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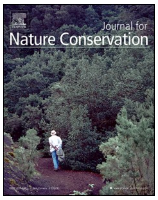

Past and present existence of *Spermophilus citellus* in Hungary with a forecast of its population using time series models

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ABSTRACT

The European ground squirrel (EGS) is an endangered burrowing rodent of Central and South-Eastern European dry grasslands with a declining population trend. Its prehistoric and historical distribution ranges and population trend have not been analysed until now. In this study we addressed these gaps and aimed to give a comprehensive view on the species history and forecast its population trend in light of past management actions. We collected data on the location and extinction of local colonies in Hungary from archaeological, geographical, and document archives and Hungarian monitoring databases. Statistical analysis focused on forecasting the trend and quantifying the change in the number of populations since 1964 by two-times interrupted autoregressive integrated moving average and Bayesian structural time-series models.

Paleontological evidence indicated widespread distribution of the genus *Spermophilus* in Hungary in the last 1.45 million years. EGS has continuously inhabited this area for 2000 years. Documentary evidence supported that EGS inhabited 94 % of the area of Hungary if we assume a *meta*-population structure until the 2nd half of the XXth century. From 1964 EGS colonies showed a sharply declining trend until 2012. After 2012, the trend levelled out, however, the analysis could not exclude random fluctuations behind that positive change in the trend. The halt in decline may be attributed to the start of coordinated conservation reintroductions. Results indicated that translocations could provide a useful tool for species protection despite failures of translocations, though further data will be required to clearly accept or refute this metapopulation.

1. Introduction

Natural history encompasses the study of the (evolutionary) history, ecology, and behaviour of a species (Greene, 2005). In addition to other sources within that domain, paleontological evidence from fossils, documentary evidence from place names, and population time series data can serve as information sources from different time frames to put the whole picture together on the natural history of species or other taxa.

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Those studies provide direct knowledge about organisms which can help us understand their spatiotemporal dynamics, the patterns and changes in the distribution, abundance, and behaviour of populations across space (shrinking, expanding, stable) and time (short-term or long-term periods) (Hammond & Kolasa, 2014). These quantitative methods are suitable for assessing conservation status by measuring the direction of population trends or estimating the risk of extinction (Mace & Lande, 1991; Thompson et al., 1994), and rely on detailed knowledge about the natural history and long term population trends of a species. Assessment of a species' conservation status is important because it provides a basis for policy development and allocation of resources for conservation actions. That information also helps us manage the populations of threatened species properly (Gedeon, 2011). Conservation of biodiversity and the long term survival of populations of keystone species contribute to ecosystem functions and services (food security, human well-being and health) (European Commission, 2021). Therefore, the gradual decrease in the number of or disappearance of keystone, often ecosystem engineer burrowing, megafauna species, such as the European ground squirrel (*Spermophilus citellus*) (Linnaeus, 1766) (EGS hereafter) (Lindtner et al., 2019), from natural ecosystems results in intensified ecosystem deterioration. For this reason, the disappearance of mammalian biopedturbators has been considered one of the most important drivers of the collapse of Australian grasslands (Elridge & Soliveres, 2022; Fleming et al., 2014). From that perspective, the long term population trend of those keystone grassland species goes beyond their simple presence or absence and becomes an important topic concerning the long term conservation of grassland ecosystems, and in the case of EGSs, of the Pannonian ecoregion.

1.1. *Paleontological evidence: Fossils*

Paleontological evidence can show the former occurrence of taxa that have gone locally extinct but there were recent populations in their distribution area. The quantification of evidence is difficult due to different levels of disposal, preservation, and recovery of animal remains for different species. In other words, paleontological faunal cannot provide quantitatively reliable information about the abundance of a species and the sites of excavations do not represent a random selection of locations (Conolly et al., 2012). However, animal remains in bone assemblages uncovered in excavations can show the occurrence of species indicating tolerable environmental conditions for that species (Albarella, 1999) within a specific time period determined from sediment layers or by carbon-14 dating. Moreover, paleo-zoological records provide evidence about the presence of a taxon but the absence of taxa in paleontological remains may not indicate the absence of that taxon in an area, as incorrect sampling techniques or unfavourable conditions for fossilisation could fail to show the taxon's presence (Lyman, 2008). Consequently, a careful approach is to use paleontological evidence in the sense of a qualitative indicator (with binary output) of the former presence of a taxon.

1.2. *Documentary evidence: Place names*

Documentary evidence, which are non-scientific, descriptive written records about animal populations' location, is another form of data that can show the current or former presence of animals. Among the indirect evidence of the presence of EGS, place names play an important role, many of which are based on the floral and faunistic characteristics of the sites and often preserve the memory of a situation that has existed for many centuries. The name remains attached to the place as long as the area does not undergo a radical change and the inhabiting population there shows relative continuity.

Animals and plants occurring in the Pannonian ecoregion were often mentioned in detailed maps produced in the XVIIIth and XIXth centuries. In the hierarchy of geographical and cartographical nomenclature microtoponyms (small geographical units, field names and the names of the outskirts of settlements, which we call place names in the following (Bölcskei et al., 2017), are the ones that usually refer to animals or plants (Faragó, 2014; Hough, 2008; Pásztor, 2013) in the landscape. These names are frequently formed from demotic vocabulary and preserve a rich collection of the local history about the outskirts of settlements (Faragó, 2014; Hough, 2008). The origin of those place names comes from personal experiences and reflections of local people on the natural environment including wild animals (Poole, 2015). Therefore, place names can be used as indicators of the recent or former presence or distribution of animals (Cox et al., 2002; Poole, 2015; Tattoni, 2019). Although paleontological and documentary evidence provide data on the history and location of animal populations they cannot be used to quantitatively investigate animal population trends, and as a result the use of this kind of data needs careful approach.

1.3. *Time series data: Trend analysis*

In biology, trend analysis is the study of long term change in population size (mean abundance) or distribution range and as a result it can show decreasing, increasing, or fluctuating spatio-temporal population trends (Davitt et al., 1999; Sturludóttir, 2015). Absence-presence data is required at minimum to delineate the spatial distribution range of a species. For absence-presence sampling it is recommended to sample large areas with low effort rather than small areas with large effort (Chandler & Scott, 2011). One of the main reasons is that animals, which tend to aggregate, can be easily missed if only small areas are meticulously investigated. Moreover, the large over small area approach better fits long term, historical data on animal populations, which do not have quantitative dimensions (abundance) but only the frequency of occurrences (presence). This large over small area approach is also favourable when animal populations live in colonies (clumping) (like EGS) rather than being individually dispersed because large areas can contain a few colonies but many individuals.

1.4. *The European ground squirrel*

The EGS is a medium-sized, hibernating species that favours short-grass natural meadows. Recently it is linked, inter alia, to semi-natural managed grasslands, such as airfields, golf courses, recreational areas, and vineyards. These managed grasslands provide refuge for EGS while their natural grassland habitat has been shrinking (Váczi and Altbäcker, 1999). The EGS is a key engineering species of the steppic ecosystem (Lindtner et al., 2019) and endemic to Central and South-Eastern Europe. Its importance to ecosystem functions and services has not been studied as intensively as other ground dwelling *Sciurids* and burrowing mammals of, for instance, Australia (Fleming et al., 2014) and North America (Augustine et al., 2023). However, recent results have indicated that EGS changes soil physical and chemical characteristics significantly (Lindtner et al., 2019). EGS is also an important prey species for several endangered top predators, such as the Imperial eagle (*Aquila heliaca*) (Horváth, 2009), the Saker falcon (*Falco cherrug*) (Bagyura et al., 2004), the Steppe polecat (*Mustela eversmanii*) (Sainsbury et al., 2024), and the Marbled polecat (*Vormela peregusna*) (Gorsuch & Larivière, 2005), contributing more to their nesting success or litter survival compared to other prey (e.g. pigeons). The distribution range of the EGS consists of two distinct areas divided by the Carpathian Mountains. The border between the two phylogenetic lineages is in Bulgaria (Říčanová et al., 2011). The western part extends from Southern Poland (reintroduced colonies) through the Czech Republic and Eastern Austria through Slovakia and Hungary into the Pannonian part of Romania and Serbia. The eastern part of the range includes the Trans-Carpathian region of Ukraine, Romania, and part of Moldova, Bulgaria, and the Western Balkan countries including the southeastern part of Northern Macedonia. It also inhabits the northeastern part of Greece and the European part of Turkey. It is a relatively well-studied species with unusually good historical records because it used to be common and has had a continuous association with human communities, which provided a rich source of information about its early presence in Hungary in addition to paleontological evidence. Paleontological excavations in Hungary resulted in several ground squirrel findings (Kordos & Krolopp, 1980; Kretzoi, 1964; Sinitsa & Pogodina, 2019). Moreover, minor place names (field names, microtoponyms), works of ethnographers and writers, and later XX^th^ century documentaries of pest control authorities, etc. stored and provided evidence about the former occurrence of EGS colonies (Aybes & Yalden, 1995; Webster, 2001). These place names included the approximate location of EGS colonies. After the species was declared protected and then strictly protected by law (Council Directive 92/43/EEC, 1992; IUCN, 2015; Környezetvédelmi Minisztérium, 2001) it became an important flagship species of nature conservation, and field naturalists and amateur or professional conservationists or citizen scientists purposely recorded locations of colonies (Váczi, 2021). However, because it was a common pest in earlier times that was considered abundant and, as a result, inexhaustible until the end of the 1970s (Grulich, 1960), specimens were rarely collected and stored in museums or collections.

1.5. Aims

In consistence with the species' and burrowing mammals' importance in the maintenance of grasslands, our comprehensive aim was to study the species' past and present existence and abundance in Hungary, to predict the fate of the population based on quantitative data on the number of colonies since 1964, and by that to encourage and improve future conservation decisions and practices. Our more specific aims fell into two distinct parts: (1) To comprehend the presence and distribution area of EGS from prehistoric times through to modern days, specifically in two epochs (prehistoric, based on paleontological evidence from the last 1.45 million years; historic, from the XVII^th^ century until 1963, based on documentary evidence). (2) To determine the trend of colony numbers of EGS from 1964 until 2020, and to predict the perspectives of its future population in Hungary based on quantitative data on the number of colonies annually.

2. Materials and methods

We gathered paleontological, historical, or recent, direct or indirect data on the locations of colonies and the estimated date of their local extinctions for the period between 1964 and 2020. We attempted to collect ground data from different sources available for free for research or educational purposes: data sources included archaeological and geographical databases, biotic databases from national park directorates, the Hungarian Biodiversity Monitoring System (HBMS), regional reports and documentaries, and personal records of field naturalists and conservation experts. Prehistorical data about the species consisted of paleontological findings of the species complex (i.e. *Spermophilus citellus* and *citelloides*) in Hungary.

2.1. Study area and data collection

Data was gathered on the occurrences (presence) of EGS colonies in Hungary. The data referred to EGS presence as indicated either directly or indirectly. Direct data included observations of EGS at any locality. Direct data were georeferenced with x and y coordinates (point or polygon), mainly localised by GPS tools and collected by professional conservationists, researchers or volunteers (validated by specialists). Indirect data included records of EGS's presence from place names that could indicate the approximate location of EGS colonies (Aybes & Yalden, 1995). In these cases the approximate location of the colony could be extracted from the source but it was not possible to localise the colony with an exact georeferenced point or polygon. These types of data could still be valid and indicate a colony unambiguously because there has been only one ground squirrel species in Hungary, therefore the species' name in Hungarian could only refer to EGS. Thanks to the geomorphological features they create, life history and ecological characteristics (sociality, hibernation, semi-fossorial, grassland habitat) of the species colonies could have always been differentiated from other burrowing rodents like European hamsters (*Cricetus cricetus*), common voles (*Microtus arvalis*), and Eurasian blind mole-rats (*Nannospalax* spp.), which has helped us to accept the place names of colony occurrences as valid locations of the species in Hungary.

Both indirect and direct data were collected from four different types of sources: (1) fossil records of *Spermophilus* spp. specimens (Pazonyi, 2004, 2011); (2) databases of Hungarian place and field names (Földrajzinév-tár, 1978; Magyar Nemzeti Múzeum, 2017; Központi Statisztikai Hivatal Könyvtár és Dokumentációs Szolgálat, 1987; Lechner Tudásközpont, 2024; Magyar Királyi Központi Statisztikai Hivatal, 2024; Országos Széchenyi Könyvtár, 2024; Benkő, 1970); (3) survey data and regional reports of country wide EGS mapping, biotic databases of the HBMS and national park directorates (Váczi, 2006, 2019; Vadonleső Csoport, 2019); and (4) personal records of field naturalists, conservation experts, publications, and reports in local papers (Arcanum Adatbázis Kiadó, 2024).

Data were divided into three time periods: (i) the first period was indicated by paleontological evidence (fossils), and represented the prehistorical period of ground squirrel and EGS presence in Hungary (indirect data; approximate location of colonies and age of ground squirrel fossils based on the work of Pazonyi (2006); (ii) the second period was indicated by place names derived from historical times data from the XVIII^th^ century until 1963 (indirect data; location of colonies); (iii) and the third period, based on records of EGS colonies, this included both direct and indirect, quantitative, country wide data from 1964 until 2020.

In the 1^st^ period, paleontological remains of ground squirrels (i.e. *Spermophilus citellus* and *citelloides*) recovered in Hungary were considered indirect data of the *Sciuridae* group. Although paleontological evidence indicated the presence of four different species in Hungary (*S. citellus*, *S. citelloides*, *S. major*, *S. primigenius*) during the Pleistocene and Holocene, only EGS is currently present in the area. *S. citelloides*, which is the youngest fossil species except for *S. citellus*, went extinct 15000 years ago (Sinitsa et al., 2021). As the habitat requirements and ecological needs of *S. citelloides* and EGS were similar (grasslands or forest steppe), we did not differentiate *S. citellus* and *citelloides* for our historical review. Our approach to paleontological findings of ground squirrels was to approximately locate prehistorical ground squirrel remains and then we aimed to describe the floral characteristics and specific environment of those specific time periods focusing on the ecological needs of ground squirrels (Murie & Michener, 1984; Pazonyi, 2004; Sebe et al., 2021). For this descriptive part of our work we primarily used the so-called "Ecological Units" as defined in Pazonyi (2006). The most important of these for this work is Ecological Unit 1, which encompasses the present-day mammalian fauna communities of the Carpathian Basin, and thus has the most reliable interpretation. Ecological Unit 1 consists of a significant proportion of species that prefer grassland, such as *S. citellus*, and species that prefer woody-shrubby (forest-steppe) vegetation. The habitat distribution of the species indicates that the unit is characterised by wooded steppe vegetation. Over the last 1450 thousand years, this ecological unit has been identified several times in the Carpathian Basin and has always been associated with a ground squirrel species (Table 1). *S. primigenius* was found in the oldest sites, *S. citelloides* in the younger sites, and *S. citellus* in the last 2000 years.

Records from the 2^nd^ period are represented by the database of historic occurrences until 1963. Each record contained the approximate location of the colony or group of colonies connected to each other. This period contained information, including minor place names (Aybes & Yalden, 1995) for EGS from the XVIII^th^ century until 1963 and is based on the common noun "ground squirrel" ("ürge" or "irge") found in geographic field names (minor place names) (Bába & Nemes, 2014;

Table 1

Locations of ground squirrel (*S. citellus, S. citelloides* and *S. primigenius*) remains from paleontological excavations since 1964. Each location and time period were characterised by similar environmental conditions. The original description, characterisation and differentiation of environmental conditions, so called Ecological Units, during the last 1.45 million years can be found in Pazonyi (2011) (Kordos & Krolopp, 1980; Kretzoi, 1964; Sinitsa & Pogodina, 2019).

Localities and layers	**Estimated age (ka)**	**Species (number of specimens)**				**References**
		S. citellus	*S. citelloides*	*S. spp.*	*Spermophilus pimigenius*	
Rigó-lyuk layer 1	0.2	6				Kordos 1984
Rigó-lyuk layer 2	0.3	5				Kordos 1984
Rigó-lyuk layer 3	0.5	4				Kordos 1984
Rigó-lyuk layer 4	0.8	6				Kordos 1984
Rigó-lyuk layer 5	1.2	3				Kordos 1984
Rigó-lyuk layer 6–7	1.8	2				Kordos 1984
Nagyoldal Hole layer 0	2.0	1				Kordos 1981
Tata	100		2			Kretzoi 1964
Bajót Rock-shelter 3	101			4		Kordos 1994
Nagyharsányhegy 4	500				*	Jánossy 1986
Villány 6	640				5	Jánossy 1986
Osztramos 8	1200				15	Jánossy 1986
Újlaki hegy	1200				1	Jánossy & Topál 1990
Osztramos 2	1400				2	Jánossy 1986

Notes: Numbers represent the number of specimens found in the specific locality. * shows unknown number of specimens. Each locality and layer belonged to Ecological Unit 1 (Pazonyi, 2011).

Földrajzinév-tár, 1978; Kiss, 1983; Kovács, 2019). As a result of the historical, indicative nature of the data and the species' widespread distribution in the past (when it was considered an agricultural pest), this period was not differentiated into sub-periods (XVIIIth – XIXth centuries or more recent XXth century until 1963). The place names for EGS indicated the species without confusion but we assumed that not all EGS colonies' occurrences were named and stored in those compiled resources therefore we did not calculate frequency of EGS for specific areas or counties. These indirect records were able to show the coarse-scale occurrence distribution of EGS in Hungary (Aybes & Yalden, 1995; Boisseau & Yalden, 1998; Cox et al., 2002). Assuming a formal network of *meta*-population structure of the species (Hanski, 1998; Spitzenberger & Bauer, 2001; Gedeon et al., 2017) in the Pannonian ecoregion (Horváth et al., 2012) we assumed that if a place name referring to an EGS colony was found in a county then within that county EGS colonies – without anthropogenic or geographic dispersal barriers, such as large rivers, industrial sites, etc. – could disperse into new areas. Any colonisable grassland patches within a county could be occupied by EGS within the metapopulation structure (connected landscape patches) in this 2nd period. Recent developments in digitalizing the names of geographical areas and archaeological sites of Hungary have created the opportunity to search for entries containing "ürge" or "irge" in databases with references to localities. As EGS has been the only extant ground squirrel species in the area of Hungary since human occupancy, each finding of "ürge" or "irge" in place names should refer to EGS.

Data covering the 3rd period between 1964 and 2020 could be statistically analysed. For this period we determined the total number of existing colonies in each year (Fig. 1). In the following year this number of "active" colonies was reduced by the number of colonies gone extinct or increased by the number of new (introduced, re-introduced, discovered or rediscovered) colonies. We used records of EGS occurrences as point data after 1963 because the metapopulation structure with dispersal corridors collapsed (Gedeon et al., 2017) and the landscape was converted into habitable patches surrounded by uninhabitable areas. It is necessary to discuss here what is meant by an 'extinct colony' (absence) or a colony itself (presence). Literature indicates (Holekamp, 1984; Wiggett & Boag, 1989) that EGS have a limited (<2km) male-biased dispersal. Therefore, if EGS colonies were less than 2 km apart they were considered as one colony, while at greater than 2 km apart they were considered to be distinct colonies. During this 3rd period nature conservation made two important measures. In 1982, EGS became protected, then in 2012, they became strictly protected by law. It is likely that legal protection brought more attention to the species which likely increased records or data about the species.

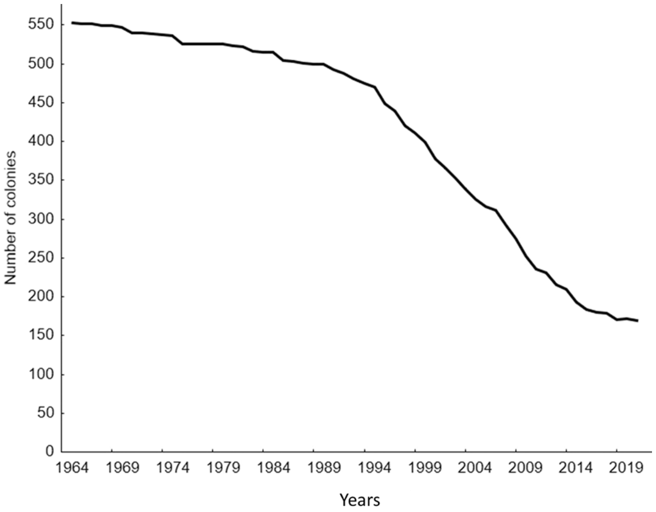

Fig. 1. The estimated number of EGS colonies in Hungary between 1964 and 2020.

2.2. *Statistical analysis of data between 1964 and 2020*

2.2.1. *Identification of change (or break or turning) points in the dataset*

In our data period of 1964 to 2020 the conservation status of the species changed from pest to protected (1982) and then to strictly-protected (2012). Additional economic or countrywide management actions or changes (i.e. industrialization of agriculture, systematic reintroductions and translocations) could also have drastically altered the survival success of colonies and as a result the number of EGS colonies within the country, but it is difficult to link these effects to a single year. Consequently, we considered these changes or actions to be 'interventions', and divided our dataset into consecutive pre-intervention and post-intervention periods (Wauchope et al., 2021). To reliably split our time series data into distinct periods, and then to retrospectively compare our time series data (observed values) with predicted theoretical values based on the specific pre-intervention period's trend, we identified structural change or break points in our time series data from 1964 to 2020. Time series data represented the number of colonies in Hungary for 57 years. If structural change points identified in the time series were close to or overlapped with intervention dates (1982, 2012) then we considered them as interventions with measurable consequences on the survival of the species. We eventually integrated those interventions into our further analysis, identifying pre- and post-intervention periods.

Our structural change point analysis method was based on a modified Chow test to investigate changes in the slope of the time series data using the R package *strucchange*. This approach tests the hypothesis that the parameters of a certain regression model remain constant over all observations. In other words, the null hypothesis states the absence of breakpoints, and the alternative hypothesis is that observations change over time either once or several times. The function *strucchange* test performs the Quandt (1961) likelihood ratio (QLR) test. This is an extension of the Chow test where F-test statistics are calculated for all breakpoints (Jayatissa, 1977; Zeileis et al., 2002). If the p value was less than 0.05 then we could conclude that the data contained a change point at a certain year. Change points (k) then were used to split the time series into $(k + 1)$ periods. We eventually scrutinized the relationship between the identified change points and the conservation actions (interventions). If a conservation action's year coincided with the year of the identified change point or the closest change point identified to the year of the conservation intervention, then we accepted that point as a confirmed change point. This procedure helped us find interpretable, statistically and theoretically the likeliest structural change points or interventions.

2.2.2. Estimation of the effect of the intervention on the number of EGS populations

Based on the intervention (change point) analysis, we were interested in investigating the impact of the interventions on the number of colonies (survival and country level abundance of EGS represented by the total number of colonies) over time (Wauchope et al., 2021). We applied a Bayesian structural time series (BSTS) model that could predict the counter-factual response in a dummy control dataset that would have occurred if no intervention had happened. The dummy control dataset was in strong correlation with the observed dataset. It included pre- and post-intervention data values, and the latter was predicted by single-series times-series ARIMA models. We selected the best, specific ARIMA model based on the auto-arima function in R which defines, compares, and ranks several models based on their AIC (Akaike Information Criterion) and BIC (Bayesian Information Criterion) values. This procedure can guarantee an automated best model selection procedure.

To carry out the BSTS analysis and infer the causal impact of the interventions we used the *CausalImpact* R package (Brodersen et al., 2015, 2016). The 'causal impact' name of the package refers to the difference between the observed and theoretical (unobserved) values of the response variable (number of colonies). Theoretical, unobserved sequence of values is estimated from a specified multivariate probability distribution, when direct sampling is difficult or impossible. This would have happened without the intervention. This modelling approach fits well with experimental designs where a randomised experiment is unavailable like in our dataset. To formulize this procedure, we first defined the year of interventions and then divided the dataset into pre-intervention and post-intervention periods depending on the number of change points identified. The tool inspects the data and builds a Bayesian structural time series model for inferences using a Gibbs sampler, which is a modified Markov Chain Monte Carlo algorithm. Further details about the modelling approach and its application in the R environment are found in Brodersen et al., (2015) and Big Things Conference (Brodersen, 2016).

2.2.3. Forecasting the population trend

We used the estimated number of EGS colonies in Hungary from 1964 to 2020. Data points were equally spaced in time and ordered chronologically. Therefore, they constituted a time series of data. We used the ARIMA or Box-Jenkin's time series analysis method (Eric & Len, 2013; Geurts et al., 1977) to develop an autoregressive integrated moving average (ARIMA: p, d, q) model to forecast the number of colonies based on the past 57 years. ARIMA is one of the most common methods to predict future values in a time series if certain assumptions are met (Schaffer et al., 2021). A good ARIMA model has only non-systematic errors that do not contain any useful information to improve predictions of the model (white-noise error; stationarity). Compared to other forecasting modelling techniques, such as exponential smoothing, ARIMA models can capture autocorrelations in the data which results in improved fit to the data and reduced white-noise errors. One of the important assumptions in an ARIMA model is the continuity between the past and future trends, therefore forecasting into the future becomes more tenuous with time. We aimed to forecast the trend for 20 years arbitrarily. Although ARIMA models are mathematically complex approaches, since the availability of automated model selection procedures embedded in statistical software, such as in the R or Statistica – Tibco programs, they have been available to less experienced forecasters and can outperform manual model selection procedures (Ord & Lowe, 1996; Stellwagen & Tashman, 2013).

As compared to an ARMA model, which is an extension of an autoregressive model (AR) to include "moving average" terms (MA), an ARIMA model allows greater flexibility. In ARIMA model building, there are three parameters to be estimated: the order p of the autoregressive component, the order d of differencing, and the order q of the moving average component. The general description and stages of building an ARIMA model until the most parsimonious model has been identified are well described in various resources (Schaffer et al., 2021). Therefore, we briefly summarize the procedure we followed to analyse our time-series dataset.

For the Box-Jenkins (ARIMA) method the data must satisfy stationarity. Therefore, we applied as many differencing (d) as necessary to fulfil this prerequisite. We tested stationarity by applying the autocorrelation (ACF) and the partial autocorrelation (PACF) functions (Ord & Lowe, 1996; Pyper & Peterman, 1998). Autocorrelation describes the number of colonies (y) at time t in relation to the previous year's colony number (y_{t-1}). This is the autocorrelation at lag 1. Autocorrelations at further lags (2, 3, …, n) correspond to relationships between y_t and y_{t-n}. Partial autocorrelation describes the relationship between the number of colonies (y) at time t and the number of colonies (y) at lag 1, 2,…, n once we have controlled for the correlations between all of the successive years between this year and year t.

Since there were break points in the time series data, we applied interrupted time-series ARIMA (iARIMA) modelling. The aim of the iARIMA was to incorporate the impact of the interruption on the forecasting, and the future number of EGS colonies in Hungary over the next 20 years (intervention effect). We applied a permanent, abrupt intervention which implies that the overall mean of the time series shifted after the intervention. In our time series data and period of 57 years we identified two validated interventions which then were used in iARIMA (see in breakpoint analysis). Both interventions were supposed to have long term (permanent) effects on the number of populations. The effect of the interventions on conservation status and management of the species will be addressed in the discussion section.

Compared to the Bayesian structural time series (BSTS) analysis, we identified a global iARIMA model for the whole dataset and then forecasted the number of EGS colonies. The aim of using two approaches was to compare the results and see if they end up with different conclusions. While BSTS analysis forecasts the number of colonies in Hungary in the absence of the interventions and determines how the observed number of colonies (with intervention) diverges from the predicted number of colonies (without the intervention), iARIMA involved both interventions in the "global" model and determined the diversion based on the whole dataset. Eventually, after the model fitting and best model selection procedure (Schaffer et al., 2021), so called 'diagnostic checking' (Chatfield & Xing, 2019), we used the final, best model to forecast the future trend of the Hungarian EGS population. Based on that result we also made recommendations on future EGS conservation status and management.

3. Results

3.1. Prehistory of the ground squirrels

During the last 1.45 million years there were five periods when the climatic conditions supported grasslands or woody grasslands in modern-day Hungary: 1) the last 6 k years, 2) the period from 7.5-10 ka, 3) the period from 98.5-102 ka, 4) the period from 475-750 ka, and 5) the period from 1150-1450 ka. Within these periods, ground squirrel remains were recovered from the small mammal material of several sites (Table 1). Although the palaeontological data were scattered, the geographical distribution of remains supported their early presence in these periods in large parts of the country from the foothills of the Villány Hills (south-western part of the country) through parts of the Transdanubian Range (Vértes, Gerecse and Buda Hills) and even to the Bükk Mountains and Aggtelek karst in the north-eastern part of the country, since the Middle Pleistocene (ca. 1450 kya BP; Table 1) (Kordos & Krolopp, 1980; Kretzoi, 1964; Sinitsa & Pogodina, 2019). These species occupied the same or similar ecological niches as EGS does today.

The paleontological evidence (Sümegi & Hertelendi, 1998; Sümegi & Krolopp, 1995) indicated that ground squirrels were widespread in Hungary and the EGS first appeared in this region, in the Great Hungarian Plain particularly, at the end of the Holocene (2000 ya). Based on the palaeontological database EGS findings from this period are not only known from this region but also from the Vértes and Gerecse Hills and the Aggtelek Karst. In addition, it has also been argued that EGS reached this area even earlier, at the end of the Pleistocene or beginning of the Holocene period after *S. citelloides* (which also had a range that covered almost the entire country) had gone extinct in this area ca. 15 ka (Sinitsa et al., 2021; Sinitsa & Pogodina, 2019). EGS probably spread in the Pannonian ecoregion earlier between 15 and 20 ka, and by 2 ka it probably became a widespread species in the region.

3.2. Historical presence of EGS in Hungary up to 1963

There have been a number of derivatives or compound words from the Hungarian word for EGS (“ürge”) in place names from the Middle Ages until the 1960s (Hungarian Geographic Name Database; Archaeological database). The word “ürge” first appeared in writing in 1469 (and its less frequent variant, “irge” in 1588) and its use in Hungarian has been continuous and common ever since. Unfortunately, data containing information on the spatial distribution of their usage was not available in those early resources. It is a loaned word from the Old Turkic language (Róna-Tas, 1996), which is also supported by a similar, recent Turkish version of ground squirrel (“örge” (Turkish) vs. “ürge” (Hungarian)) in the Khakas and Tuvan languages in Siberia (Benkő et al., 1970; Benkő, 1993). The importance of the word’s etymology is that when Hungarian people reached the Carpathian Basin, they could identify ground squirrels and integrate that know-how into place names (Dall’Ò, 2019). Another detail that increases the weight and spatial credibility of place names is that Hungarian lacks general place names formation as a grammatical function to form place names in contrast to Indo-European languages. In Hungarian some place name formant (principally “-s”) indicates the presence of its substrate (i.e. animals, plants) in a specific location more than simply identifying topographical features (Bényei, 2012).

Our search of these Hungarian terms for EGS resulted in 217 records (Fig. 2). That frequency in geographical names puts the ground squirrel among the top ranked place names related to terrestrial wildlife (i.e. excluding birds and wetland fauna).

Place names indicated that EGS occurred in all but one county (County Békés covers 6 % of the total territory). List of place names

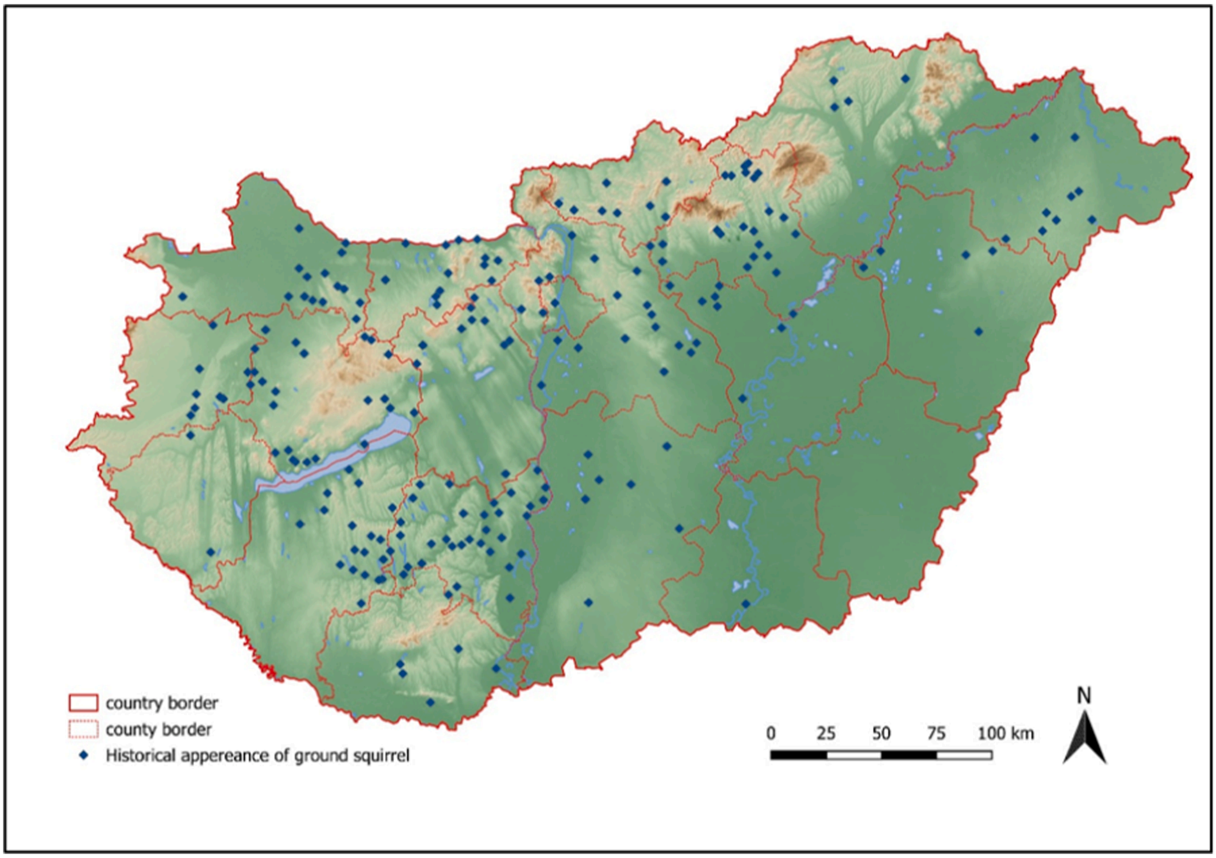

Fig. 2. The distribution of place names involving ground squirrel (“ürge”). Place names refer to *Spermophilus citellus* unambiguously as this has been the only ground squirrel species in Hungary for at least 2000 years.

formed from the word ground squirrel ("ürge"), their frequency of occurrences and additional explanatory notes about them are discussed briefly in Supplementary Table 1 and Fig. 1. In summary, we identified 89 different place name groups formed from ground squirrel ("ürge"). Simple derivations ("ürgés" = a place with or characterised by ground squirrels) or compound place names formed from "ürge" and common topographic features (see in Supplementary Fig. 1) constituted about 60 % of all cases. That 60 % consisted of 9 groups from the 89 categories. There was also only one reference to the hunting of ground-squirrels and there were no place names referring to catching, trapping or deluging, which was one of the most common traditional hunting methods of ground-squirrels. There were two villages (Kunsziget, Tápiószecső) in our records that were nicknamed mockingly "ürgés" (a place characterised by ground-squirrels) by the surrounding villages because EGS was a frequent food in those villages and it indicated poverty and underdevelopment.

3.3. Structural change points (interventions) in the time series data

The QLR (extended Chow) test revealed 4 breakpoints in the time series data, corresponding to the years 1984, 1994, 2002, and 2010 ($F = 285.26$, $p < 2.2e\text{-}16$). Preliminarily, we identified two intervention dates between 1964 and 2020: 1982, when the species became protected, and 2012, when the species became strictly protected. The latter was also considered the first year of systematic, soft-release translocations based on experimental studies and translocation guides (Gedeon, 2011; Gedeon et al., 2011, 2012; Tokaji, 2012). Therefore we considered 1984 and 2010 as meaningful change points in the dataset. Those dates divided our dataset into pairs of pre- and post –intervention periods. The other two change points found by the QLR test were left out of consideration as they could not be interpreted or connected to anthropogenic or natural phenomena or actions that happened in specific years although there could be unknown factors.

3.4. Estimation of the effect of the interventions in 1984 and 2010 on the number of EGS populations based on the BSTS model

During the first post-intervention period, after 1984, the average number of colonies was approximately 457. By contrast, in the absence of the intervention, we would have expected 494 colonies on average (SD = 3.9). The 95 % interval of this counterfactual prediction is [486, 502]. Subtracting this prediction from the observed number of colonies yields an estimate of the causal effect the intervention had on the number of colonies. This effect is −37 (SD = 3.9) with a 95 % interval of [-45, −29]. In relative terms, the response variable showed a decrease of −7% (SD = 0.73 %). The 95 % interval of this percentage is [-9%, −6%]. This means that the negative effect observed during the intervention period is statistically significant. The probability of obtaining this effect by chance is very small (Bayesian one-sided tail-area probability $p = 0.001$). This means the causal effect can be considered statistically significant (Fig. 3).

During the second post-intervention period, after 2010, the average number of colonies was approximately 190. In the absence of an intervention in 2010, we would have expected 160 (SD = 22) colonies on average. The 95 % interval of this counterfactual prediction is [114, 205]. Subtracting this prediction from the observed number of colonies yields an estimate of the causal effect the intervention had on the number of colonies. This effect is 31 (SD = 22) with a 95 % interval of [-15, 76]. In relative terms, the response variable showed an increase of + 21 % (SD = 18 %). The 95 % interval of this percentage is [-7%, +67 %]. This means that, although the intervention appears to have a positive effect, this effect is not statistically significant when considering the entire post-intervention period as a whole. (Individual years or shorter stretches within the intervention period may of course still have had a significant effect.) The probability of obtaining this effect by chance is $p = 0.087$. This means the effect may be spurious and would generally not be considered statistically significant (Fig. 4).

3.5. Forecasting the population trend beyond 2020

Based on the ARIMA time-series modelling approach, we developed the best model to forecast the annual number of EGS colonies in Hungary until 2027. Our dataset covered a period of 57 years from 1964 until 2020. The number of EGS colonies in Hungary declined since 1964 with two major, significant interruptions (conservation interventions), one in 1984, 2 years after the species became protected- and another in 2010, when more evidence-based translocations started in Hungary (Gedeon, 2011; Tokaji, 2012). Variance seemed stable over time,

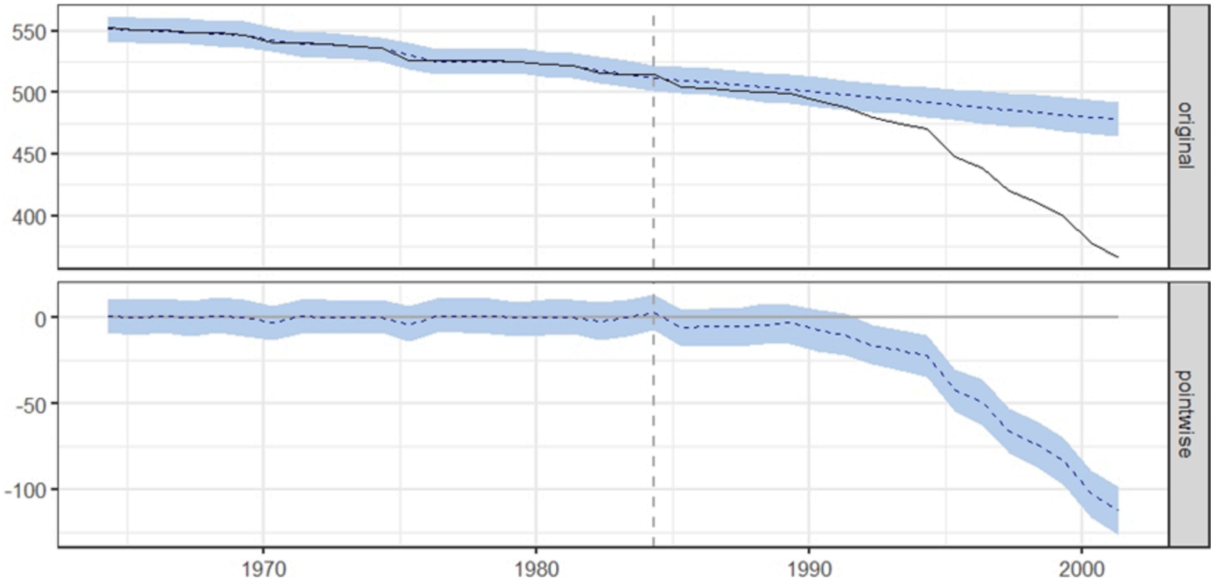

Fig. 3. Estimated effect of the intervention in 1984 on the number of EGS colonies in Hungary. The top panel ("original") shows our observed data (solid line) and counterfactual estimate (dashed line) without the intervention in 1984. Both the original and the counterfactual data show a downward trend but with distinct slopes. The second panel ("pointwise") shows the difference between the observed data and the counterfactual estimate (dashed curve, pointwise causal effect increases up to about −110). The X axis corresponds to the calendar years. The change point is in 1984, which is marked by the vertical dashed line.

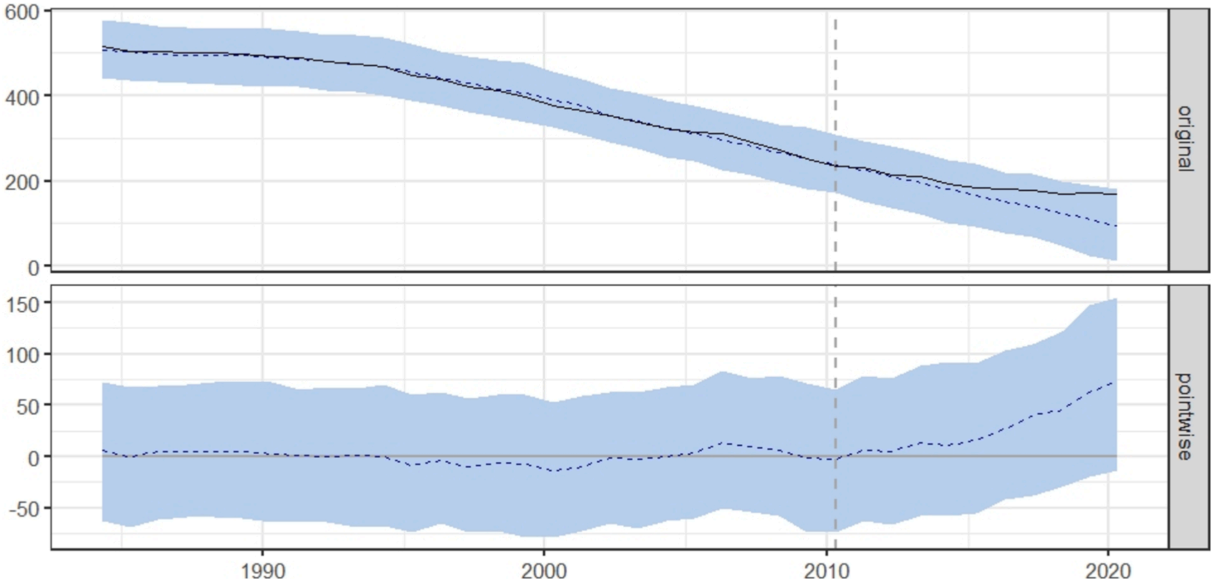

Fig. 4. Estimated effect of the intervention in 2010 on the number of EGS colonies in Hungary. The top panel ("original") shows our observed data (solid line) and counterfactual estimate without the intervention in 2010 (dashed line). The counterfactual data show a downward trend but the observed data levels off after the intervention. The shaded area shows posterior predictive expectation of the counterfactual with pointwise 95% posterior probability intervals. The second panel ("pointwise") shows the difference between the observed data (solid line) and the counterfactual estimate (dashed line; pointwise causal effect increases up to about 75). The shaded area of the inferred impact series shows a weak but progressive widening of the posterior interval, which emerges from the model structure and also agrees with the a priori intuition that predictions should become increasingly uncertain. The dashed vertical line shows the change point in 2012.

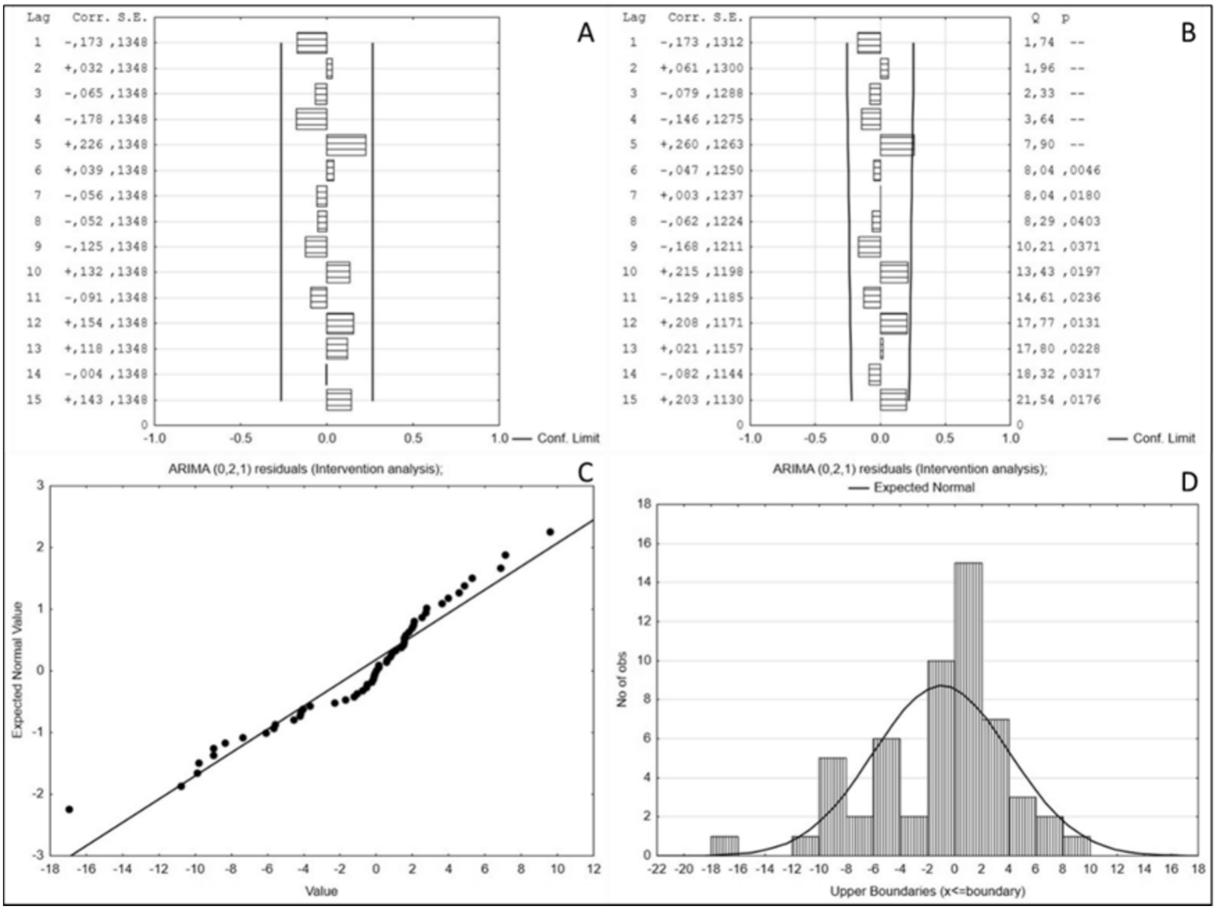

Fig. 5. A-B: Partial autocorrelation (A) and residual autocorrelation (B) and function plots from iARIMA(0, 2, 1) showed no significant spikes or gradual decays at any lags. (C): Normal probability plot indicated normal distribution of the residuals. (D): The distribution of the residuals also approximated the normal distribution well.

therefore no data transformation was needed to improve the model performance. The automated model selection procedure using the function forecast::auto.arima resulted in a final, interrupted single variable ARIMA model of order (p = 0, d = 2, q = 1) (Hyndman, 2012). Additional, manual selection (TIBCO Software Inc., 2024) of the best model based on ACF and PACF correlograms also resulted in the same iARIMA model (0, 2, 1). This means that data was differenced twice (d = 2) to stabilize the variance, remove the trend, and reach stationarity. During model validation, the residual analysis did not show any pattern or remaining autocorrelation (Revels et al., 2017). There was no evidence of any residual serial dependency in the data (Fig. 5. A, B) and the distribution of the residuals approximated the normal distribution reasonably well (Fig. 5. C, D).

From the iARIMA(0, 2, 1) forecast, it appears that the number of local populations will increase after 2020. However, and unfortunately, the lower 90 % prediction interval of the model went under zero in 2027. That meant that the model was unable to show significant change and values under zero could mean total extinction of the species. Since this may occur in 2027, it suggested that the model needs further data in the following years to narrow down the prediction interval for the future value (Fig. 6).

4. Discussion

By collecting paleontological, historical, and current data on the occurrences of EGS in Hungary we intended to show the history of ground squirrels starting from the age of the first fossils until recently. When possible, we aimed to show the temporal change of the size of the Hungarian population. The progress of the number and distribution of EGS colonies in Hungary helped us give an updated, comprehensive picture on the conservation status of the Hungarian EGS population. Finally, we gave a careful prediction on the future trend of the EGS population in Hungary for the upcoming decades based on a review of all data from prehistoric times until present. Although all data and models to show past, present, and future numbers of colonies and corresponding local extinctions were purely descriptive in nature because this study could not consider what mechanisms or factors had affected the number of local extinctions, this study is the first important step to determine the conservation status and trend of ground squirrel populations in Hungary.

4.1. Prehistory of ground squirrels in Hungary

Paleontological evidence and recent findings of ground squirrel (*Spermophilus* spp.) specimens (Sinitsa et al., 2021) indicate that they have colonized the Carpathian Basin successfully and this group has become a widespread, common burrowing rodent of this region (Hegyeli, 2020). It plays a similar ecological, engineering role in grassland ecosystems as prairie dogs or other ground squirrels in the Holarctic region. EGS first appeared in this region, more specifically on the Great Hungarian Plain around the Vértes and Gerecse Hills and Aggtelek karst, around 2000 years ago at the latest and has been present since then. However, ground squirrels show large ecological plasticity and as a result they could have inhabited the Pannonian ecoregion (Kordos & Krolopp, 1980; Kretzoi, 1964; Sinitsa & Pogodina, 2019) since the Middle Pleistocene (ca. 1450 kya BP). Within this period the climate and corresponding vegetation favoured the presence and expansion of ground squirrels. Most fossil specimens identified from this period belonged to *S. citelloides* and *citellus* (Sebe et al., 2021; Sinitsa & Pogodina, 2019). The extinct *S. citelloides* was morphologically and ecologically similar to the recent spotted souslik (*S. suslicus*) considered as her sister taxon (Sinitsa et al., 2021). Until the appearance of EGS in the Late Holocene fossils of *S. citelloides* represented the *Sciurinae* (Sebe et al., 2021). Although *S. citellus* and *S. citelloides* were clearly differentiated based on skull shape, lower jaw and body size, they inhabited this region within similar environmental conditions. From the viewpoint of our analysis, this indicates a habitable area for EGS from as early as the Late Pleistocene, but due to the ecological similarities between these two species and competition, a sympatric existence was not possible (Popova et al., 2019). Therefore, EGS likely followed and expanded in this region after the extinction of *S. citelloides*, which coincided with a rise in temperature and a shift to the modern, thermophylous flora and fauna (Pécsi and Kordos, 1987). It is difficult to estimate the expansion rate of small rodents (i.e. voles, mice) but empirical studies showed a range of expansion rate from 0.75 km to 3 kms per year or 50,000 km^2/40 years (Schmelzer & Schmelzer, 2022; Filip et al., 2023; White et al.,

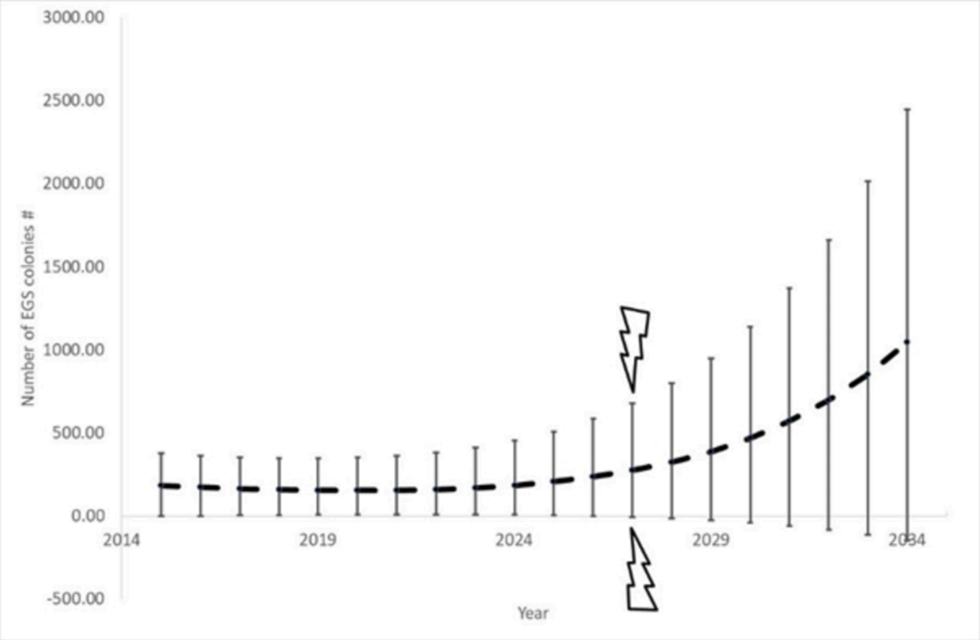

Fig. 6. Forecast of the number of EGS colonies in Hungary using the iARIMA(0, 2, 1) model from 2021. The lower 90% prediction interval of the model crossed the zero line in 2027. Further prediction was unnecessary as a result of the non-significant, otherwise apparently positive (increasing) trend of the number of populations in Hungary. The lightning symbol shows the year when our model's lower prediction interval crosses the zero line and becomes non-significant.

2012). This suggests that a larger sized ground dwelling species, such as EGS, with special life history (hibernating, social) and biogeography (temperate, Eurasian shortgrass habitat), could have expanded its range at least at around the same rate after *S. citelloides* went extinct. That could have meant a fast expansion of the species into favourable areas. Consequently, its expansion from 2000 years ago until modern ages (XVIth or XVIIth centuries) could seem a plausible scenario, and as a result its widespread distribution based on place names' occurrences does not seem unexpected. Several extrinsic factors, such as woody grasslands, grasslands, and riparian corridors could have made expansion of the EGS feasible (Barnes & Hoffman, 2023; Pacifici et al., 2020). The woody grassland habitat probably facilitated expansion through a heterogeneous landscape, which points in the direction of a widespread species in the Carpathian Basin as soon as competitors disappeared from the area (Crone et al., 2019; Santini et al., 2013). During human expansion and the extensive agricultural activity (grazing livestock system) of early settlers in this area around 2000 years ago forested areas were converted into grasslands or maintained steppe-like vegetation. Human management could have provided additional habitat for EGS and other steppic small mammals to expand further in the Carpathian Basin (Schmelzer & Schmelzer, 2022; Sinitsa & Pogodina, 2019). Since animal remains could have drifted from their place of origin to depositional areas, we did not analyse paleontological evidence quantitatively even though the exact location and age of fossils were available.

Molecular phylogenetic and population genetic studies also support the above-presented colonization and expansion timeline (Rammou et al., 2023, Ben-Slimen et al., 2012). The EGS population is divided into two mitochondrial lineages, the 'northern' and 'southern' groups, with a strong geographical division. The younger, northern lineage was established in the Carpathian Basin about 0.1–0.15 Mya (Rammou et al., 2023) but it shrank and expanded several times from 0.3 Mya till nowadays (Gündüz et al., 2007; Gedeon et al., 2017; Popova, 2019). That fluctuation of effective population size could explain the relatively lower genetic diversity in the northern group (Spitzenberger and Bauer, 2001; Ben-Slimen et al., 2012) despite its large distribution range in Central-Eastern Europe. That northern lineage includes the populations of Central-Eastern Europe, Romania, Moldova, Northern Macedonia and western and northern Bulgaria. The older, southern group has a more conservative distribution, covering southern Bulgaria, Greece, European Turkey, and western Balkan regions. This is characterised by higher haplotype and genetic diversity (Kryštufek et al., 2009; Říčanová et al., 2013), however its distribution range is not significantly larger. Further evidence indicates that the Balkan (Northern Macedonia and Serbia) served as a refuge for EGS during unfavourable conditions to re-colonize the Pannonian grasslands, nonetheless it might have survived the warm and humid early Holocene period in the Carpathian Basin (Říčanová et al., 2013).

4.2. Historical records of EGS

Place names indicated the widespread occurrence of EGS in the first half of the XXth century. However, the distribution of those place names was uneven with higher and lower density areas. Though the absence of place names cannot be taken as strong evidence about the absence of the animal in that region, it was interesting to see that it was missing from only one county of Hungary, which lies on the southern edge of its northern-distribution area (IUCN, 2015). This finding is in accordance with the periphery-core hypothesis, which would suggest a decreased density and abundance of populations at the periphery of the species' range (Britnell et al., 2024; Lloyd et al., 2013). The larger distribution range of place names in the farther past compared to the current one indicates the shrinking of the EGS distribution area from historic times until 1964, when our quantitative analysis started.

Place names indicated geographical features in agreement with the known ecology of EGS (Frajer & Fiedor, 2018; Gedeon, 2011; Ben-Slimen et al., 2012; Katona et al., 2002; Rammou et al., 2021; Váczi, 2006). For example, they inhabit non-forested, drier, undulating landscape, where EGS occupies higher elevations, southerly exposed sides, and often co-exists (or co-existed) with humans indicating that the species does not avoid the presence of humans. Several current colonies in Austria, Czech Republic (Moravia and Bohemia), and Hungary still show this phenomenon.

Place names indicated a larger historical area than the current area of distribution (Fig. 3) without their exact age of existence (Bánki et al., 2023). At the beginning of our quantitative analysis, in the 1960s, we already saw a steady decline. Before the socialist agricultural reform occurred in 1949 agricultural activity was characterised by a sustainable privately owned and cultivated agriculture. Animal husbandry and pasture farming maintained favourable EGS habitats all over the country. It is likely that EGS grassland habitats overlapped with agricultural lands and farms for centuries without dramatic, negative consequences on the Hungarian population. That landscape changed when a state-directed agricultural modernisation and industrialization started in 1949–1950 with its most intensive period lasting until 1962 (Gedeon et al., 2017; Kovács, 2013). This resulted in the abandonment of sustainably cultivated small lands (meadows) and farms. In other words, the former socio-economic characteristics that had been in effect for centuries and favoured the presence of EGS or other small mammal fauna changed, and the landscape became unfavourable for the steppic mammal fauna. The period before 1949, which involves several centuries and the birth of place names, was likely characterised by a metapopulation structure. The landscape of steppic and woody steppic flora favoured the expansion and maintenance of the EGS population. Certain studies found that place names might not have always denoted resident fauna correctly when new settlers tried to denote and name local flora and fauna based on their prior knowledge coming from a different area (Tent, 2023). However, the 217 place names found in our study should have reflected the distribution of EGS more reliably since the Hungarian language has been spoken by most people in this region since the 9th century (895 CE), when the Hungarian Conquest of the Carpathian Basin occurred by nomad shepherd cultures (Pécsi & Kordos, 1987). Therefore, the co-existence of culture including its local people and language and fauna have been occurring more-or-less continuously since that time. In other words, place names consisting of the word 'ground squirrel' ('ürge' in Hungarian) should have come from Hungarian indigenous people living in this area. Another important spatial feature of the list of place names is that they did not show strong clustering (though uneven distribution). This indicates and supports the inference that EGS was a widespread fauna member for thousands of years in Hungary. Consequently, we carefully say only that the species was widespread in Hungary in modern times, until the end of the World War II, when agricultural activity changed the Hungarian environment to be unfavourable to EGS for the first time in the last 2000 years.

4.3. Records of EGS presence between 1964 and 1982

Compared to other countries, though in different times, we can say that EGS was present in large numbers and widespread in Hungary from 1964 to 1982, though early reliable estimations of the real number of colonies for countries within the distribution range have not been widely available in the literature. Estimates on the EGS population from neighbouring countries or Greece reported continuous distribution from the 1950s, which decreased to close to 100 local populations per country by the early 2000s (Matějů et al., 2008; Petluš et al., 2021; Rammou et al., 2021). As a consequence of the real or exaggerated damage caused by ground squirrels on cultivated lands they were considered an agricultural pest (Veszelka, 1959). Rural communities got rewards for dead specimens, and state owned agricultural collectives implemented large-scale pest-control measures during those decades. During these culling campaigns tens of thousands of animals were killed, similar to prairie dogs in the US (Magyar Filmhiradó, 1948; Magyar Világhiradó, 1936).

During this period, EGS went extinct in Germany in the Eastern part of Erzgebirge in 1961 (Tiergarten Nürnberg, 2024). Germany was the north-western edge of the EGS distribution range. Another indicator of the widespread presence of EGS around this period was its consumption by poor people in Hungary. This custom was still recognizable in the early years of 2000 and cookbooks contained recipes for "ürgepörkölt" (EGS stew) (Színes Gyöngyök, 2016; Szolnok Megyei Jogú Város Önkormányzata, 2016) in the 2010s.

The slow decline of the number of populations until the first breakpoint shown by the BSTS analysis is in accordance with this narrative on the widespread distribution, usage and culling of the species, a period when the species' conservation and long term survival seemed an unimportant issue. However, the BSTS analysis showed clearly that even without a breakpoint, where the slope of the decline increased, the entire population showed a declining trend with about 10 % decrease until the 1990s (Fig. 4). The difference between this "normal" decline and the effect after the breakpoint in 1984 was about −27 % which means that its decline had been going on for at least many decades and had started long before its conservation concerned state nature conservation and unknown factors worsened its decline. That base declining trend had likely been going on in other countries as well, though we had no hard evidence for that phenomenon as trend analysis has not been carried out in other countries yet (Grulich, 1960; Hegyeli, 2020; Mateos-González et al., 2023; Ružić, 1978; Tokaji, 2012).

4.4. Records of EGS presence after 1984

Our first breakpoint detected was 1984, close to 1982, the year the species received legal protection which was a response to its significant decline that nature conservation observed in its decreased ratio in raptors' prey (Szitta, 1996; Horváth et al., 2018; Petlus et al., 2021). Records on EGS colonies after 1982 contained locality (coordinates) and colonies' (potential) area of occupation. However, those records still lacked a standardized and systematic data collection procedure on the abundance of local populations. Nevertheless, it resulted in more accurate data on its country-scale presence. Legal protection implicitly demonstrated that its ecosystem role and importance was recognised before it later became recognised as an ecosystem engineer flagship species (Lindtner et al., 2019; Szitta, 1996). An even more intensified decline in the following decades (Figs. 1 and 3) indicated that legal protection was unable to level off the decline of the EGS populations just like it did not work effectively in the US (Ferraro et al., 2007). Although there were only speculations about this general, widespread decline on a large geographic scale, its function in grassland ecosystems showed an intensifying need for halting or reversing this process. We did not address the underlying causes of this decline -whether anthropogenic, climatic, ecological, or other factors- in the analyses as it was outside the scope of this study. International meetings, such as the Madjarovo Conference (entitled the "Ecology and conservation of the European souslik (*Spermophilus citellus*)), 25–28 October 2002, Bulgaria) supported the increased international attention of conservationists and researchers alike on this species or family Sciuridae so we can call this period the dawn of the international protection of the species in its entire distribution area (i.e. Sousliks of Eurasia, 2005, Russia; 1st European Ground Squirrel Meeting, 2006, Hungary).

4.5. Records of EGS presence since 2000

In 2000, a country-wide quantitative estimation of local population density started by applying a transect-line burrow census method (Váczi, 2019; Váczi et al., 2015; Hubbs et al., 2000), aiming to give a relative, change sensitive estimation of population density. Since then, the systematic annual monitoring of the Hungarian EGS populations has been carried out in the framework of the HBMS (Váczi, 2006, 2019; Váczi et al., 2015). According to results of the first years of the HBMS there were no data to support that the Hungarian EGS population declined significantly at the national level (Váczi, 2006) which could be interpreted as a relatively stable population (Janák et al., 2013) with highly asynchronous local fluctuations and extinctions. That status quo appears to have changed and current results of the HBMS or reports of national park rangers have shown several local extinctions of EGS populations in Hungary and a significantly declining trend on permanent sampling sites (Csonka & Riezing, 2004; Riezing, 2021; Váczi, 2019). Several authors argue that habitat destruction and abandonment of grassland management has been mainly responsible for the shrinking of the Hungarian EGS population (Bihari et al., 2000; Janák et al., 2013; Kis et al., 1998; Matějů et al., 2008; Rammou et al., 2021). However, those studies investigated these hypotheses for individual colonies, not for larger areas or several populations simultaneously.

Since 2012 EGS has been strictly protected in Hungary (IUCN global category is "Endangered" and "Critically Endangered'' in the north-western portion of its range) (Koshev, 2008; Ćosić,et al., 2024). It is considered "Vulnerable" in Bulgaria and "Endangered" in Austria (Hegyeli, 2020). The EGS is listed in Appendix II of the Bern Convention and Annexes II and IV of the EU Habitats Directive. Declines have been reported (Hegyeli, 2020) from various parts of the range, particularly from the Pannonian ecoregion. In the last decades several conservation programs have attempted to reintroduce (from Hungary to Poland, 2005; Germany, 2006) or translocate animals into suitable habitats with the aim of establishing new colonies on former habitats (Ben-Slimen et al., 2012; Hulová & Sedláček, 2008) but long term success has not been monitored in many cases. Therefore, those experiences did not provide quantitative data on the survival rates of released animals, nevertheless the new colonies' survival was recorded and used for our study. Analysis of our model predicted an increase in the estimated number of colonies after the breakpoint in 2010. On the other hand, the analysis showed that although the intervention appears to have caused a positive effect, this effect was not statistically significant when considering the entire post-intervention period as a whole. Individual years or shorter stretches within the intervention period may of course still have had a significant effect. This means the effect may be spurious and could generally not be considered statistically significant (Fig. 5). We can therefore carefully imply that a positive change might have started as a consequence of the widespread translocations, but results cannot confirm that. Further years can provide data to support or disapprove the positive effect of translocations on the entire population in the Pannonian ecoregion if these actions receive financial support from national or international organisations or governments, such as the European Union's LIFE Programme, and data management will fit to FAIR data principles so that researchers will be able to analyse (meta) data for large spatial and temporal scales (European Commission, 2024).

4.6. Forecast of the EGS population in Hungary

Our best statistical model (iARIMA(0, 2, 1) following Box-Jenkin's methodology (GeeksforGeeks, 2024) to forecast the future trend of the EGS population in Hungary showed that a positive trend could have started in 2010, when an intervention was identified. That result was in accordance with the BSTS analysis about the effect of the intervention that we summarised in paragraph 4.5. Although our dataset was still too short after the intervention to provide statistically significant predictions a turning point was observable, and it could indicate the cumulative effect of past conservation translocations (Altbäcker & Nagy, 2017; Gedeon et al., 2011; Gedeon et al. 2012). Eventually, the average population size turned from decreasing to increasing in 2021, which seems promising for the future of the EGS population.

On the other hand, as a result of the non-significant prediction we were unable to exclude the effect of random fluctuations that are unrelated to the intervention. Too short follow up times or too long intervention periods could also hide the signal under the variance of the data (Minaker et al., 2016). Furthermore, the fewer the number of colonies were during those 57 years the more dramatic effect that decrease or increase could have had on the entire population. In other words, the likelihood of losing another colony from the viewpoint of probability and as a result of randomly behaving factors on any colonies (in this regard points in space) decreased as the colony numbers decreased from year to year (Krauth, 2021).

5. Conclusions

In this study we reviewed the history and updated the conservation status of EGS based on palaeontological, documentary and quantitative data about its presence in Hungary. However, the results could reflect a broader trend pertaining not only to the Pannonian ecoregion (Lukács et al., 2016) but its northern and southern distribution peripheral areas (Rammou et al., 2023). The time series analysis of the number of colonies in Hungary indicated two breakpoints that could be linked to two interventions in the past. The later breakpoint coincided with the start of systematic conservation reintroductions of EGS providing evidence for an overall positive effect of conservation reintroductions despite failed actions (Gregorová et al., 2023; Kachamakova et al., 2021, 2022; Wauchope et al., 2021; Kachamakova & Koshev, 2021; Gelman & Hennig, 2017; Matějů et al., 2010). This study demonstrated that comprehensive, different sources of data incorporating the effect of past conservation measures and a complex analysis could more effectively review and comprehend the history (i.e. ups and downs) and management needs of the species and forecast its future more realistically. That enabled us to detect a “broken” trend and a potentially causal inference of a past conservation measure on the EGS population of Hungary. Unfortunately, the general trend of the last 57 years has still supported the globally experienced decline of burrowing mammals (Davidson et al., 2012). This has negative consequences on grassland ecosystem functions and services as ESG and its relatives are often true keystone and engineering species (Pereg et al., 2021; Delgado-Baquerizo et al., 2020; Nieder et al., 2018; Haussmann, 2017; Machicote et al., 2004; Reichman & Smith, 1990).

Threat maps, and the analysis of population density or size could add further information for improving the conservation of this species and other endangered burrowing rodents. Moreover, carefully designed and monitored conservation reintroductions could provide data for detailed analysis and result in more valid survival rates of reintroduced populations. It may also enable the comparison of management methods or give location specific results that may help transfer methods between different habitats or species. The results underline the importance of long term absence (extinction)-presence data of colonies to provide information on the changes in the conservation status of the targeted species, which can be used for biodiversity monitoring too.

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CRediT authorship contribution statement

Tamás Cserkész: Conceptualization, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Project administration, Funding acquisition. **Olivér Váczi:** Conceptualization, Methodology, Validation, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Project administration, Funding acquisition. **Tünde Takáts:** Investigation, Resources, Writing – original draft, Visualization, Validation, Project administration. **Piroska Pazonyi:** Investigation, Validation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Validation, Methodology. **Gábor Mikesy:** Investigation, Validation, Resources, Data curation, Writing – original draft, Writing – review & editing, Methodology, Visualization. **Eric C. Brevik:** Writing – original draft, Writing – review & editing. **Lajos Nagy:** Data curation, Writing – original draft. **András István Csathó:** Data curation, Writing – review & editing. **Attila Németh:** Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing. **Tamás Szitta:** Investigation, Resources. **Csaba Kiss:** Resources, Data curation. **Annamária Laborczi:** Validation, Methodology. **János Mészáros:** Methodology, Writing – original draft, Visualization. **Csongor Gedeon:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2025.126836.

Data availability

Data will be made available on request.

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