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The expansion wave of an invasive predator leaves declining waterbird populations behind

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Abstract

Aim: Theory predicts that the evolutionary adaptations of prey to reduce predator pressure often fail in confrontation with non-native predators; thus, their predation usually leads to sharp declines of prey populations. However, over time, prey can develop anti-predator adaptations, reduce predator impact and recover its population. We analyse the numerical response of multiple prey species to the impact of a non-native predator on a large spatiotemporal scale.

Location: Poland.

Methods: Long-term population dynamics of 13 waterbird species breeding in 123 sites were analysed with reference to the present and historical distribution of mink over 40 years. We rescaled the temporal waterbird dynamics to the time elapsed since the mink colonized each site.

Results: The steepest waterbird declines were recorded up to 15 years after establishment of the mink population, and in that period, waterbird abundance averaged across the 13 studied species declined by 50% but certain species showed different patterns: the abundance of eight species declined linearly or nonlinearly, whereas the breeding populations of five other species did not change significantly. Over time, the abundance of some declining species increased slightly and tended to stabilize at a lower level. The temporal pattern of waterbird dynamics averaged across species correlated closely with temporal changes of mink density with a 4-year time-lag. A projection of the observed patterns shows that waterbird decline following the expansion of mink has the shape of a wave travelling from the north to the south of Poland.

Main conclusions: We conclude that the impact of the invasive American mink should be considered an important factor affecting waterbird populations at a large geographical scale. The waterbird vulnerability to mink predation is species-specific, and over time the negative impact grows weak as mink population densities decline.

KEYWORDS

American mink, biological invasion, *Neovison vison*, population dynamics, predation, spatiotemporal scale

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1 | INTRODUCTION

Predation is an important timeless factor that affects animal productivity, drives distribution and the abundance of animals, and has evolutionary consequences (Jędrzejewska & Jędrzejewski, 1998; Newton, 1993). The top–down effect of predation is modified by geographical and ecological parameters, for example latitude or environmental heterogeneity (Bartholomew, Diaz, & Cicchetti, 2000; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009), but the most important mechanism shaping prey's vulnerability to predation is the evolution of its defence strategies during predator–prey co-existence (e.g. Lima, 2009; Lima & Dill, 1990; Winnie & Creel, 2007). Spatial and temporal niche segregation, anti-predator behaviour, camouflage, etc., are adaptations that are being permanently screened by natural selection. Such adaptations, evolved from short-term behavioural plasticity, mitigate predators' impact and prevent constant declines in numbers or restrictions in the ranges of prey populations resulting from predation.

These adaptations, however, are usually ineffective in confrontation with introduced and rapidly expanding invasive non-native predators, which often inhabit predator-free habitats, use different hunting strategies and behave in different ways to native predators. Thus, already developed anti-predator adaptations and strategies may perform poorly in reducing the impact of the new predators, as they are often too "conservative" to adjust to the higher predation pressure in a short period of time. As a consequence, predation by invasive predators often leads to a sharp decrease in productivity, an increase in mortality, site abandonment, population declines or even the total extermination of a prey species (Blackburn, Petchey, Cassey, & Gaston, 2005; Hilton & Cuthbert, 2010; Macdonald & Strachan, 1999). The high impact of invasive predators on prey is explained by the naïve prey hypothesis (Salo, Korpimäki, Banks, Nordström, & Dickman, 2007). Although there are some examples of successful adaptation of native species to the heavy impact of invasive predators (e.g. Barros, Romero, Munilla, Pérez, & Velando, 2016; Brzeziński, Natorff, Zalewski, & Żmihorski, 2012; Nordström & Korpimäki, 2004), these adaptations can be developed over time and are usually preceded by a decline in prey populations. At the beginning, prey adaptations to invasive predator impact are short-term, invoking anti-predator behavioural changes via learning (e.g. plasticity in habitat selection) but over time may evolve towards long-term, permanent adaptations. Moreover, the facility of prey response may depend on the degree of similarity of an introduced predator to any native predator (predator similarity hypothesis; Ehlman, Trimmer, & Sih, 2019).

Over the last decades, numerous predator species have been intentionally or accidentally introduced outside their natural range to many regions of the world. They impact native fauna and are a growing problem for biodiversity conservation worldwide (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016). For some ecosystems, global assessment of the ecological impact of invasive species has been made (e.g. Cameron, Vilà, & Cabeza, 2016; Gallardo, Clavero, Sánchez, & Vilà, 2016); for others, our knowledge is still very limited and usually based on several local studies lacking a wide spatial and temporal approach (Simberloff et al., 2013). Native birds are among the animals most impacted; however, their decline or extinction has been well documented mainly on islands or in small mainland areas (Blackburn et al., 2005), most often showing the decline or extinction of rare species. In contrast, empirical evidence of the impact of invasive predators on populations inhabiting vast areas of a continent is lacking from several regions, and it is not clear if the patterns observed for local and insular populations can be scaled up to larger spatial scales. The lack of information about the large-scale impact of invasive species on birds results mostly from inaccurate data on the birds' dynamics, the lack of a spatiotemporal relation between bird numbers and the progress of predator expansion, and difficulties in distinguishing between predator impact and other factors. The large-scale evaluation of invasive predator impact on native birds requires information on bird population dynamics in relation to the time that has passed since the predator arrived in a specific area.

One of the invasive predators that has a destructive impact on native fauna is the American mink *Neovison vison*. The expansion of mink in Europe is the result of intentional introductions in the first half of the 20th century, as well as of numerous escapes from mink farms throughout the continent (review in Bonesi & Palazón, 2007). Differences in behaviour and ecology (e.g. food habits) between American mink and native riparian predators—Eurasian otter *Lutra lutra*, polecat *Mustela putorius* and European mink *Mustela lutreola* (extinct in Poland since the 1920s)—cause this invasive species to severely impact native prey (naïve prey hypothesis). Mink predation mainly affects aquatic and semi-aquatic vertebrates, with waterbirds being among the most seriously impacted (but also mammals, e.g. water vole *Arvicola amphibius*). Waterbirds are vulnerable to mink predation mainly during the breeding season, and some species can suffer high nest losses (Niemczynowicz, Świętochowski, Brzeziński, & Zalewski, 2017). A rapid decrease in breeding success and decline of waterbird populations, as well as changes in the distribution of local nesting populations, triggered by mink predation have been documented in many areas of Europe, but mostly in relation to sea birds (Andersson, 1992; Barros et al., 2016; Brzeziński et al., 2012; Craik, 1997; Ferreras & Macdonald, 1999; Gerell, 1985; Kilpi, 1995; Magnusdottir, von Schmalensee, Stefansson, Macdonald, & Hersteinsson, 2014; Nordström et al., 2003; Oring, Lank, & Maxson, 1983). Mink can also lead indirectly to birds abandoning nesting sites (Barros et al., 2016; Nordström & Korpimäki, 2004), as most waterbird species avoid nesting at lakes colonized by American mink (Pescador, Díaz, & Peris, 2012). Moreover, according to the ideal free distribution hypothesis, waterbirds reach higher densities at sites ensuring good habitat conditions (Blums, Nichols, Hines, & Mednis, 2002; Majewski & Beszterda, 1990). Unfortunately, the mink invasion is often concentrated in those high-quality sites, thus creating an "ecological trap" and accelerating the decline in reproductive success of bird populations in areas that previously ensured high brood survival (Niemczynowicz et al., 2017). These negative effects, however, are documented almost exclusively for small local

bird populations, and few, if any, studies have documented the large-scale response of several waterbird species to the mink invasion.

In this study, we investigate the spatiotemporal dynamics of breeding waterbird communities over 40 years in relation to the ongoing invasion of the American mink. In Poland, mink expansion began at the end of the 1970s in the north of the country, and since that time the population has expanded to the south, extensively colonizing new areas (Brzeziński, Żmihorski, Zarzycka, & Zalewski, 2019). At the same time, several waterbird surveys have revealed significant declines in the density of local breeding populations compared to those recorded in the 1970s, 1980s and 1990s (e.g. Wylegała, Batycki, Krąkowski, & Cierplikowski, 2011; Wylegała et al., 2010). We supplemented these surveys with our own bird counts to obtain waterbird abundance estimates for 123 water bodies distributed across the whole country: in regions colonized by mink many years ago, those colonized recently and regions that are still mink-free. Precise information on the expansion and present distribution of the American mink in Poland (Brzeziński et al., 2019) provided us with a unique opportunity to correlate the population dynamics of selected waterbird species with the colonization and development of the invasive predator. However, simple correlations between trends of waterbird abundance and mink occurrence are not enough to attribute prey population decline to predation since other variables changing over time but not accounted for (e.g. climatic or land use factors) can drive the correlation. To deal with this problem, we correlated the temporal waterbird dynamics not only to years but also to the time elapsed since the mink colonized each site. We predict that waterbird population declines are related to the time since mink site colonization (as recorded for several local sites in Europe and South America, e.g. Andersson, 1992; Brzeziński et al., 2012; Pescador et al., 2012) and are independent of general population trends. Second, we hypothesize that the impact of mink is not constant over time: following the naïve prey hypothesis (Salo et al., 2007), it should be strongest just after colonization, but weaken later on as the prey populations adapt to the new predator (Brzeziński et al., 2012) and predator abundance starts to decrease (Brzeziński et al., 2019). Finally, knowing the spatial pattern of the mink invasion in Poland, we project decreases in waterbird population size as a response to the invasive predator on a large geographical scale.

2 | METHODS

2.1 | Waterbird surveys

We used data on the breeding populations of waterbirds collected from 1972 to 2016, published in journals, MSc theses and reports. The criterion for selection of these sites was the availability of data from two periods: before and after establishment of the mink population in the specific area (except for 14 sites in southern Poland not colonized by mink). The intervals between the surveys differed by study site and ranged from 10 to 44 years (Table S1, Figure S1). We selected only bird surveys conducted during the breeding season and which followed standard ornithological procedures (Ranoszek, 1983)—publications based on data sets obtained without recommended ornithological methods or lacking description of the methods were discarded. The large number of surveys selected makes detailed description of the methods difficult but all of them followed procedures that enabled reliable estimates of waterbird numbers. Generally, each survey included up to 10 (most often 3–6) censuses during the breeding season (April–June) when all breeding pairs of waterbirds were counted, and their number was averaged if there was more than one census per season. All the authors made an attempt to distinguish between breeding and non-breeding birds as this is crucial for reliable waterbird population estimation to exclude migrating individuals. Due to the many researchers involved, survey methods were not always strictly the same (e.g. the number of bird censuses per season differed between study sites and years), which could increase the variation in our analyses. However, we assumed that uncertainty resulting from the above-mentioned differences in survey methods were random over the study period and have equalized (over- vs. underestimates) and thus provide unbiased (although not very precise) estimates of waterbird trends. The study sites and methodology details are described in the source publications listed in Table S1.

Generally, the number and distribution of sites used for the analysis were determined by the archival data available, and we made an attempt to use all suitable data to cover the whole territory of Poland. In total, 123 sites distributed all over the country were selected (Figure 1, Table S1). Study sites represented four types of habitat: eutrophic lakes (55), reservoirs (9), fishponds (52) and rivers (7). Fishponds were single water bodies or pond complexes, and rivers were river sections of various lengths. Surveys from at least two periods were available for 51 sites; thus, it was possible to use already existing data for the analysis without needing to conduct new field studies in these areas. Only single surveys were available for the remaining 72 sites, so we counted the birds for the second time from 2013 to 2016. One- or two-day censuses were conducted at each site by canoeing the lakes and reservoirs and by walking along the shorelines of the fishponds. We did not count birds on the rivers because they were among the 51 sites where counts were made by other researchers. The censuses were carried out during the breeding season, from April to June. We made an attempt to distinguish between breeding and non-breeding individuals according to ornithological procedures (e.g. flocks of birds were excluded), and final estimations were conducted according to the ornithological methods for waterbird censuses (Chylarecki, Sikora, Cenian, & Chodkiewicz, 2015; Ranoszek, 1983).

To analyse breeding population dynamics, we included abundance estimations for 13 waterbird species: Eurasian coot *Fulica atra*, great crested grebe *Podiceps cristatus*, red-necked grebe *P. grisegena*, black-necked grebe *P. nigricollis*, little grebe *Tachybaptus ruficollis*, common pochard *Aythya ferina*, tufted duck *A. fuligula*, mallard *Anas platyrhynchos*, Eurasian teal *A. crecca*, gadwall *Mareca strepera*, northern shoveler *Spatula clypeata*, garganey *S. querquedula* and common goldeneye *Bucephala clangula* (Table 1).

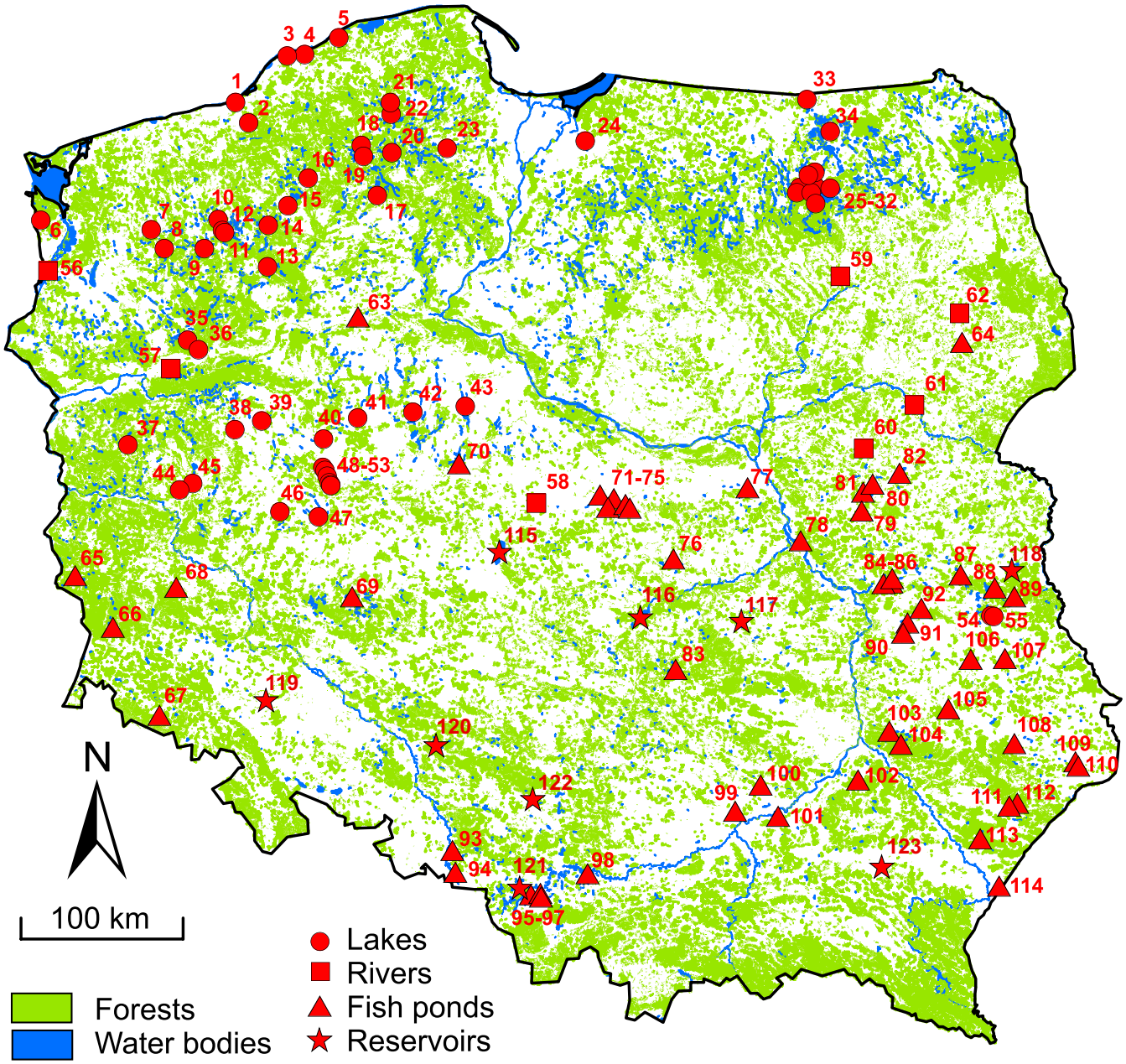


FIGURE 1 The location of the study sites in Poland used to analyse waterbird abundance. Different symbols indicate the type of water body. Numbers on the map correspond to the study site number in Table S1

2.2 | Temporal pattern of mink colonization

We obtained data on mink colonization from a reconstruction of the mink expansion in Poland (Brzeziński et al., 2019) based on mink observations in the wild, the distribution of hunted animals and questionnaires sent to hunting units as well as the offices of landscape parks, national parks and forest inspectorates. A total of 344 records were collected with the known year when mink was recorded in a certain location for the first time. On the basis of these data, we created a model of mink expansion over time (see Brzeziński et al., 2019).

Next, using the expansion model, we predicted the year of mink colonization for all 123 sites at which the bird counts were performed. As a result, for each bird survey at each site, we were able to estimate the time (years) that had elapsed since mink occurred at that site for the first time (and used zero if a site was still not colonized during the year of the bird survey at that site). Finally, we obtained a variable—the attribute of each bird survey ranging from 0 (sites not yet colonized during a bird survey) to 31 (sites colonized 31 years before the bird survey, the longest period between the year of mink colonization and the year of the last bird survey). This variable was included as an explanatory variable in further modelling.

2.3 | Statistical analysis

In order to explain the variation in abundance of 13 bird species from 123 waterbodies over 44 years, we performed two types of

TABLE 1 Number of sites, number of surveys and pooled abundance for each of the 13 waterbird species used in the analyses. The species are sorted from most to least common

Species	Years (range)	*N* sites	*N* surveys	Pooled abundance
Eurasian coot	1972–2016	122	388	27 342
Great crested grebe	1972–2016	119	403	15 629
Mallard	1972–2016	108	323	15 705
Common pochard	1972–2016	98	336	11 921
Tufted duck	1972–2016	93	325	14 429
Gadwall	1972–2016	79	298	2 715
Garganey	1972–2016	77	285	2 698
Little grebe	1972–2016	71	231	2 373
Red-necked grebe	1974–2016	69	261	1 971
Northern shoveler	1972–2016	59	245	1 341
Black-necked grebe	1972–2016	54	217	4 554
Eurasian teal	1972–2016	51	222	511
Goldeneye	1977–2016	48	120	461

analysis: (1) 13 species-specific models, in which the abundance of a certain species was the response variable and (2) one model in which abundances of all 13 species were considered jointly (but not summed) in order to test abundance changes averaged for all 13 species (hereafter "community GAMM"). Altogether we used 14 models. We used generalized additive mixed models (GAMMs) using the "mgcv" package (Wood, 2017) in R (R Core Team, 2018). We used the negative-binomial family (theta was not defined a priori) and log-link in GAMMs to address possible data overdispersion. Three explanatory variables were included in all 14 GAMMs: (1) the habitat type (fixed factor with four levels: lake, reservoir, fishpond and river), as it may affect the abundance of certain species, reflecting their habitat preferences; (2) year of survey (covariate) to investigate the potential temporal population trends of the studied species; and (3) time that had elapsed since the mink colonized a site (covariate, in years), to investigate a numerical response to mink occurrence, independent of general temporal population changes, as year is included in the GAMM as a separate variable. Year of survey and time elapsed since mink colonization were not confounded and were moderately correlated (r = 0.6) as some sites were colonized by mink as early as 1984 while others were colonized very recently (2016) or remained uncolonized; thus, these two variables can be used simultaneously in a single model. This is crucial for our study—while the year effect can be associated with other factors potentially affecting waterbirds (but not controlled in the models: climate change, land use alterations, etc.), the effect of time since mink colonization at a site cannot be easily attributed to these factors because there is hardly any environmental factor spatially and temporarily synchronized with mink expansion. This is so because, in Poland, the mink population colonized eastern and western Poland almost simultaneously and has expanded from the north to the south, mainly upstream of the largest Polish rivers: Vistula and Oder (Brzeziński et al., 2019). Therefore, neither environmental global factors (e.g. climate change) nor local disturbances (e.g. lake eutrophication) are likely to follow such a complex spatial pattern as mink expansion.

In all 14 GAMMs, both year and time since mink colonization were fitted with thin plate regression splines with an upper limit to degrees of freedom set to 5, to keep the fit relatively simple. Splines estimate a smoothing curve to the data and are useful in describing nonlinear relationships between response and explanatory variables (Wood, 2017). We expected that the response of the birds to mink occurrence would be steep at the beginning and less pronounced later on, thus leading to a nonlinear relationship between bird abundance and time since mink colonization.

We confirmed that time since mink colonization improves model performance by comparing AIC values for GAMMs with and without this variable. In GAMMs, we also fitted the random effect of year (inserted as a categorical factor), water body ID and species ID (only in community GAMM). Thus, we introduced year twice: as a covariate and random categorical variable. We did this to separate long-term population trends from random perturbations in a given year (e.g. Knape, 2016). We checked model residuals for spatial autocorrelation with the use of spline correlograms. These correlograms suggest no spatial dependency problems and are presented in Figure S2.

In each GAMM, we identified the periods of statistically significant changes in bird abundance (i.e. sections of the x-axis for which the slope of the spline is distinguishable from zero) in relation to time since mink colonization. We used the "tsgam" package (Simpson, 2018) in R for this purpose. Community GAMM was additionally visualized by showing predicted relative waterbird abundance in Poland for 1990–2015 following mink expansion (for the purpose of visualization, all remaining variables from the GAMM were kept constant).

Finally, we correlated two time trends: changes in bird abundance over time since mink colonization (as predicted by community

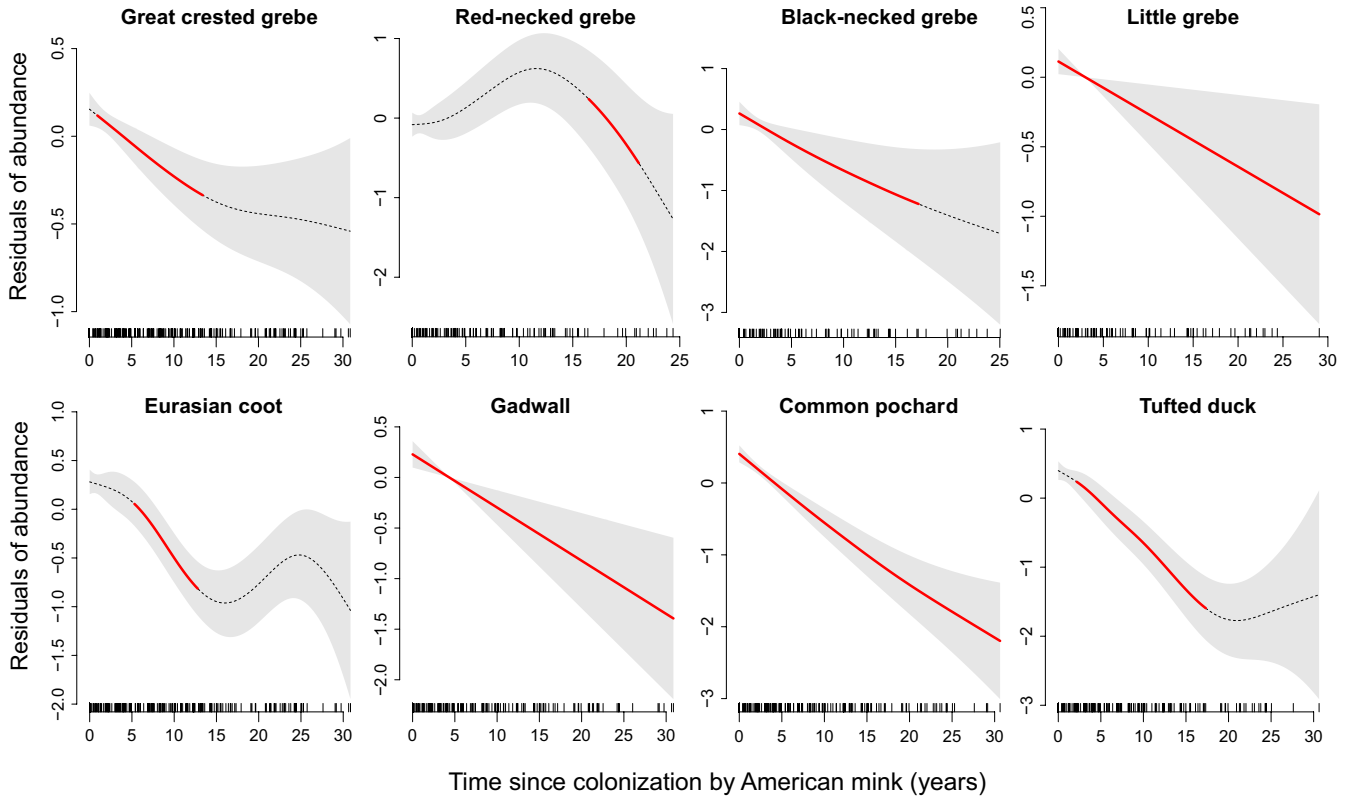


FIGURE 2 Relative changes in the abundance of eight waterbird species as a function of time since colonization by American mink as predicted by GAMMs summarised in Table 2. Curves represent the estimated smooth function, and shading denotes 95% confidence intervals. The red sections indicate periods of significant changes in the trend. The y-axis presents the partial residuals of the model after removing the effects of the other covariates. The rug plots along the x-axis show the data distribution

GAMM in this paper) and changes in mink density over time since mink colonization (taken from Brzeziński et al., 2019). We expected that a decrease in bird abundance would mirror an increase in mink density. In this correlation, we considered different time-lags (e.g. $mink_t$ vs. $birds_t$ or $mink_t$ vs. $birds_{t+1}$) and presented the lag ensuring the highest correlation coefficient.

3 | RESULTS

3.1 | Temporal variation in abundance of waterbird species

Coot, great crested grebe and mallard were the most numerous species, recorded at 122, 119 and 108 study sites, respectively (Table 1). The least numerous were Eurasian teal (51 sites) and goldeneye (48 sites). Most of the species studied showed differences in abundance between habitat types, with rivers hosting a greater abundance of coot and ducks (except tufted duck and goldeneye) (Figure S3 and Table S2). No differences were observed in the case of grebes (except great crested grebe). All species studied except one (little grebe), as well as the whole waterbird community, showed significant population trends over time. These trends were primarily negative, at least during the first half of the study period (1972–2000), but some species tended to increase in number during the last 15 years. Two species, gadwall and goldeneye, showed a linear population increase over the study period (Figure S3).

The breeding populations of 8 of the 13 waterbird species analysed were significantly associated with time since mink colonization, and these associations were primarily negative, although in most cases nonlinear (Figure 2, Table 2). The populations of four species (black-necked grebe, little grebe, gadwall and common pochard) declined linearly over the 30-year period after mink invasion, whereas the populations of three other species (great crested grebe, coot and tufted duck) declined over the first ca. 15 years after mink invasion, but then stabilized at a low level. Inserting "time since mink colonization" into the model substantially increased its parsimony for nine species (column presenting ΔAIC in Table 2). Year alone (without "time since mink colonization") was better in the case of four species (three ducks and one grebe). The abundance of five species (mallard, northern shoveler, teal, garganey and goldeneye) remained unaltered despite mink expansion, and their numbers did not change significantly over time (Table 2, Figure S4).

3.2 | Temporal variation in abundance of waterbird community

Breeding populations of all 13 waterbird species analysed together in one model showed a significant association with the time that had

TABLE 2 Summary of 14 generalized additive mixed models (13 species-specific GAMMs and community GAMM) explaining the abundance of waterbirds over time and across surveyed sites

	Habitat type (Lake = reference)			Spline fits (edf)			ΔAIC	
Response variable	River (SE)	Fishpond (SE)	Reservoir (SE)	Year of survey	Time since mink	R^2_{adj} (%)	Year	Year + Time since mink
Ducks								
Gadwall	**1.32 (0.67)***	−0.36 (0.37)	0.15 (0.64)	**1.00*** **	**1.00*** **	42.8	13.75	**0.00**
Eurasian teal	**1.33 (0.59)***	−0.38 (0.41)	0.06 (0.54)	**1.00*** **	1.00	22.9	1.00	**0.00**
Garganey	**2.63 (0.45)** ***	−0.53 (0.32)^	0.23 (0.44)	**3.22*** **	1.75	35.4	**0.00**	2.72
Mallard	**2.82 (0.61)** ***	**1.37 (0.22)** ***	**1.48 (0.45)** ***	**5.33****	2.43	70.9	**0.00**	4.19
Northern shoveler	**2.58 (0.53)** ***	−0.54 (0.36)	0.53 (0.52)	**1.00*** **	1.09	61.4	**0.00**	20.09
Common pochard	**1.74 (0.62)****	**1.68 (0.30)** ***	0.49 (0.58)	**3.27*** **	**1.49*** **	46.4	38.62	**0.00**
Tufted duck	0.82 (0.62)	**1.65 (0.33)** ***	0.51 (0.54)	**3.86*** **	**3.31*** **	58.1	69.39	**0.00**
Goldeneye	−0.42 (0.61)	0.50 (0.43)	0.39 (1.19)	**1.00***	1.00	38.9	1.50	**0.00**
Coot and Grebes								
Eurasian coot	**1.87 (0.51)** ***	**0.77 (0.24)****	0.59 (0.43)	**4.36*** **	**4.62*** **	60.8	55.58	**0.00**
Great crested grebe	−0.05 (0.61)	**−0.73 (0.24)****	0.16 (0.42)	**2.58***	**2.08****	76.1	10.49	**0.00**
Red-necked grebe	−0.13 (0.76)	0.11 (0.56)	−0.13 (0.71)	**4.49*** **	**3.19****	84.3	14.66	**0.00**
Black-necked grebe	0.38 (1.31)	0.21 (0.81)	0.79 (1.02)	**1.22****	**1.30***	39.3	**0.00**	3.11
Little grebe	0.12 (0.48)	0.60 (0.33)^	0.37 (0.46)	1.00	**1.00***	41.0	14.55	**0.00**
All species								
All species	**1.98 (0.36)** ***	**0.57 (0.18)****	**0.65 (0.32)***	**3.79*** **	**3.66*** **	47.3	42.49	**0.00**

Note: Significance: ^0.1; *0.05; **0.01; ***0.001. Significant effects are marked in bold.
Abbreviation: edf, estimated degrees of freedom.

passed since establishment of the mink population (Table 2). The model containing "time since mink colonization" was much more parsimonious in comparison with the model analysing year effect alone (Table 2, Figure S5). The decline of the breeding waterbird community was significant from ca. 3 to 15 years after establishment of the mink population, and on average, the original abundance of each species (time since mink colonization = 0) was reduced by 53% during the first 16 years following first mink occurrence (Figure 3a). Between 18 and 23 years after mink colonization, waterbird numbers increased slightly and tended to remain at a stable but low level in the following years (however, between years 24 and 30, the confidence interval is very wide).

At 123 study sites, the predicted abundance decreased from 27 000 to 12 000 pairs during the 15-year period after the mink population was established (Figure 3b, Table S3). Four species made the major contribution towards the decline in the abundance of the whole waterbird community: the abundance of coot declined from 7,668 to 2,211 pairs (71%) over a 16-year period after mink populations were established, the abundance of tufted duck declined from 3,043 to 347 pairs (89%) over 20 years after mink colonization, and the abundance of great crested grebe and common pochard declined from 4,540 to 2,288 pairs (50%) and from 2,749 to 213 pairs (92%), respectively, over 30 years after the mink population was established (Figure 3b, Table S3).

We found a lagged association between bird abundance following mink colonization and mink density over time elapsed since their populations were established (Figure 3a). Decreasing bird abundance correlated with increasing mink density, and the highest correlation was recorded for a 4-year time-lag (R^2 = 0.95): mink density at a site was highest 12 years after colonization, while waterbird abundance was lowest 16 years after establishment of the mink population in a certain area (Figure 3a).

3.3 | Spatiotemporal variation in waterbird abundance

Extrapolation of the spatiotemporal relation between the occurrence of mink and decline in waterbird populations to the broad geographical scale results in a pattern of a travelling wave of declining bird abundance following ongoing mink expansion (Figure 4). The decline in waterbird numbers started in north-eastern Poland; the wave moved to central and western Poland, and next to the south. It moved fastest upstream of large Polish rivers: the Vistula and Oder, following the main routes of mink expansion. Up to 2015, waterbird abundance decreased in about 70% of the country, compared with the 1990s. However, since 2010, the abundance of waterbirds in northern Poland has started to recover (Figure 4), as the model presented in Figure 3a predicts abundance recovery after an initial decrease.

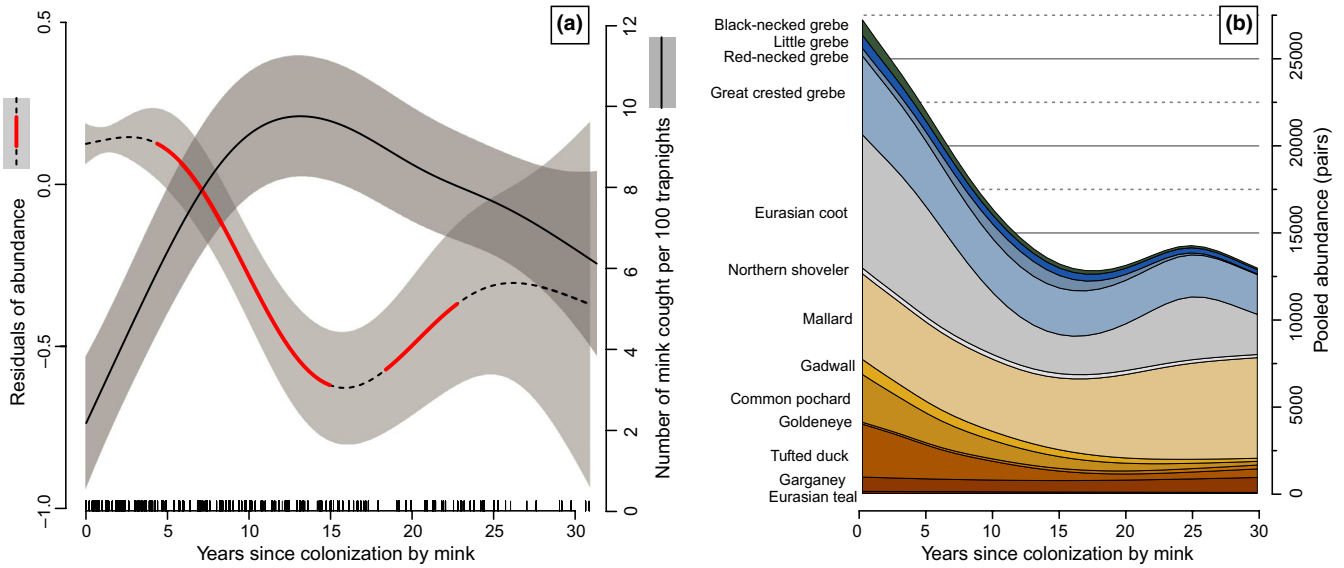


FIGURE 3 (a) Relative changes of waterbird abundance averaged across 13 species as a function of time after American mink colonization as predicted by community GAMM summarized in Table 2 (dashed curve). Curves represent the estimated smooth function and shading denotes the 95% confidence intervals. The red sections indicate the periods of significant changes in the trend. The y-axis presents the partial residuals of the model after removing the effects of the other covariates. The rug plots along the x-axis show the data distribution. Mink density, taken from Brzeziński et al. (2019), is visualized with the black solid curve. (b) Species abundance at 123 sites predicted from 13 species-specific GAMMs summarized in Table 2 inrelation to the time after mink colonization. Each species is indicated by a different colour

4 | DISCUSSION

Our study showed a quick and deep decline in the total abundance of waterbirds after the American mink colonized their breeding grounds, although a few exceptions to this rule were observed. This decline, however, was nonlinear in most cases and, generally, after a steep decline during the first 15 years, it stopped and overall community abundance started to recover. We thus confirmed the hypotheses posed in the introduction and for the first time report nonlinear patterns in a population's response to alien predators on a large temporal scale. Furthermore, extrapolation of these findings to a broader geographical scale suggests a spatiotemporal pattern resembling a wave of waterbird population decline travelling through Poland from north to south. Our analysis reveals that at a national scale, the impact of mink on waterbirds could reduce their breeding populations by even tens of thousands of pairs.

Estimating prey decline after predator expansion is challenging as, at the same time, prey populations may be decreasing or increasing due to other environmental factors. Thus, negative trends in bird abundance after the appearance of mink cannot be directly attributed to a "mink effect." Consequently, we did not use such an approach. Instead, based on the 40-year history of American mink colonization in Poland (Brzeziński et al., 2019), we calculated the number of years that had elapsed since mink appearance for each bird survey. The spatiotemporal pattern of mink expansion was unlikely to be synchronized with the impact of any other factor affecting bird populations (e.g. climatic and land use changes, hunting, other invasive species). All these factors affect bird abundance at random sites or consequently over time; thus, their possible influence is inseparable from year effect in the model but should not bias the effect of time since mink appearance.

Despite this approach, we still have uncertainty around the abundance of the populations studied. This could be linked to the type of data we have used—data sets collected by many researchers over a long time period are usually associated with some variation in methods used. This variation may reflect differences in sampling effort, timing and duration as well as researchers' experience. If the methodology changes over time, it is hard to disentangle real biological processes (e.g. population trends) from sampling bias. Fortunately, the waterbird survey methods for all studies used by us followed the same protocol, and the only potential variation we are aware of is related to unequal effort between surveys. This, however, does not show any spatial or temporal pattern and only produces additional random variation in the data analysed. Despite this random variation, we confirmed clear patterns of substantial changes in waterbird abundance.

The results of our study suggest that over a long time period, the mink invasion had a devastating impact on breeding waterbird populations. The impact differed according to species but, generally, the patterns of population change in the periods following mink colonization were similar. Our results agree with earlier findings (but on a much smaller scale) on local bird declines in areas colonized by mink (e.g. Brzeziński et al., 2012). On the other hand, not all species declined after establishment of the mink population, and a species-specific response to an alien predator may be associated with birds' life histories. Predation pressure on birds depends strongly on bird nest type and nesting site. Generally, ground-nesting birds are more vulnerable to predation than those nesting

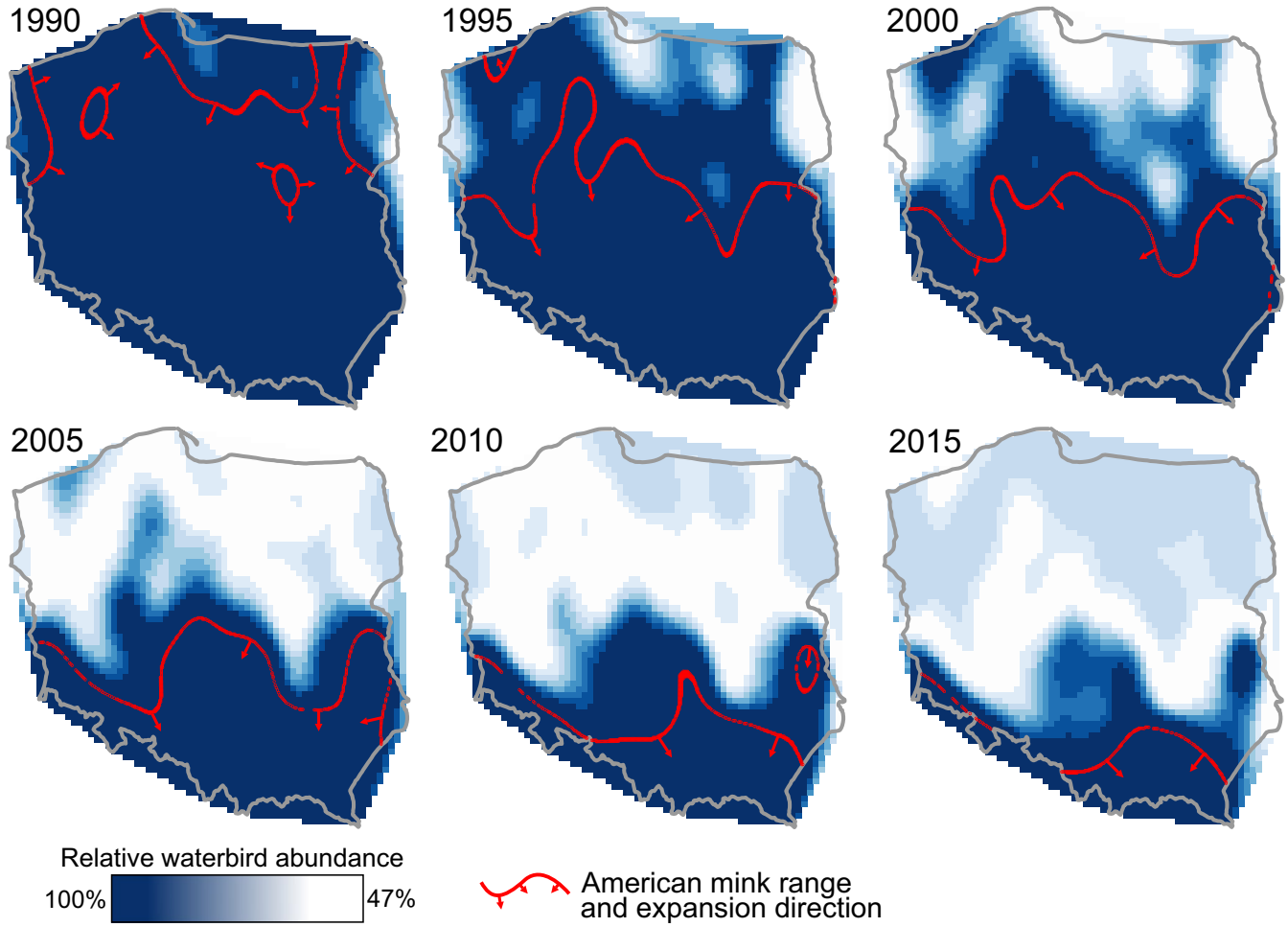


FIGURE 4 Relative waterbird abundance related to their numbers before mink colonization (white-blue gradient) in Poland in consecutive 5-year periods as predicted by the community GAMM presented in Table 2. Waterbird abundance before mink occurrence is set as 100% (blue colour). The red line indicates the American mink range calculated for a given year from Brzeziński et al. (2019)

at higher locations (Chalfoun, Thompson III, & Ratnaswamy, 2002), and populations of ground nesters may suffer greater declines due to more intensive predation compared with species using other nesting sites (Gregory et al., 2007; Kolecek & Reif, 2011; Thaxter, Joys, Gregory, Baillie, & Noble, 2010; Woinarski et al., 2017). The different nesting site preferences of waterbirds may, therefore, be an important factor influencing the probability of depredation by mink. It seems that species which build their nests in the littoral zone of water bodies are at greatest risk of mink predation because mink are mostly active along a narrow strip of river or lake bank (Brzeziński, Marzec, & Żmihorski, 2010; Melero, Palazón, Revilla, Martelo, & Gosàlbez, 2008; Yamaguchi, Rushton, & Macdonald, 2003). Our results, as well as those of some former studies (e.g. Brzeziński et al., 2012; Ręk, 2009), show that coot populations are particularly vulnerable to mink predation, and the coot may even be considered an indicator species reflecting the impact of mink on waterbird populations in a certain area. On the contrary, the waterbird species safest from mink predation are those nesting in cavities. According to this prediction, a cavity nester, the common goldeneye, was the only species that tended to increase in number after mink expansion. Duck species that are not cavity nesters but can choose nesting sites farther away from a water body shoreline can also be less impacted by mink.

The breeding populations of most common waterbird species (coot, great crested grebe, common pochard and tufted duck) declined significantly after mink invasion, with the only exception being the mallard. The lack of a relation between mink expansion and mallard abundance may be explained by the increasing fraction of mallard urban population (Engel, Keller, Leszkowicz, & Zawadzki, 1988), which may stabilize its population at a national scale. American mink avoid anthropogenic habitats (Brzeziński, Ignatiuk, Żmihorski, & Zalewski, 2018); therefore, the mallards in these habitats are safe from mink. Urban mallards may therefore have a higher breeding output and higher winter survival rate and may be constantly supplying rural populations. Moreover, mallards often nest far from water bodies and in cavities and therefore may be less vulnerable to the impact of mink. We did not record significant population declines of garganey, northern shoveler, teal or goldeneye following mink expansion, which may be partly explained by their initial low densities (they were recorded at about or less than 50% of study

sites), reducing the statistical power of the models, as well as their nesting site preferences (nesting in backwaters, midfield pools and tree cavities).

The waterbird decline averaged across all 13 species was most intense up to 15 years after the mink population was established in a certain region, with the lowest waterbird numbers being recorded 4 years after the mink populations reached their highest density. The decline was followed by a slight increase in waterbird abundance recorded between the 15th to 25th years after mink colonization. We suppose that this increase may be driven by two factors. First, the density of invasive species varies over time (Simberloff & Gibbons, 2004). In Poland, densities of local mink populations consecutively increased in colonized areas, reached their maxima after 10–15 years and then declined and stabilized at an average level (Brzeziński et al., 2019). Thus, the waterbird increase can reflect mink density decrease. Second, the birds develop strategies which enable them to avoid or minimize predation. Behavioural adaptations of naïve prey to avoid predation by invasive mink have been observed in birds and mammals (Barros et al., 2016; Brzeziński et al., 2018, 2012; Nordström & Korpimäki, 2004) but such adaptations can be induced by many other invasive species, for example black rats *Rattus rattus* (Vanderwerf, 2012) and European starlings *Sturnus vulgaris* (Lawrence, Paris, Briskie, & Massaro, 2017). Choosing safer nesting sites by changing nesting height, colonial breeding or nesting in the vicinity of human settlements has been identified as a strategy to increase their productivity and survival (Brzeziński et al., 2012; Lawrence et al., 2017; Vanderwerf, 2012).

Our findings on the spatiotemporal effect of mink on waterbirds correspond well with recent waterbird population trends. For instance, in Poland, population declines were recorded for tufted duck and red-necked grebe in the years 2008–2016, whereas the breeding populations of mallard, great crested grebe and coot increased in that period (Chodkiewicz et al., 2018). These estimates are consistent with our results if we take into account the last 10 years. In Europe, coot, great crested grebe, pochard and garganey are considered to have been in decline since the beginning of the 21st century; populations of mallard, tufted duck, northern shoveler and goldeneye are rather stable; and red-necked grebe and gadwall populations are increasing (BirdLife International, 2017). Some of these trends reflect our results and may suggest that mink also impacted bird abundance in other parts of Europe. However, the mechanisms driving these changes on a continental scale are largely unknown and can differ in various regions. The increases have been explained by lower hunting pressure, improved environmental conditions and protection of wetlands, but also by increasing temperatures and the intensification of fish production (Lemoine, Bauer, Peintinger, & Böhning-Gaese, 2007; Martínez-Abraín, Jiménez, Gómez, & Oro, 2016; Pagel, Martínez-Abraín, Gómez, Jiménez, & Oro, 2014; Reif, 2013). On the other hand, declines have been attributed to climate change, habitat alterations, reduced food resources and hunting pressure (Fernandez, Selma, Aymerich, Sáez, & Fructuoso, 2005; Lehikoinen, Rintala, Lammi, & Pöysä, 2016; Long, Székely, Kershaw, & O'Connell, 2007; Pöysä, Rintala, Lehikoinen, & Väisänen, 2013; Rönkä, Saari, Lehikoinen, Suomela, & Häkkilä, 2005; Ward, Semel, & Herkert, 2010). Surprisingly, American mink predation is not often considered a possible factor driving the negative trends among waterbirds, and our results suggest that the current view on waterbird population trends needs to be updated by including this important ecological factor.

Based on our model, we estimated declines in waterbird numbers from about 27 000 pairs to 12 000 pairs, which is more than 50%. The Polish populations of the 13 waterbird species analysed were estimated to be between 251 300 and 448 200 breeding pairs in 2008–2012 (Chodkiewicz et al., 2015), when most of the country was already colonized by mink. This then indicates that waterbird populations have been reduced by at least tens of thousands of breeding pairs. Also, other groups of waterbirds, such as waders, rallids, gulls and terns, can be impacted by mink predation (Craik, 1997; Kilpi, 1995; Niemczynowicz et al., 2017), so the reduction in the total waterbird community may be even larger. Assuming a similar overall level of bird number reductions in other countries colonized by mink (e.g. Russia, Germany or Sweden; Bonesi & Palazón, 2007), we conclude that mink predation may cause a dramatic decline in the global population of several waterbird species. This underlines the need for actions to mitigate the negative impact of the American mink and to protect waterbirds. Our data also suggest that the most severe period of mink impact on waterbirds is up to 15 years after colonization; therefore, any protective activities should be conducted particularly in this period.

5 | CONCLUSIONS

Tens of mammalian species have been introduced and successfully expanded their range on a global scale (DAISIE, 2009), and there are several well-documented cases of mammalian impacts on native prey populations, not only across small oceanic islands (e.g. Woinarski et al., 2017). However, most of the impacts on a larger geographical scale are largely unknown, despite the fact that at least some of them may affect native prey on a similar scale to the American mink. Unfortunately, the lack of long-term, precise data on the expansion of invasive predators and native prey dynamics often prevents the discovery of their real impact. For that reason, the decline of native species is often falsely attributed only to other factors (e.g. climate change, habitat destruction). In publications analysing the long-term changes in waterbird abundance in Europe, American mink predation is mentioned as a factor contributing to the population declines of certain species (e.g. pochard; Fox et al., 2016). However, such statements are rarely based on empirical data. Certainly, it has been confirmed that mink can impact waterbird populations locally, but at a large European scale, waterbird dynamics in relation to mink expansion have not been analysed. Overall, our study fills this gap and shows that most waterbirds are vulnerable to mink predation, and their large-scale declines can be related to the expansion of this invasive predator. Because waterbirds are an important component of trophic food webs, responsible for organic matter turnover and providing numerous ecosystem services (Green & Elmberg, 2014), a large

reduction in their abundance may significantly affect freshwater ecosystems and may trigger a cascade of environmental changes in large parts of Europe, as well as in parts of South America and Asia, which are already colonized by American mink.

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DATA AVAILABILITY STATEMENT

Data will be available from the Dryad Digital Repository upon acceptance.

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BIOSKETCHES

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SUPPORTING INFORMATION

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

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