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Research Article

Effect of plant-related threats on lizards of open sand steppes: a snapshot at the beginning of the spread of a novel invader

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Abstract

Grasslands have undergone significant loss of area and species diversity worldwide. The spread of invasive alien plant species further exacerbates the degradation of these ecosystems. Reptile populations are particularly affected by changes caused by invasive plants. Pannonian sand steppe grasslands, typical of the lowland regions within the Central European Carpathian Basin, are distinctive habitats that are rapidly shrinking in extent. These grasslands provide habitats for numerous grassland specialists, such as the Balkan wall lizard (*Podarcis tauricus*). Over the last few years, a new invader, the sand dropseed (*Sporobolus cryptandrus*), native to the North American prairies, has appeared in this community and spread aggressively. In addition, shrub encroachment due to pasture abandonment and reforestation has further reduced the area of these communities. In this study, we explored how the densities of two lizard species, the Balkan wall lizard and the Eastern green lizard (*Lacerta viridis*), a potential competitor of the Balkan wall lizard inhabiting these open grasslands, respond to increasing coverage of non-native invasive plants and the encroachment of woody vegetation. We surveyed lizard populations at six sites and assessed the effects of these threats using single-visit *N*-mixture models. The results showed varied effects on the abundance of the two lizard species: sand dropseed negatively affected the Balkan wall lizard, while woody encroachment positively influenced the Eastern green lizard.

Key words: *Asclepias syriaca*, biological invasions, grasslands, invasive alien species (IAS), nature conservation, reptiles, *Sporobolus cryptandrus*, woody plant encroachment

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Introduction

Grasslands are among the most threatened terrestrial ecosystems worldwide. Large portions of these areas were converted to crop fields during the 19th–20th centuries, leading to a significant global loss of grassland habitats (Matson et al. 1997; Hoekstra et al. 2005). In the majority of the remaining grasslands, traditional livestock grazing was replaced by intensive farming accompanied by mechanised hay harvest and other yield-maximising technologies (Isselstein et al. 2005). These processes resulted in

a significant loss of species diversity and declining ecosystem functioning across the remaining grassland fragments, driving many grassland specialists towards extinction (Hilpold et al. 2018; Mizsei et al. 2020). Other factors, such as river regulations and water management practices that disregarded ecological needs, disrupted natural hydrological cycles and increased aridity, further exacerbated by climate change-induced extreme weather events, especially prolonged droughts (Jánosi et al. 2023). In addition to these threats, the introduction or arrival of non-native species has altered communities of flora and fauna (Horwitz et al. 2008; Seastedt and Pyšek 2011; Hendrickson et al. 2019). These alterations affect both species diversity and ecological integrity profoundly, underscoring the need for conservation activities that counterbalance these threats, particularly those affecting sensitive grassland specialist species (Watkinson and Ormerod 2001; Gustavsson et al. 2011).

A growing body of research demonstrates that the incursion of non-native plants into native vegetation causes significant alterations to species richness, composition and structure (Fletcher et al. 2019), as well as to the abundance of animals (Eyre et al. 2009; Seastedt and Pyšek 2011; Bateman and Ostoja 2012; Drake et al. 2016). However, the effect of invasive plants on fauna is not consistently negative, positive or neutral (Martin and Murray 2011; Gray and Steidl 2015). Three main types of underlying mechanisms have been identified in determining the impact of non-native plants: 1) changes in habitat structure and heterogeneity, 2) alteration of herbivory and predator–prey interactions, and 3) modification of reproductive success (Levine et al. 2003; Martin and Murray 2011). Animals with limited dispersal ability, low recruitment rate and narrow niches are more likely to respond strongly negatively to the spread of invasive plants (Litt and Pearson 2022). However, the encroachment of native shrubs can also have negative effects on the vertebrate fauna of grasslands (Blaum et al. 2007; Stanton et al. 2018); for example, it could negatively affect herpetofaunal diversity (Stanton et al. 2018).

Reptile populations are declining globally, with nearly 20% of species threatened by extinction (Gibbons et al. 2000; Cox et al. 2022). The main causes are habitat loss and degradation (Paterson et al. 2021; Doherty et al. 2020), changes in land use (Cordier et al. 2021), the spread of invasive species (Bellard et al. 2016), diseases, environmental pollution, overexploitation of habitats, and climate change (Gibbons et al. 2000; Böhm et al. 2013; Ceballos et al. 2015), as well as overexploitation (Auliya 2003; Auliya et al. 2016). Reptiles are predicted to respond negatively to plant invasions due to their generally small body size, limited mobility, breeding strategies and habitat specialisation (Litt and Pearson 2022). However, there remains a lack of knowledge regarding the specific impacts and underlying processes of this interaction (Martin and Murray 2011). This issue warrants attention, as plant invasions can occur on short timescales (Daehler 2009), and reptiles are pivotal to ecosystem functioning and can be monitored as indicators of ecosystem change and biodiversity loss (Cortes et al. 2014).

Reptile species are often elusive, behaviourally cryptic, and display strong thermoregulatory responses to microclimatic conditions, all of which contribute to low detectability in field surveys (Mazerolle et al. 2007; Durso et al. 2011; Ward et al. 2017). This poses a major challenge when assessing population responses to rapid environmental changes such as biological invasions or habitat degradation, especially when detection may vary spatially and temporally. To overcome this limitation, model-based approaches that account for imperfect detection, such as *N*-mixture models, are increasingly applied in herpetological studies (van Wyk and

Maritz 2025). In our study, we adopted a single-visit *N*-mixture framework well suited for reptile monitoring where repeated visits may not be feasible and where disturbance minimisation is a priority (Sólymos and Lele 2016). This approach enables robust inference about abundance while explicitly accounting for variation in detectability and supports conservation-focused evaluations of how habitat changes influence reptile populations (Duarte et al. 2018).

Over the past decade, several exotic plant species have become established on the dry sandy grasslands of Central Europe (Csiky et al. 2023). Many of them spread particularly on grasslands, such as common milkweed (*Asclepias syriaca*) (Meinhardt et al. 2024) or woody black locust (*Robinia pseudoacacia*) (Chikowore et al. 2021). Approximately half of the world's invasive perennial grasses use the C4 photosynthetic pathway, a trait that can enhance their spread under future climate scenarios involving more frequent heatwaves (Díaz Cando et al. 2025). Despite this, C4 perennial bunchgrasses are uncommon among native European flora (Sage et al. 1999; Weber 2017). A recently emerging invasive species, the sand dropseed (*Sporobolus cryptandrus*), native to North America, has attracted attention due to its potential ecological impacts (Kröel-Dulay et al. 2024). While other invasive species are more likely to spread in disturbed habitats (Kröel-Dulay et al. 2024), this species also spreads rapidly on non-degraded grasslands with high conservation value. Its establishment is associated with a sharp decline in plant diversity, the loss of less competitive species and the displacement of native perennial bunchgrasses. Due to these impacts, it is increasingly recognised as a transformer species (Maltsev et al. 2017; Demina et al. 2018; Török et al. 2021; Hábenczyus et al. 2022). Recent findings also indicate that while sand dropseed may have neutral or positive effects on certain predatory arthropods, such as spiders and ground beetles, overall, it negatively impacts herbivorous insects of high conservation value, especially orthopterans and true bugs (Szabó et al. 2025).

In this study, we explored the response in the densities of two lizard species on dry sandy grasslands to the threats posed by sand dropseed and common milkweed, as well as to the encroachment of native shrubs and trees on historically almost treeless meadows. To provide timely insights at the early stage of invasion, we designed this work as a rapid assessment using a targeted, time-efficient sampling framework suitable for conservation planning under data-limited conditions. Given their ecological traits, we expected the grassland specialist Balkan wall lizard (*Podarcis tauricus*) to respond negatively to vegetation changes caused by invasive species and woody encroachment. In contrast, the more generalist Eastern green lizard (*Lacerta viridis*), which utilises structurally more closed habitats, was predicted to show neutral or even positive responses to increasing vegetation closure.

Methods

Study area and study species

Our study area is located in the sandy grasslands of the Kiskunság National Park, Central Hungary, where large untilled grasslands remain despite the significant loss of this ecosystem during the 19th–20th centuries (Fig. 1A). These grasslands are dominated by the priority habitat type of Pannonian sand steppes listed in the European Union Habitat Directive (habitat type code 6260; Annex I). This habitat type is considered to be in "unfavourable-bad" conservation status (U2), a habitat in peril of

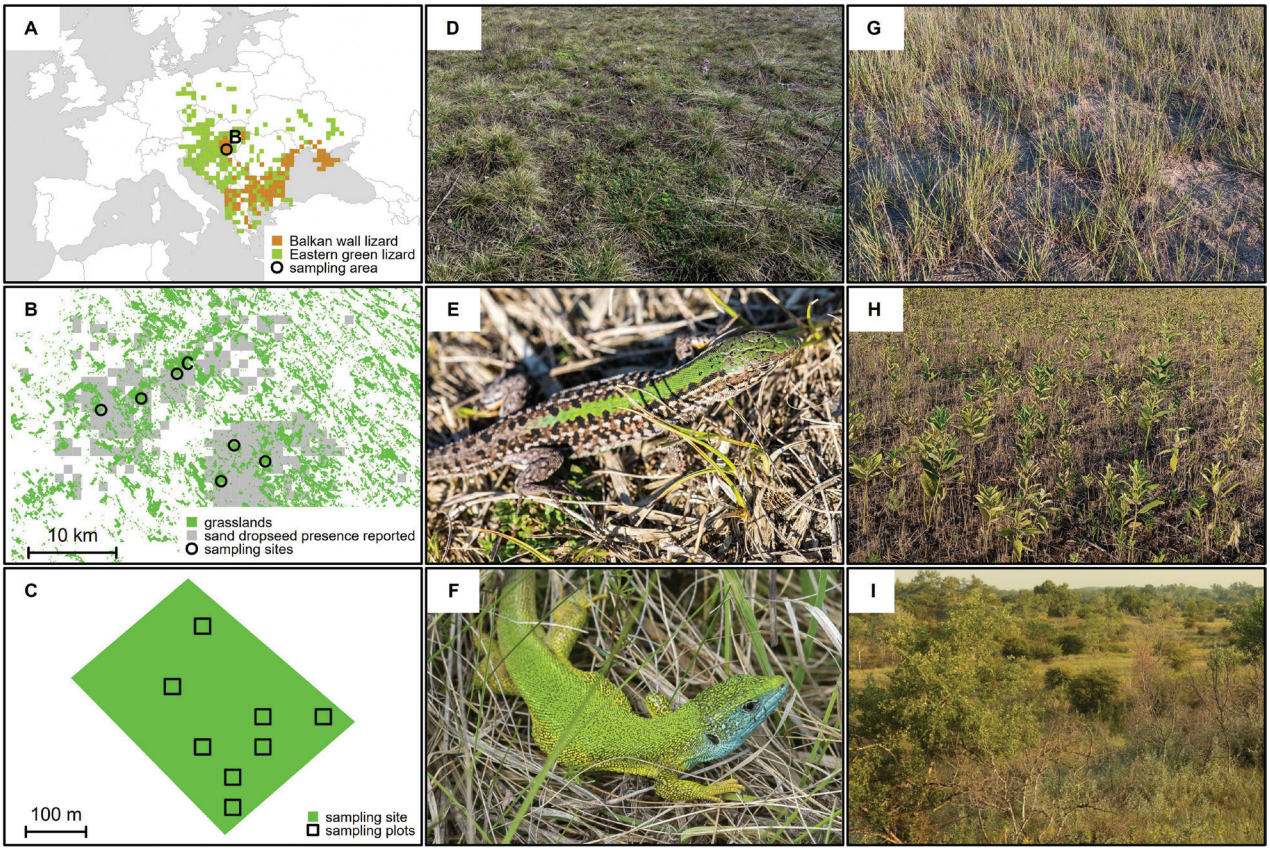

Figure 1. Distribution of the studied lizard species (modified from Sillero et al. 2014) and the location of the sampling area (panel **A**), the location of the sampling sites (panel **B**), and an example of random sampling plots at one of the sampling sites (panel **C**). Examples of the surveyed grassland habitats: **D.** High-nature-value open sand steppe without invasive plant species; **G.** Sand-drop-seed-dominated grassland; **H.** Common-milkweed-dominated grassland; **I.** Encroachment of woody vegetation. Representative individuals of the studied lizard species: Balkan wall lizard (panel **E**) and Eastern green lizard (panel **F**). Photographs **D–H** by E. Mizsei; **I** by B. Bancsik.

disappearing (European Environment Agency 2013). Our study sites were selected in the core of this habitat type, where one of the most important threats is aridification due to altered weather patterns, water abstraction, the spread of invasive species, and encroachment by woody vegetation following a substantial reduction in grazing intensity after the abandonment of traditional grazing practices.

Among the invasive alien plant species, the common milkweed (*Asclepias syriaca*) is widespread across the area (Fig. 1H). However, this species requires disturbance to spread and thrive. It grows mostly on degraded meadows, roadsides, and formerly overgrazed, burnt, or ploughed sandy grasslands and is less prone to invade intact grasslands (Avramov et al. 2024). Conversely, the sand dropseed (*Sporobolus cryptandrus*) can successfully infest undisturbed plant communities, such as primary open sand grasslands with high conservation value (Kröel-Dulay et al. 2024; Fig. 1G). This species was first detected in 2016 in our study area and subsequently spread explosively. Besides these, woody species such as the non-native invasive black locust (*Robinia pseudoacacia*), tree of heaven (*Ailanthus altissima*), and honey locust (*Gleditsia triacanthos*), as well as the native silver poplar (*Populus alba*) and common hawthorn (*Crataegus monogyna*), encroach upon the grasslands (Fig. 1I).

We surveyed the two most common reptile species occurring in the study area, the Balkan wall lizard (*Podarcis tauricus*) and the Eastern green lizard (*Lacerta viridis*) (Fig. 1A, E, F). The Balkan wall lizard is restricted to open sandy and loess grasslands

in this part of its distribution range (Mizsei et al. 2020). These habitats are characterised by sparse, low vegetation cover, where soil conditions and aridity prevent complete closure of both herbaceous and woody vegetation. The Eastern green lizard is a generalist species occupying a wide range of habitats, from grasslands to forests and from wet to dry conditions (Mizsei et al. 2020; Vacheva et al. 2020).

Sampling design

We conducted a preliminary mapping of sand dropseed based on previous observations in the study area (Kröel-Dulay et al. 2024). In July 2024, we identified n = 6 separate grassland habitats (study sites) suitable for our study design, showing various levels of invasive plant presence and encroachment (including intact grassland patches) and apparent reptile abundance, and selected these as study sites (Fig. 1B). The average area of each selected site was 10.5 ± 4.1 ha (mean ± SD).

To create a randomised sampling design, we plotted a 25 × 25 m grid over each study site. To avoid the undesired selection of neighbouring sampling plots, we removed every second row and column of grid cells (Fig. 1C). We then summarised the sand dropseed records within the grid cells and scaled the numbers to a range between 0 and 1. Finally, we randomly selected n = 8 25 × 25 m sampling plots at each study site from the grid cells stratified by sand dropseed presence to ensure the inclusion of plots with no or low coverage, as well as plots with high coverage of this plant. Altogether, we selected n = 48 sampling plots across the six study sites.

Data collection

We conducted our surveys in September 2024. The surveyors (n = 6 or 7) walked slowly across each sampling plot along parallel transects (25 m long and approximately 4 m apart), moving in a row from the southern border of the 25 × 25 m sampling plot towards the northern border. All reptile individuals observed were recorded by the first surveyor who spotted them, noting the species, age (juvenile, subadult, or adult), sex, coordinates, date, and time using the OpenBioMaps Android application (Bán et al. 2022).

At each plot, we recorded the focal plant-related threats targeted in this study. We estimated the relative cover of sand dropseed, common milkweed, and woody vegetation in each plot by visually assessing and counting the number of 5 × 5 m grid squares (within each 25 × 25 m plot) in which the target plant groups were present. To account for the level of vegetation degradation, we determined the naturalness value of each sampling plot on an ordinal scale from 0 to 1 based on the vegetation's compositional, structural, and functional diversity. The naturalness-based quality of a habitat was developed along with the vegetation classification system in Hungary (Bagi et al. 1997). Low values indicate a degraded natural state characterised by reduced species richness and homogenised structure, while high values indicate near-complete species composition typical of the habitat type and high ecological functioning (Bagi et al. 1997; Horváth et al. 2008; Illyés et al. 2008).

To account for variation in reptile detectability during the surveys, we used data from a custom-built automated meteorological station equipped with eight operative temperature loggers, located approximately 20 km from the study sites. Operative temperature is the environmental temperature available to an individual of an ectothermic species within a given time frame (Kearney and Porter 2020; Falaschi

2021). Thermoregulatory conditions, which influence a reptile's activity and thus its detectability, strongly depend on this variable. The temperature data were collected at two-minute intervals from eight thermometers (BTP-06 temperature sensors connected to a BEL-06 ecologger unit, Boreas Ltd., Hungary), four exposed to full sun and four placed in the shade of vegetation (Mizsei et al. 2023).

Statistical analysis

To assess the influence of vegetation-related variables on reptile abundance, we applied single-visit *N*-mixture abundance models (Sólymos et al. 2012; Sólymos and Lele 2016). *N*-mixture models are particularly useful for studying species with imperfect or low detectability, as they explicitly account for detection probability (p), thereby reducing bias in abundance estimates (Madsen and Royle 2023). Single-visit *N*-mixture models estimate detection and abundance simultaneously by assuming that separate sets of covariates influence each process. In our models, vegetation variables were included in the abundance submodel (reflecting habitat effects), while operative temperature and observer effort were included in the detection submodel (reflecting short-term activity and survey conditions).

We fitted separate models for the two lizard species using the same model structure. The sum of reptile detections per survey (one survey per sampling plot) was used as the dependent variable. Explanatory variables for latent abundance (abundance submodel) included sand dropseed cover, milkweed cover, woody plant cover, and naturalness, while the mean operative temperature during the survey and the number of surveyors (survey effort) were included as explanatory variables for detection (detection submodel). In the models, we did not differentiate between the age and sex of individuals. All explanatory variables were scaled to a mean of 0 and a standard deviation of 1. In the global model including all variables, we performed a step selection to identify the most parsimonious candidate models based on an information-theoretic framework using the Akaike Information Criterion (AIC; Burnham and Anderson 2002). To fit the models, we used the *detect* package (Sólymos et al. 2023) in R 4.4.2 (R Core Team 2024).

We acknowledge that *N*-mixture models can be sensitive to violations of their assumptions and may be affected by identifiability issues (Goldstein and de Valpine 2022; Link et al. 2018). To assess the robustness of our findings, we conducted an additional analysis using generalised linear mixed models (GLMMs) with Poisson error distribution and log link function, assuming perfect detection. Predictor variables were standardised, and models were fitted using the *glmmTMB* package. Model selection was performed using AIC, and model averaging was applied for models within $\Delta AIC < 2$. The results, including model selection tables and averaged coefficients, are provided in the Suppl. material 1.

Results

The habitat features of the sampling plots showed a mean naturalness of 0.58 ± 0.04 (±SE). Sand dropseed was detected in 75% of the sampling plots (n = 36) with a mean cover of $25.5 \pm 4.8\%$ (±SE), common milkweed was present in 31% of the sampling plots (n = 15) with a mean cover of $12.6 \pm 2.9\%$ (±SE), and encroachment of woody vegetation was observed in 62.5% of the sampling plots (n = 30) with a mean cover of $9.0 \pm 1.7\%$ (±SE).

We observed n = 56 Balkan wall lizard and n = 28 Eastern green lizard individuals during the surveys (n = 48). The Balkan wall lizard was detected in 62% (n = 30) of the sampling plots, and the Eastern green lizard in 37.5% (n = 18). In terms of age structure, Balkan wall lizard observations consisted predominantly of adults (63.4%), followed by juveniles (23.9%) and subadults (12.7%). For the Eastern green lizard, the observed individuals were 75.6% adults and 24.4% juveniles.

Model selection for the abundance and detectability of the Balkan wall lizard revealed that the most parsimonious model included operative temperature as a covariate of detectability and naturalness, sand dropseed cover, and common milkweed cover as covariates of abundance (Table 1). Operative temperature showed a marginally significant positive influence on the detectability of Balkan wall lizards (Table 1). Sand dropseed cover had a significant negative effect, while common milkweed cover had no significant effect on abundance (Table 1, Fig. 2). The mean detection probability of the Balkan wall lizard was 0.82 (95% confidence interval, CI: 0.58–0.91). The estimated mean density for the sampling plots was 48.5 individuals/ha (CI: 11.5–78.5 individuals/ha).

The most parsimonious model for the abundance and detectability of the Eastern green lizard included survey effort as a covariate of detectability and woody encroachment and naturalness as covariates of abundance (Table 1). Survey effort had no effect

Table 1. Coefficient estimates for detectability (logit link) and abundance (log link) of the Balkan wall lizard and the Eastern green lizard.

Species	Submodel	Variable	Estimate	SE	z	p
Balkan wall lizard	Detectability	(Intercept)	-1.4769	0.8166	-1.8087	0.0705
		operative temperature	0.5915	0.3607	1.6397	0.1011
	Abundance	(Intercept)	1.6487	0.5289	3.1174	0.0018
		sand dropseed cover	**-0.5828**	**0.2176**	**-2.6789**	**0.0074**
		common milkweed cover	0.168	0.1242	1.3529	0.1761
Eastern green lizard	Detectability	(Intercept)	-0.2769	0.995	-0.2783	0.7808
		survey effort	0.4934	0.7632	0.6464	0.518
	Abundance	(Intercept)	0.0584	0.36	0.1623	0.871
		woody encroachment	**0.4979**	**0.153**	**3.2541**	**0.0011**
		naturalness	0.3985	0.2703	1.474	0.1405

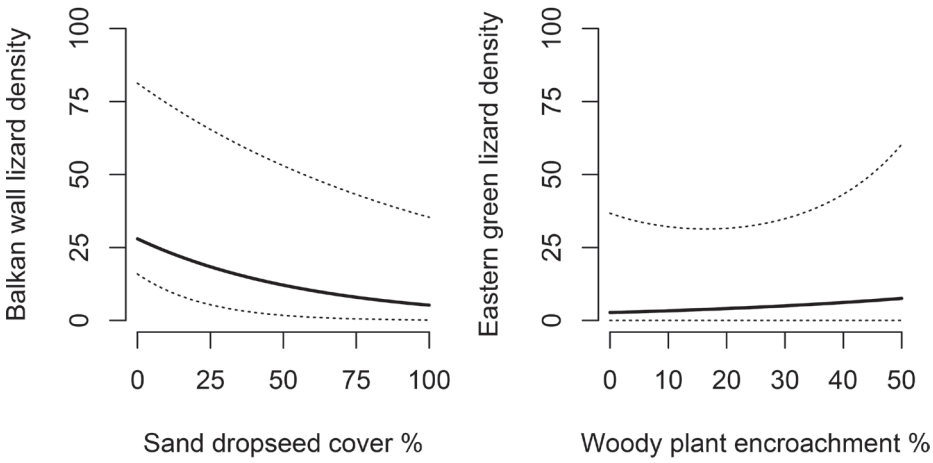

Figure 2. Effect of sand-dropseed cover on Balkan wall lizard and woody-plant encroachment on Eastern green lizard density (individuals/ha; dotted lines indicate 95% confidence intervals).

on detectability. For abundance, woody encroachment showed a significant positive influence, while naturalness had no effect (Table 1, Fig. 2). The mean detection probability of the Eastern green lizard was 0.51 (CI: 0.28–0.77). The estimated mean density for the sampling plots was 11.2 individuals/ha (CI: 3.1–26.5 individuals/ha).

Results from complementary GLMM analyses (Suppl. material 1) yielded the same direction and similar magnitude of effects for the key predictors, supporting the robustness of the patterns inferred from the *N*-mixture models.

Discussion

Habitat selection by reptiles strongly depends on the structural features of vegetation available to them (Doherty et al. 2020; Mizsei et al. 2020, 2024). Our results suggest that the abundance of the open grassland specialist Balkan wall lizard was negatively influenced by the increasing cover of the invasive sand dropseed, while the abundance of the Eastern green lizard was not affected by the presence of invasive plants; however, it was positively influenced by the encroachment of woody vegetation. The results highlight that an explosively spreading exotic plant or alteration of vegetation structure through succession can affect native reptile communities over a short time frame.

Changes in vegetation composition that alter structural features are likely to influence reptile populations (Howland et al. 2014; Cosendey et al. 2019; Mizsei et al. 2020; Móré et al. 2024). Our results accord with findings of other studies showing that the impact of invasive plants on reptiles is not always negative (Martin and Murray 2011; Stellatelli et al. 2013; Gray and Steidl 2015). The common milkweed had no effect on the abundance of the two reptiles we surveyed, but the sand dropseed influenced the Balkan wall lizard. Encroachment of woody vegetation usually negatively impacts species specialised for treeless habitats (Ratajczak et al. 2012); however, in our survey, we did not detect such a negative impact on the Balkan wall lizard. On the other hand, encroachment by woody plants had a positive effect on the generalist Eastern green lizard, which prefers shrubby grassland and forest–steppe mosaics (Heltai et al. 2015).

The two main influential plant-related habitat features we identified were the cover of the invasive sand dropseed and the encroachment by native woody vegetation. In the Balkan wall lizard, the negative effect of sand dropseed cover can be explained by two key mechanisms: 1) changes in habitat structure and 2) alterations of the trophic network. On open sand steppes, sand dropseed invasion alters the microhabitat structure and plant community composition (Kröel-Dulay et al. 2024). Firstly, the monodominant patches of sand dropseed exhibit lower structural heterogeneity compared with native open sand grassland communities. This may decrease thermal landscape heterogeneity and influence the availability of shelters from predators, both of which are crucial in the ecology of lizards (Carter et al. 2015; Bateman and Riddle 2020). Secondly, the more homogeneous and non-native vegetation supports lower arthropod diversity and abundance, limiting prey availability and reducing the carrying capacity of the habitats (van Hengstum et al. 2014; Kajzer-Bonk et al. 2016; Cornelis et al. 2023). Additionally, the invasion can lead to a homogenisation of grassland communities and a decline in native plant diversity, which may further reduce microhabitat variety and ecological niche availability for grassland specialists. However, further investigations are needed to assess differences among microhabitats provided by native grass species and sand dropseed.

This study aimed to provide a rapid assessment of whether native reptiles are threatened by a new invader, the non-native sand dropseed. Consequently, the sampling design prioritised speed over comprehensiveness and therefore involved several limitations. First, survey plots were stratified to span the observed range of sand dropseed cover, which may have resulted in an under-representation of other plant-related threats, such as common milkweed and woody encroachment. Further stratification based on these variables could yield more robust estimates of their effects. This likely explains the absence of a significant detected impact of encroachment on the abundance of the Balkan wall lizard, which contradicts field observations suggesting that this species tends to avoid woody vegetation. Second, the study was limited in terms of spatial replication, with only six sites and eight sampling plots per site, and used a relatively small spatial scale (25 × 25 m). Third, estimation of naturalness was based on the field experience of the surveyors using a standardised visual assessment method applied in Hungarian grassland monitoring. While this approach ensures consistency within the national framework, its reproducibility may be limited across other habitat types or outside the region. Increasing the sample size, expanding the spatial scale, and including additional sites could improve the reliability of parameter estimates. Finally, the surveys lacked temporal replication. While single-visit *N*-mixture models offer a practical solution for rapid assessments, they rely on strong assumptions about the separation of abundance and detection processes. Our supplementary GLMM analyses demonstrate that our main findings are robust to these assumptions, but future monitoring should employ repeated surveys or open-population models to refine abundance and recruitment estimates. Conducting repeated within-season surveys would help to refine abundance estimates and assess short-term variability, while extending monitoring across multiple seasons or years could reveal longer-term trends and improve our understanding of how plant-related threats influence reptile populations.

The explosive spread of sand dropseed and its threat to grasslands draw attention to the need for effective strategies against new invaders. Due to the widespread presence it has gained within a few years, its total eradication is unrealistic; thus, other objectives could be set. Detailed mapping and monitoring of sand dropseed colonies are needed to determine the patterns and drivers of their invasion and to predict future spread for developing preventive management strategies. In the case of intact grasslands or high-density populations of sand dropseed, the prevention of further spread could be achieved by blocking dirt roads and minimising traffic, as sand dropseed mostly spreads along sandy dirt roads where its seeds are carried by vehicles (Kröel-Dulay et al. 2024). Founder plant individuals and small populations could be eradicated manually, while in large populations, management methods (e.g. grazing, mowing, burning, chemical treatment, and their combinations) should be tested soon, as effective control measures for sand dropseed have not yet been identified despite recent attempts. Uncontrolled spread of this invasive plant may have a detrimental effect on the unique steppe fauna and flora of the Central European sandy grasslands.

Conclusion

Our study highlights significant species-specific responses of reptiles to invasive plants and habitat changes in the sand steppes of Hungary. The Balkan wall lizard responds negatively to the non-native invasive sand dropseed; its abundance

decreases in the presence of this plant, likely due to alterations in habitat structure and reduced prey availability. On the other hand, the Eastern green lizard is not affected by the presence of sand dropseed and benefits from the encroachment of native woody vegetation, suggesting a preference for structurally more diverse habitats. These findings emphasise the complexity of invasive species studies and the need for targeted conservation strategies that consider the specific needs of, and threats to, particular species. Given the rapid spread and ecological impact of sand dropseed, effective management practices are urgently needed to mitigate its effects and preserve the biodiversity of these unique grassland ecosystems.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

The data collection was carried out as part of the independent research of the Kiskunság National Park Directorate.

Use of AI

No use of AI was reported.

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Author contributions

Edvárd Mizsei: conceptualisation, investigation, formal analysis, visualisation, writing – origi-nal draft, writing – review and editing. Csongor Adorjáni: conceptualisation, investigation, writing – review and editing. Barnabás Bancsik: investigation, writing – review and editing. Gergő Kovács: investigation, writing – review and editing. Gergő Rák: conceptualisation, investigation, writing – review and editing. Gergely Babocsay: conceptualisation, funding acquisition, writing – review and editing. Mátyás Budai: conceptualisation, investigation, writing – review and editing.

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Data availability

Data and R code files associated with this study are available in the Zenodo repository at (https://doi.org/10.5281/zenodo.15471556).

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Supplementary material 1

Supplementary information

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