI_i is the Species Temperature Index of species *i*, and *S* is the number of species with available STI values in that year. The year 2021 was excluded from all CTI calculations.

To assess the robustness of CTI trends to species dominance, we recalculated CTI after excluding the most abundant species (Dunlin *C. alpina*), which accounts for a large proportion of total abundance and strongly influences community-level metrics.

2.6. Statistical Analyses

Temporal trends in climate variables, total abundance and CTI were assessed using linear regression models (PAST software v. 5.2: [36]), whereas species-level trends were estimated using TRIM (see above).

3. Results

3.1. Climate and Sea Level Trends

Mean winter temperature at Tessera station showed moderate interannual variability over the study period (1993–2022), with values fluctuating around a long-term mean of 5.9 ± 1.1 °C. No significant linear trend was detected (r = 0.17, $p > 0.05$).

3.2. Overall Patterns of Abundance and Community Structure

Over the study period (1993–2022, excluding 2021), the total number of wintering waders showed marked interannual variability, ranging from approximately 11,500 individuals in the early 1990s to a maximum of nearly 67,000 individuals in 2018 (Figure 2; Supplementary Material Table S1). Despite this variability, an overall increasing trend emerged from the late 1990s onwards, with particularly high values recorded after 2010; TRIM classified the overall trend as a moderate increase, with an estimated annual growth rate of 3.5% /yr.

Species richness ranged between 12 and 21 species per winter. The lowest values were recorded in the early years of the time series, whereas from the late 1990s onwards richness consistently fluctuated around 19–21 species. In contrast, community structure showed pronounced variability. The Shannon diversity index ranged between approximately 0.3 and 1.17, with lower values generally associated with years of high total abundance, reflecting increased dominance by a limited number of species. Conversely, higher diversity values occurred in years with a more even distribution of individuals among species.

Interannual similarity between consecutive winters, expressed as the Jaccard index based on species presence–absence, was consistently high (generally 0.70–0.90). An exceptionally high value (0.95) was observed between 2020 and 2022, despite the absence of data for 2021.

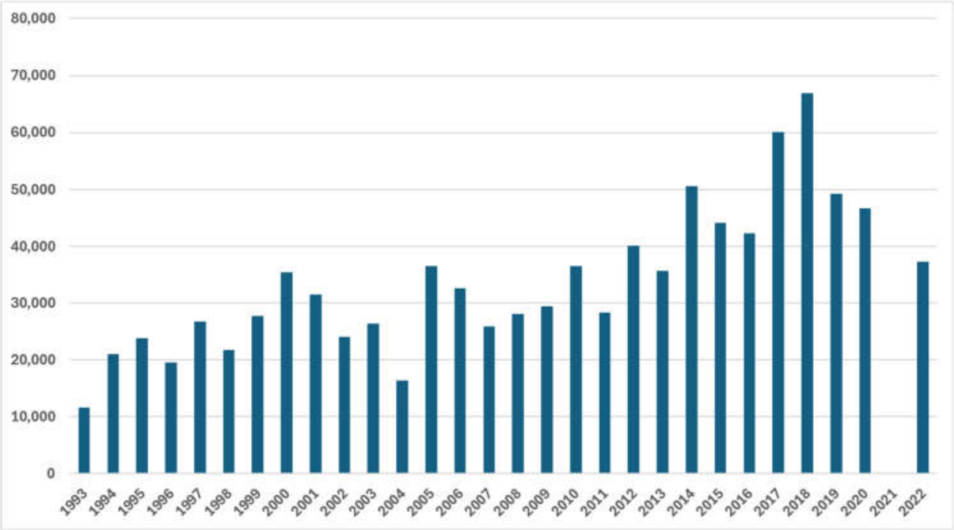

Figure 2. Total number of wintering waders counted in the Venice Lagoon between 1993 and 2022. No count was conducted in 2021.

3.3. Main Species Contributing to Wintering Wader Abundance

The wintering wader assemblage was strongly dominated by a limited number of species. The most abundant species was Dunlin, with a cumulative total exceeding 800,000 individuals over the study period. This species accounted for a considerable proportion (83.6%) of all waders counted and largely determined the temporal pattern of total abundance, particularly in years with exceptionally high totals (Figure 3). Its numerical dominance also contributed to low Shannon diversity values in several winters.

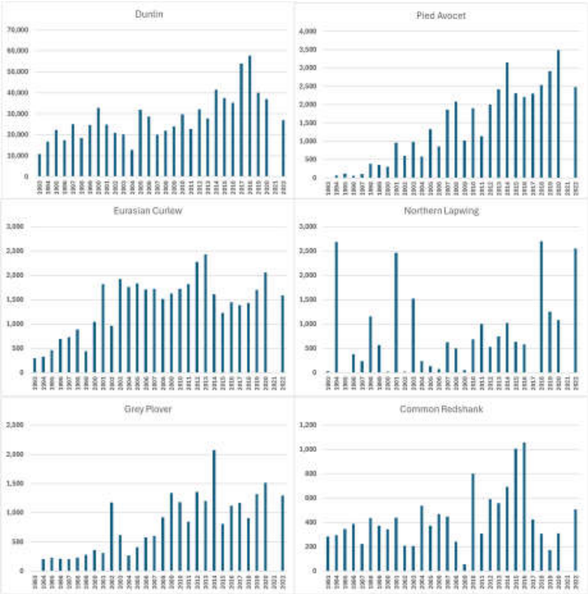

Figure 3. Annual counts of the main wader species accounting for at least 1% of total abundance over the study period.

A second group of species, clearly less abundant than *C. alpina* but still of major importance, included Pied Avocet *Recurvirostra avosetta* and Eurasian Curlew *Numenius arquata*, both with cumulative totals slightly above 40,000 individuals (ca. 4%). Intermediate abundances were recorded for Northern Lapwing *Vanellus vanellus* and Grey Plover *Pluvialis squatarola*, both exceeding 20,000 (about 2.0%) individuals cumulatively. A further group of regularly occurring but less abundant species included Common Redshank *Tringa totanus*, Spotted Redshank *Tringa erythropus*, European Golden Plover *Pluvialis apricaria* and Common Greenshank *Tringa nebularia*. These taxa contributed to species richness and temporal continuity of the assemblage. Kentish Plover *Anarhynchus alexandrinus* ranked among the ten most abundant species despite its relatively low cumulative total. Finally, although much less abundant, two species (Eurasian Oystercatcher *Haematopus ostralegus* and Ruddy Turnstone *Arenaria interpres*) showed a remarkable strong increase, rising from near absence until the early 2000s to several hundred individuals within the following decade (Figure 4).

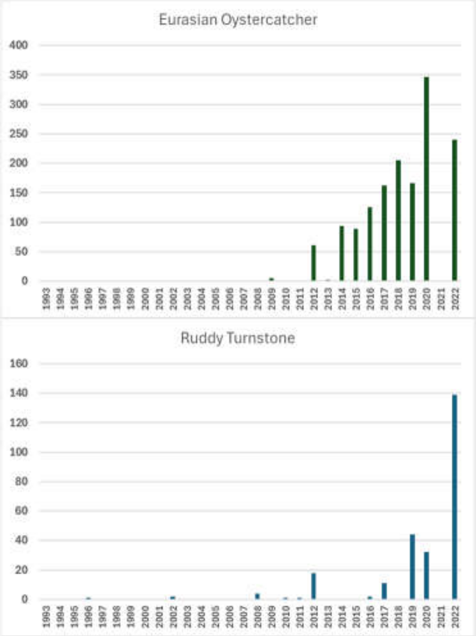

Figure 4. Annual winter counts of Eurasian Oystercatcher and Ruddy Turnstone in the Venice Lagoon.

Overall, the assemblage structure was highly uneven, with strong dominance by *C. alpina* and a limited number of additional species contributing most of the remaining abundance. Interannual changes in total numbers were associated with fluctuations in a few dominant taxa.

3.4. Eco-Functional Guilds

Probing benthic feeders remained by far the most abundant guild (88% of the total) throughout the study period, consistently accounting for the majority of individuals in most winters. Non-benthic and generalist feeders (6.5%) and surface/visual feeders (5.5%) contributed smaller proportions of the assemblage, although their relative importance varied among years.

All three eco-functional guilds showed significant positive trends over the study period (1993–2022, excluding 2021), although with different magnitudes. Probing benthic feeders, which dominated the assemblage in terms of abundance, increased at a rate of +3.2% yr^{-1} ($p < 0.01$) and were classified as showing a moderate increase. Surface/visual feeders exhibited a higher rate of increase (+4.7% yr^{-1}, $p < 0.01$), also corresponding to a moderate increase, but with greater interannual variability in abundance. The strongest increase was observed for non-benthic and generalist feeders, which showed a growth rate of +6.7% yr^{-1} ($p < 0.05$) and were classified as a strong increase.

3.5. Species-Level Trends

Species-level TRIM analyses conducted on the 19 species recorded in at least 10 winters revealed a predominance of increasing trends, although with substantial interspecific variability. Four species showed strong increases, all with high annual growth rates (ranging from +9% to +39% yr^{-1}; $p < 0.01$; Table 1). An additional five species exhibited moderate increases, with annual changes between +3.1% and +11.8% yr^{-1} ($p < 0.05$–0.01). In contrast, only one species showed a significant decline, with a moderate negative trend (−6% yr^{-1}; $p < 0.05$). One species was classified as stable, while the remaining eight species were classified as uncertain because of non-significant or highly variable trends.

Table 1. TRIM trends for 19 species, 1993-2022 (no data in 2021).

Scientific name	No. of winters	Annual change (%)	Judgment	*P*
Actitis hypoleucos	29	4.7	Moderate increase	<0.05
Anarhynchus alexandrinus	29	-2.6	Uncertain	
Arenaria interpres	11	39	Strong increase	<0.01
Calidris alba	19	21	Strong increase	<0.01
Calidris alpina	29	3.1	Moderate increase	<0.01
Calidris minuta	24	-4	Uncertain	
Calidris pugnax	10	-3.3	Uncertain	
Charadrius hiaticula	27	-1.7	Uncertain	
Gallinago gallinago	29	-6	Moderate decline	<0.05
Haematopus ostralegus	11	26	Strong increase	<0.01
Numenius arquata	29	4.7	Moderate increase	<0.05
Pluvialis apricaria	14	2	Uncertain	
Pluvialis squatarola	29	6.5	Moderate increase	<0.01
Recurvirostra avosetta	28	9	Strong increase	<0.01
Tringa erythropus	29	3.4	Uncertain	
Tringa nebularia	26	11.8	Moderate increase	<0.05
Tringa ochropus	15	2.2	Uncertain	

Tringa totanus	29	2	Stable
Vanellus vanellus	29	7	Uncertain

3.6. Community Temperature Index (CTI)

The CTI calculated for wintering waders (26 species with available STI values) showed a significant increasing trend over time (slope = 0.033 yr^{-1}, $r = 0.58$, $p = 0.001$; Figure 5 and Supplementary Material Table S2). However, this pattern was not robust to the removal of the dominant species *C. alpina*. When this species was excluded, the CTI trend became non-significant ($p = 0.11$). The exclusion of *C. alpina* also resulted in increased interannual variability of CTI values. For example, the decrease in CTI between 1993 and 1994 after exclusion of this species was associated with a marked increase in *Vanellus vanellus*, a species with a relatively low STI value.

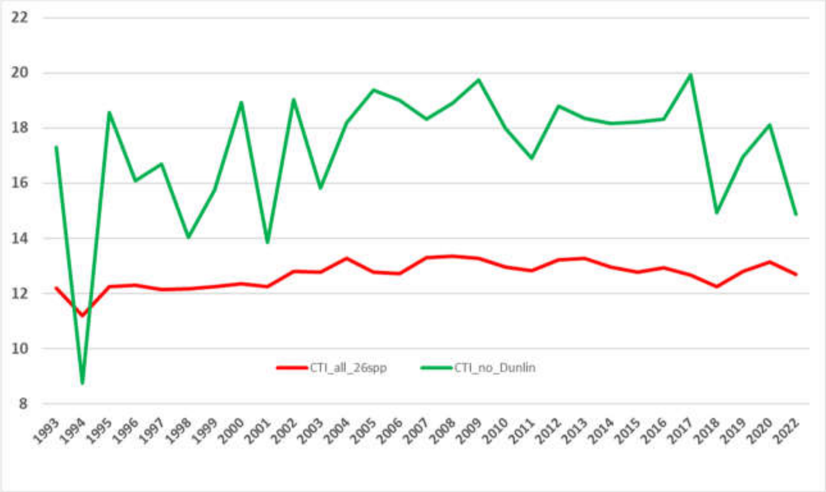

Figure 5. Temporal trends in the Community Temperature Index (CTI) of wintering waders in the Venice Lagoon, 1993–2022, excluding 2021. The red line shows CTI calculated using all species with available STI values (n = 26), whereas the green line shows CTI after excluding the dominant species, Dunlin.

3.7. Spatial Distribution

The spatial distribution of wintering waders was strongly structured across macro-areas, with the open lagoon consistently supporting the largest proportion of individuals in most years. On average, the open lagoon accounted for most of the total abundance (71% of the total individuals), frequently exceeding 50% of all counted individuals, whereas fish farms represented the second most important component (26%), with highly variable contributions among years. Minor wetlands and the littoral strip contributed only marginally (both <2%).

Temporal trends differed among habitat types. Wader abundance in the open lagoon showed a strong and significant increase over time (linear regression: $r = 0.85$, $p < 0.001$). In contrast, fish farms exhibited a significant declining trend ($r = -0.48$, $p = 0.008$). Minor wetlands showed no significant temporal trend ($p = 0.61$), while the littoral strip hosted low and variable numbers.

4. Discussion

The analysis of a 30-year time series (1993–2022) reveals that the wintering wader assemblage of the Venice Lagoon is characterized by a combination of increasing abundance and progressive structural simplification, expressed as increasing dominance and reduced evenness.

Total abundance increased significantly over the study period (+3.5% yr^{-1}), while species richness remained relatively stable. This pattern—stable richness coupled with increasing abundance—is consistent with findings from long-term ecological studies showing that local biodiversity often remains relatively constant despite substantial changes in community structure

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[13–15]. In the Venice Lagoon, however, this apparent stability masks a clear reorganization of the assemblage, driven primarily by changes in relative abundance rather than by species turnover.

A key result of this study is the marked increase in dominance. The most abundant species (*C. alpina*) accounted for a very large proportion of total individuals over the whole study period and largely shaped interannual variation in total abundance. This pattern indicates a progressive concentration of individuals in a limited number of taxa, leading to increasing unevenness without a parallel loss of richness, a pattern consistent with broader evidence that local assemblages may undergo marked compositional reorganization even when richness remains relatively stable [13–15]. Similar dynamics have been documented in other ecological systems, where dominant species disproportionately influence community-level metrics and temporal trajectories [13,15].

The species-level analyses further support this interpretation. Although several species exhibited positive trends, the overall increase in abundance was largely driven by a limited number of taxa, most notably *C. alpina*. This finding reflects a general ecological principle: community-level trends often emerge from asynchronous dynamics among species, rather than from uniform responses across the assemblage, as also shown in other ecological systems [15].

The analysis of the Community Temperature Index (CTI) provides additional insight into the drivers of community change. The significant increase in CTI observed over the study period suggests an apparent shift towards species with higher thermal affinities, consistent with large-scale climate-driven redistribution patterns documented in European bird populations [12,17,37].

However, the sensitivity analysis clearly demonstrates that this apparent thermophilization is not robust to the removal of the dominant species *C. alpina*. When this species is excluded, the CTI trend becomes non-significant, indicating that the observed increase is largely driven by a single highly abundant *taxon* rather than by a coherent community-wide response. The strong interannual variability observed in CTI after exclusion of *C. alpina*, including abrupt changes such as the marked decrease between 1993 and 1994 driven by fluctuations in *V. vanellus*, further highlights the sensitivity of the index to changes in the relative abundance of individual species.

These results are consistent with previous studies showing that community-weighted indicators, such as the CTI, can be strongly driven by dominant species and by covariation among species traits, potentially biasing their interpretation and leading to overestimation of climate-driven change when species-specific contributions are not explicitly disentangled [19,22,38]. From an ecological perspective, this finding is particularly relevant for wader assemblages, which are often highly uneven and dominated by a few numerically abundant species [39,40]. In such systems, changes in dominance structure can strongly affect synthetic indicators such as CTI, potentially obscuring underlying ecological processes. The Venice Lagoon thus represents a clear example of how community-level metrics must be interpreted in the context of species-specific dynamics.

Functional patterns provide further insight into these dynamics. Probing benthic feeders dominated the assemblage and showed a significant positive trend, confirming the central role of intertidal habitats in supporting wintering waders in the Venice Lagoon. Surface/visual feeders and non-benthic/generalist feeders also increased significantly, although they represented much smaller proportions of the assemblage and showed greater interannual variability. This pattern indicates that the overall increase was not restricted to a single functional group, but the assemblage remained strongly structured around species exploiting benthic resources in exposed or shallow sediments. Because benthic feeders depend on invertebrates associated with tidal flats and shallow soft-bottom habitats, their abundance is closely linked to benthic productivity, sediment characteristics and the availability and duration of tidal-flat exposure. Similar relationships between wader abundance, benthic resources and habitat availability have been documented in other wetland systems [1,41].

The spatial analysis supports this interpretation, revealing a clear increase in wader abundance in the open lagoon and a concurrent decline in fish farms. This pattern indicates a progressive redistribution of individuals towards natural tidal habitats. In contrast, other waterbird groups, such as dabbling ducks, often benefit from managed wetlands and artificial habitats. In Mediterranean systems such as the Camargue, water management and habitat configuration have been shown to strongly influence waterbird distribution, with managed wetlands favouring certain guilds over others [42].

In the Venice Lagoon, the increasing importance of the open lagoon likely reflects the continued availability of extensive intertidal areas and benthic feeding habitats. At the same time, the decline in fish farms suggests a reduced role of managed habitats for waders, which are less dependent on artificial food provisioning and more closely tied to natural foraging conditions. These patterns should also be interpreted in light of ongoing environmental changes, including sea-level rise and modifications in tidal dynamics, which can influence the extent and duration of tidal-flat exposure and thus affect habitat availability for foraging waders. In the Venice Lagoon, the observed deepening of tidal flats [43] and the projected sea-level rise for the northern Adriatic (approximately +22 cm by 2050 [9] will likely reduce both the extent and exposure time of tidal flats, causing severe negative consequences for wintering waders.

Large-scale climatic forcing may also contribute to the observed patterns. Waders are highly mobile and respond to both local habitat conditions and broader flyway-scale processes. Changes in winter severity and temperature gradients across Europe can influence distribution patterns and site selection, leading to interannual variability superimposed on longer-term trends [37,44]. The relative contribution of local habitat changes and large-scale climatic drivers cannot be fully disentangled in the present study, as both processes likely act simultaneously and interactively in shaping the observed patterns.

The marked increase observed in the Venice Lagoon during the last 15 years for two species, Eurasian Oystercatcher and Ruddy Turnstone, may however reflect partially different mechanisms. In the case of Eurasian Oystercatcher, breeding populations have increased locally during the last decade [45], and some individuals may currently remain in the lagoon throughout the year, wintering close to their breeding sites. Because ringing activity on this species in the Venice Lagoon has been extremely limited, this hypothesis cannot presently be verified. More generally, the species has shown increasing wintering numbers in Italy, with a strong increase reported for 2009–2018 [7]. This national pattern is consistent with, but does not prove, the local increase observed in the Venice Lagoon.

For Ruddy Turnstone, the increase as a wintering species appears to have started more recently, both in the Venice Lagoon and more broadly in Italy. National winter counts increased from 27 individuals in 1991–1995 to 134 in 2001–2005 and 218 in 2006–2010 [46]. In the Venice Lagoon, its increasing abundance may partly reflect the large availability of hard substrates (gabions and containment poles) associated with artificial saltmarshes, which are regularly used by the species as feeding substrates (pers. obs.).

Overall, the results of this study indicate that the Venice Lagoon supports a numerically increasing but structurally simplified wader assemblage, in which long-term changes are primarily driven by: (i) increasing dominance of a limited number of species; (ii) differential responses among functional groups; (iii) spatial redistribution towards natural tidal habitats; and (iv) apparent, dominance-driven thermophilization.

These findings have important implications for the interpretation of long-term monitoring data. In particular, they highlight that: (i) stable species richness does not necessarily imply ecological stability; (ii) community-level indicators such as CTI must be interpreted in the context of assemblage dominance structure; and (iii) species-level and functional approaches are essential for disentangling the mechanisms underlying community change.

More broadly, the Venice Lagoon appears to follow patterns observed in other European and Mediterranean wetlands, where climate-driven redistribution, habitat configuration and trophic structure interact to shape long-term waterbird assemblages. Future research should aim to further disentangle these drivers by integrating long-term ecological datasets with detailed information on habitat dynamics, hydrology, benthic productivity and tidal-flat availability.

Supplementary Materials: The following supporting information can be downloaded at: Preprints.org. Table S1: Wintering waders 1993_2022; Table S2: CTI_waders_with_without_dunlin.

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