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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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2 the spread of a novel invader

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15

16 **Abstract**

17 Grasslands have been subject to a significant loss of area and species diversity worldwide.
18 The spread of invasive alien plant species further exacerbates the degradation of these
19 ecosystems. Reptile populations are particularly affected by changes caused by invasive
20 plants. Pannonic sand steppe grasslands are characteristic communities of Central Europe, but
21 their extent is shrinking rapidly. These grasslands provide habitat for numerous grassland
22 specialists such as the Balkan wall lizard (*Podarcis tauricus*). Over the last few years, a new
23 invader, the Sand dropseed (*Sporobolus cryptandrus*), native to the North American prairies,
24 appeared in this community and spread aggressively. In addition, shrub encroachment due to
25 pasture abandonment and reforestation further reduced the area of these communities. In this
26 study, we explored how densities of two species of lizards, the Balkan wall lizard and the
27 Eastern green lizard (*Lacerta viridis*), inhabiting these open grasslands respond to potential
28 plant-related threats, such as the increasing coverage of non-native invasive plants and the
29 encroachment of woody vegetation. We surveyed lizard populations at six sites and assessed
30 the influence of these threats using single-visit n-mixture models. The results showed varied
31 effects on the abundance of the two lizard species. Sand dropseed negatively affects the
32 Balkan wall lizard, and woody encroachment positively influences the Eastern green lizard.

33 There is a need for further research to refine the understanding of invasive plant impacts on
34 native wildlife, and to develop effective management strategies to control the spread of
35 invasive species like the Sand dropseed.

36

37 **Keywords**

38 *Ascpelias syriaca*, biological invasions, grasslands, invasive alien species (IAS), nature
39 conservation, reptiles, *Sporobolus cryptandrus*, woody plant encroachment

40

41 **Introduction**

42 Grasslands are among the most threatened terrestrial ecosystems worldwide because, being
43 suitable for agriculture, a large portion was converted to crop fields during the 19-20th
44 centuries, leading to a significant loss of grassland area worldwide (Matson et al. 1997;
45 Hoekstra et al. 2005). In most areas, on the remaining grasslands, traditional livestock
46 grazing was replaced by intensive farming accompanied by mechanised hay harvest and other
47 yield-maximising technologies (Isselstein et al. 2005). These processes resulted in a
48 significant loss of species diversity and declining ecosystem functioning across the remaining
49 grassland fragments, thus many grassland specialist organisms were pushed towards
50 extinction (Hilpold et al. 2018; Mizsei et al. 2018, 2020). Other factors, such as river
51 regulations and ecophobic water management, disrupted natural hydrological cycles and
52 increased aridity, exacerbated by climate change-induced extreme weather events, especially
53 prolonged droughts (Jánosi et al. 2023). In addition to these threats, non-native species
54 emerged and altered communities of flora and fauna (Horwitz et al. 2008; Seastedt and Pyšek
55 2011; Hendrickson et al. 2019). These alterations profoundly influence biodiversity and
56 ecological integrity, underscoring the need for conservation activities that counterbalance the
57 threats to grassland habitats, particularly the ones affecting sensitive specialist species
58 (Watkinson and Ormerod 2001; Gustavsson et al. 2011).

59 A growing body of research demonstrates that the incursion of non-native plants into native
60 vegetation causes significant alterations to species richness, composition, structure (Fletcher
61 et al. 2019) and abundance of animals (Eyre et al. 2009; Seastedt and Pyšek 2011; Bateman
62 and Ostojá 2012; Drake et al. 2016). However, the effect of invasive plants on the fauna is

63 not consistently negative, positive, or neutral (Martin and Murray 2011; Gray and Steidl
64 2015). Three main types of underlying mechanisms were identified in determining the impact
65 of exotic plants: changes in habitat structure and heterogeneity, alteration of herbivory and
66 predator-prey interactions, and modification of reproductive success (Levine et al. 2003;
67 Martin and Murray 2011). Animals with limited dispersal ability, low reproductive rate and
68 narrow niches are more likely to respond strongly negatively to the spread of invasive plants
69 (Litt and Pearson 2022). However, encroachment of native shrubs can also have negative
70 effects on vertebrate fauna of grasslands, for example, it could negatively affect
71 herpetofaunal diversity (Stanton et al. 2018).

72 Reptile species are declining globally, with nearly 20% of species threatened by extinction
73 (Gibbons et al 2000; Cox et al. 2022). The main threats causing these declines are habitat loss
74 and degradation (Paterson et al. 2012; Doherty et al. 2020), the spread of invasive species
75 (Bellard et al. 2016), diseases, environmental pollution, overexploitation of habitats, climate
76 change (Gibbons et al. 2000; Böhm et al. 2013; Ceballos et al. 2015), and overexploitation
77 (Auliya 2003; Auliya et al. 2016). Reptiles are predicted to respond negatively to plant
78 invasions due to their small body size, limited mobility, breeding strategies, and habitat
79 specialisation (Litt and Pearson 2022). However, there remains a lack of knowledge
80 regarding the specific impacts and underlying processes (Martin and Murray 2011). This
81 issue warrants attention as plant invasions can come off in short timescales (Daehler 2009),
82 and reptiles are pivotal in ecosystem functioning and can be monitored as indicators of
83 ecosystem change and biodiversity loss (Cortes et al. 2014).

84 Over the past decade, several exotic plant species have become established on the dry sandy
85 grasslands of Central Europe (Csiky et al. 2023). Many of those spread particularly on
86 grasslands such as the Common milkweed (*Asclepias syriaca*) (Meinhardt et al. 2024) or the
87 woody Black locust (*Robinia pseudoacacia*) (Chikowore et al. 2021). Approximately half of
88 the world's invasive perennial grasses use the C4 photosynthetic pathway, a trait that can
89 enhance their spread under future climate scenarios involving more frequent heatwaves (Díaz
90 Cando et al. 2025). Despite this, C4 perennial bunchgrasses remained uncommon within the
91 European flora (Sage et al. 1999; Weber 2017). A recently emerging invasive species, the
92 Sand dropseed (*Sporobolus cryptandrus*), native to North America, has attracted attention
93 due to its potential ecological impacts. While other invasive species are more likely to spread
94 in disturbed habitats (Kröel-Dulay et al. 2024), this species also spreads rapidly on non-
95 degraded grasslands with high conservation value. Its establishment is associated with a sharp

96 decline in plant diversity, the loss of subordinate species, and the displacement of native
97 perennial bunchgrasses. Due to these impacts, it is increasingly recognised as a transformer
98 species (Maltsev et al. 2017; Demina et al. 2018; Török et al. 2021; Hábcenyus et al. 2022).
99 In this study, we explored the response in the densities of two lizard species on dry sandy
100 grasslands to the threats posed by the Sand dropseed and Common milkweed, as well as by
101 the encroachment of native shrubs and trees on historically almost treeless meadows.

102 **Methods**

103 *Study area and study species*

104 Our study area is located in the sandy grasslands of the Kiskunság National Park, Central
105 Hungary, where large unbroken grasslands remained despite the significant loss of that
106 ecosystem during the 19th-20th centuries (Fig. 1 A). These grasslands are dominated by the
107 priority habitat type of Pannonic sand steppes listed in the European Union Habitat Directive
108 (habitat type code 6260; Annex I). This habitat type is considered to be in “unfavourable-
109 bad” conservation status (U2), a habitat in serious danger of disappearing (European
110 Environment Agency 2013). Our study sites are selected in the core of this habitat type,
111 where one of the most important threats to this area is aridification due to altered weather
112 patterns, water management system focusing on draining, the spread of invasive species, the
113 encroachment by woody vegetation and the drastic drop in grazing intensity or the
114 abandonment of traditional grazing practices.

115 Among the invasive alien plant species, the Common milkweed (*Asclepias syriaca*) is
116 widespread across the area (Fig. 1 H). However, this species requires disturbance to spread
117 and thrive. It grows mostly on degraded meadows, roadsides, formerly overgrazed, burnt or
118 ploughed sandy grasslands, while it does not invade most intact grasslands (Avramov et al.
119 2024). Conversely, the Sand dropseed (*Sporobolus cryptandrus*) can successfully infest
120 undisturbed plant communities, such as primary open sand grasslands with high conservation
121 value (Kröel-Dulay et al. 2024; Fig. 1 G). This species was first detected in 2016 in the
122 studied area and subsequently spread explosively. Besides these, woody species, such as the
123 non-native invasive Black locust (*Robinia pseudoacacia*), Tree of heaven (*Ailanthus*
124 *altissima*) and Honey locust (*Gleditsia triacanthos*), and the native Silver poplar (*Populus*
125 *alba*) and Common hawthorn (*Crataegus monogyna*) (Fig. 1 I) encroach the grasslands.

126 We surveyed the two most common reptile species occurring in the study area, the Balkan
127 wall lizard (*Podarcis tauricus*) and the Eastern green lizard (*Lacerta viridis*) (Fig. 1 A, E, F).
128 The Balkan wall lizard is restricted to open sandy and loess grasslands in this part of its
129 distribution range (Mizsei et al. 2020). These habitats are characterised by sparse, low
130 vegetation cover, where soil conditions and aridity prevent complete closure of both
131 herbaceous and woody vegetation. The Eastern green lizard is a generalist species occupying
132 a wide range of habitats from grasslands to forests, from wet to dry habitats (Mizsei et al.
133 2020; Vacheva et al. 2020).

134 *Sampling design*

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

140 To create a random sampling design, we generated a 25 \times 25 m grid for each study site. To
141 avoid the possible selection of neighbouring sampling plots, we removed every second row
142 and column of grid cells (Fig. 1 C). Then we summarised the Sand dropseed records within
143 the grid cells and scaled the numbers to a range between pr = 0-1. Finally, we randomly
144 selected n=8 25 \times 25 m sampling plots at each study site from the grid cells stratified by Sand
145 dropseed presence, to ensure the inclusion of plots with no or low coverage as well as plots
146 with high coverage of the species. Thus, we designated n=48 sampling plots for the six study
147 sites.

148 *Data collection*

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

155 At each plot, we recorded the focal plant-related threats targeted in this study. We estimated
156 the relative cover of the Sand dropseed, the Common milkweed and the woody vegetation.

157 To account for the level of degradation of the vegetation, we determined the naturalness
 158 value of each sampling plot on an ordinal scale from 0 to 1 based on the vegetation's
 159 compositional, structural, and functional diversity. Naturalness-based quality of a habitat was
 160 developed along with the vegetation classification system in Hungary (Bagi et al. 1997). Low
 161 values indicate a degraded natural state characterised by lower species richness and
 162 homogenised structure, while high values indicate near-complete species composition typical
 163 for the habitat type, and high ecological functioning (Bagi et al. 1997; Horváth et al. 2008;
 164 Illyés et al. 2008).

165 To account for reptile detectability during the surveys, we used the data from an automated
 166 meteorological station collecting operative temperature data cc. 20 km from the study sites.
 167 Operative temperature is the environmental temperature that is available to an individual of
 168 an ectotherm species at the given time frame (Kearney and Porter 2020; Falaschi 2021).
 169 Thermoregulatory conditions, which influence a reptile's activity and thus its detectability,
 170 strongly depend on this variable. The temperature data were collected at two-minute intervals
 171 from eight thermometers (BTP-06 temperature sensors connected to a BEL-06 ecologger
 172 unit, Boreas Ltd., Hungary), four exposed to full sun and four placed in the shade of
 173 vegetation (Mizsei et al. 2023).

174 *Statistical analysis*

175 To assess the influence of vegetation-related variables on reptile abundance, we applied
 176 single-visit n-mixture abundance models (Sólymos et al. 2012; Sólymos and Lele 2016). N-
 177 mixture models are particularly useful for studying species with imperfect or low
 178 detectability, as they explicitly account for detection probability (p), thereby reducing bias in
 179 abundance estimates (Madsen and Royle 2023). We fitted separate models for the two lizard
 180 species with the same formula. The sum of reptile detections per survey (one survey per
 181 sampling plot) was used as the dependent variable. Explanatory variables for latent
 182 abundance (abundance submodel) included the cover of Sand dropseed, Milkweed, woody
 183 plants, and naturalness, while the mean operative temperature during the survey and the
 184 number of surveyors (survey effort) were included as explanatory variables for detection
 185 (detection submodel). In the models, we did not differentiate between the age and sex of
 186 individuals. All explanatory variables were scaled to a 0 mean and a standard deviation of 1.
 187 On the global model including all variables, we performed a step selection to identify the
 188 most parsimonious candidate models based on an information-theoretic framework based on

189 the Akaike Information Criterion (AIC; Burnham and Anderson 2002). To fit the models, we
 190 used the ‘detect’ package (Sólymos et al. 2023) in R 4.4.2 (R Core Team 2024).

191 **Results**

192 The habitat features of the sampling plots showed a mean naturalness of 0.58 ± 0.04 (\pm SE).
 193 The Sand dropseed (*Sporobolus cryptandrus*) was detected in 75% of the sampling plots
 194 ($n=36$) with a mean cover of $25.5 \pm 4.8\%$ (\pm SE), the Common milkweed (*Asclepias syriaca*)
 195 was present in 31% of the sampling plots ($n=15$) with a mean cover of $12.6 \pm 2.9\%$ (\pm SE), and
 196 we observed encroachment of woody vegetation in 62.5 % of the sampling plots ($n=30$) with
 197 a mean cover of $9.0 \pm 1.7\%$ (\pm SE).

198 We observed $n=56$ Balkan wall lizard (*Podarcis tauricus*) and $n=28$ Eastern green lizard
 199 (*Lacerta viridis*) individuals during the surveys ($n=48$). The Balkan wall lizard was detected
 200 in 62 % ($n=30$) of the sampling plots, and the Eastern green lizard in 37.5 % ($n=18$).

201 The model selection for the abundance and detectability of the Balkan wall lizard revealed
 202 that the most parsimonious model included operative temperature for detectability,
 203 naturalness, Sand dropseed cover, and Common milkweed cover for abundance (Table 1).
 204 Operative temperature showed a marginally significant positive influence on the detectability
 205 of Balkan wall lizards (Table 1). Sand dropseed cover showed a significant negative effect on
 206 abundance, while Common milkweed showed a non-significant positive influence (Table 1,
 207 Fig. 2). The mean detection probability of the Balkan wall lizard was 0.82 (95 % confidence
 208 interval, CI: 0.58–0.91). The estimated mean density for the sampling plots was 48.5
 209 individuals/ha (CI: 11.5–78.5 individuals/ha).

210 The most parsimonious model for abundance and detectability of the Eastern green lizard
 211 included the survey effort in the detection submodel, and woody encroachment and
 212 naturalness in the abundance submodel (Table 1). Survey effort showed a non-significant
 213 positive effect on detectability; for abundance, woody encroachment showed a significant
 214 positive influence while naturalness had a non-significant positive effect on abundance
 215 (Table 1, Fig. 2). The mean detection probability of the Eastern green lizard was 0.51 (CI:
 216 0.28–0.77). The estimated mean density for the sampling plots was 11.2 individuals/ha (CI:
 217 3.1–26.5 individuals/ha).

218 **Discussion**

219 Reptiles usually strongly depend on the structural features of vegetation when selecting a
220 habitat (Doherty et al. 2020; Mizsei et al. 2020, 2024). Our results suggest that the abundance
221 of the open grassland specialist Balkan wall lizard was negatively influenced by the cover of
222 the invasive Sand dropseed, while the abundance of the Eastern green lizard was not affected
223 by the cover of invasive plants, however, it was positively influenced by the encroachment of
224 woody vegetation. The results highlight that an explosively spreading exotic plant or
225 alteration of vegetation structure by succession can influence native communities within a
226 short period.

227 Changes in vegetation that alter structural features are likely to influence reptile populations
228 (Howland et al. 2014; Cosendey et al. 2019; Mizsei et al. 2020; M3r3e et al. 2024). Our results
229 align with findings of other studies, which show that the impact of invasive plants on reptiles
230 is not always negative (Martin and Murray 2011; Stelatelli et al. 2013; Gray and Steidl
231 2015). The Common milkweed did not affect the two reptiles we surveyed, and the Sand
232 dropseed did not influence the generalist Eastern green lizard. Encroachment of woody
233 vegetation usually strongly impacts species specialised for treeless habitats (Ratajczak et al.
234 2012), however, in our survey, we did not detect a negative impact of woody plant
235 encroachment on the Balkan wall lizard. On the other hand, our results showed a positive
236 effect of encroachment on the generalist Eastern green lizard, which prefers shrubby
237 grassland and forest steppe mosaics (Heltai et al. 2015).

238 The two main plant-related influential habitat features we identified were the cover of the
239 invasive Sand dropseed and the encroachment by native woody vegetation. In the case of the
240 Balkan wall lizard, the negative effect of the Sand dropseed cover can be explained by two
241 key mechanisms: changes of habitat structure and alteration of the trophic network. On open
242 sand steppes, the Sand dropseed invasion alters the microhabitat structure and the community
243 composition (Kr3el-Dulay et al. 2024). Firstly, the mono-dominant patches of Sand dropseed
244 exhibit lower structural heterogeneity compared to native open sand grassland communities.
245 This may decrease thermal landscape heterogeneity and influence the availability of shelters
246 from predators, both crucial in the ecology of lizards (Carter et al. 2015; Bateman and Riddle
247 2020). Secondly, the more homogenous and non-native vegetation supports lower arthropod
248 diversity and abundance, limiting prey availability and reducing the carrying capacity of the
249 habitats (van Hengstum et al. 2014; Kajzer-Bonk et al. 2016; Cornelis et al. 2023). However,
250 further investigations are needed to assess differences among microhabitats provided by
251 native grass species and the Sand dropseed.

252 This study aimed to provide a rapid assessment of whether native reptiles are threatened by a
253 new invader, the non-native sand dropseed. Consequently, the sampling design prioritised
254 speed over comprehensiveness and therefore involved several limitations. First, survey plots
255 were stratified to span the observed range of sand dropseed cover, which may have resulted
256 in an underrepresentation of other plant-related threats such as common milkweed and woody
257 encroachment. Further stratification based on these variables could yield more robust
258 estimates of their effects. This likely explains the absence of a significant detected impact of
259 shrub encroachment on the abundance of the Balkan wall lizard, which contradicts field
260 observations suggesting that this species tends to avoid woody vegetation. Second, the study
261 was limited in spatial replication, with only six sites and eight sampling plots per site, and
262 used a relatively small spatial scale (25 × 25 m). Third, naturalness was estimated based on
263 the subjective field experience of the surveyors, which may restrict the reproducibility of this
264 variable across other habitat types. Increasing the sample size, expanding the spatial scale,
265 and including additional sites could improve the reliability of parameter estimates. Finally,
266 the surveys lacked temporal replication. Conducting repeat surveys within a season would
267 help to refine abundance estimates and assess short-term variability, while extending
268 monitoring across multiple seasons or years could reveal longer-term trends and improve our
269 understanding of how plant-related threats influence reptile populations.

270 The explosive spread of Sand dropseed and its threat to grasslands draw attention to the need
271 for effective strategies against new invaders. Based on its widespread presence gained in a
272 few years, total eradication is unrealistic, thus, other aims could be targeted. Detailed
273 mapping and monitoring of the Sand dropseed colonies are needed to determine the patterns
274 and drivers of its invasion and predict future spread to develop preventive management
275 strategies. In the case of intact grasslands or high-density populations of Sand dropseed, the
276 prevention of further spread could be done by blocking dirt roads and minimising traffic, as
277 Sand dropseed mostly spreads along sandy dirt roads carried by vehicles (Kröel-Dulay et al.
278 2024). Founder plant individuals and small populations could be eradicated manually, while
279 in large populations, management methods (e.g. grazing, mowing, burning, chemical
280 treatment and their combinations) should be tested soon, as despite recent attempts, the
281 effective methods to control Sand dropseed are still not identified. Uncontrolled spread of this
282 invasive plant may have a detrimental effect on the unique steppe fauna and flora of the
283 Central European sandy grasslands.

284 **Conclusion**

285 Our study highlights significant species-specific responses of reptiles to invasive plants and
286 habitat changes in the sand steppes of Hungary. The Balkan wall lizard responds negatively
287 to the non-native invasive Sand dropseed; its abundance decreases in the presence of this
288 plant, likely due to alterations in habitat structure and reduced prey availability. On the other
289 hand, the Eastern green lizard is indifferent to the presence of the Sand dropseed and benefits
290 from the encroachment of native woody vegetation, suggesting a preference for structurally
291 more diverse habitats. These findings emphasise the complexity of ecological interactions
292 and the need for targeted conservation strategies that consider the specific needs of and
293 threats to particular species. Given the rapid spread and ecological impact of Sand dropseed,
294 effective management practices are urgently needed to mitigate its effects and preserve the
295 biodiversity of these unique grassland ecosystems.

296

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301

302 **Additional information**

303 *Conflict of interest*

304 The authors have declared that no competing interests exist.

305 *Ethical statement*

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311 *CRedit authorship contribution statement*

312 Edvárd Mizsei: Conceptualisation, Investigation, Formal analysis, Visualisation, Writing -
313 Original Draft, Writing - Review & Editing. Csongor Adorjáni: Conceptualisation,
314 Investigation, Writing - Review & Editing. Barnabás Bancsik: Investigation, Writing -
315 Review & Editing. Gergő Kovács: Investigation, Writing - Review & Editing. Gergő Rák:
316 Conceptualisation, Investigation, Writing - Review & Editing. Gergely Babocsay:
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327 *Data availability*

328 Data and R code files related to this study are available at the Zenodo repository
329 (<https://doi.org/10.5281/zenodo.15471556>).

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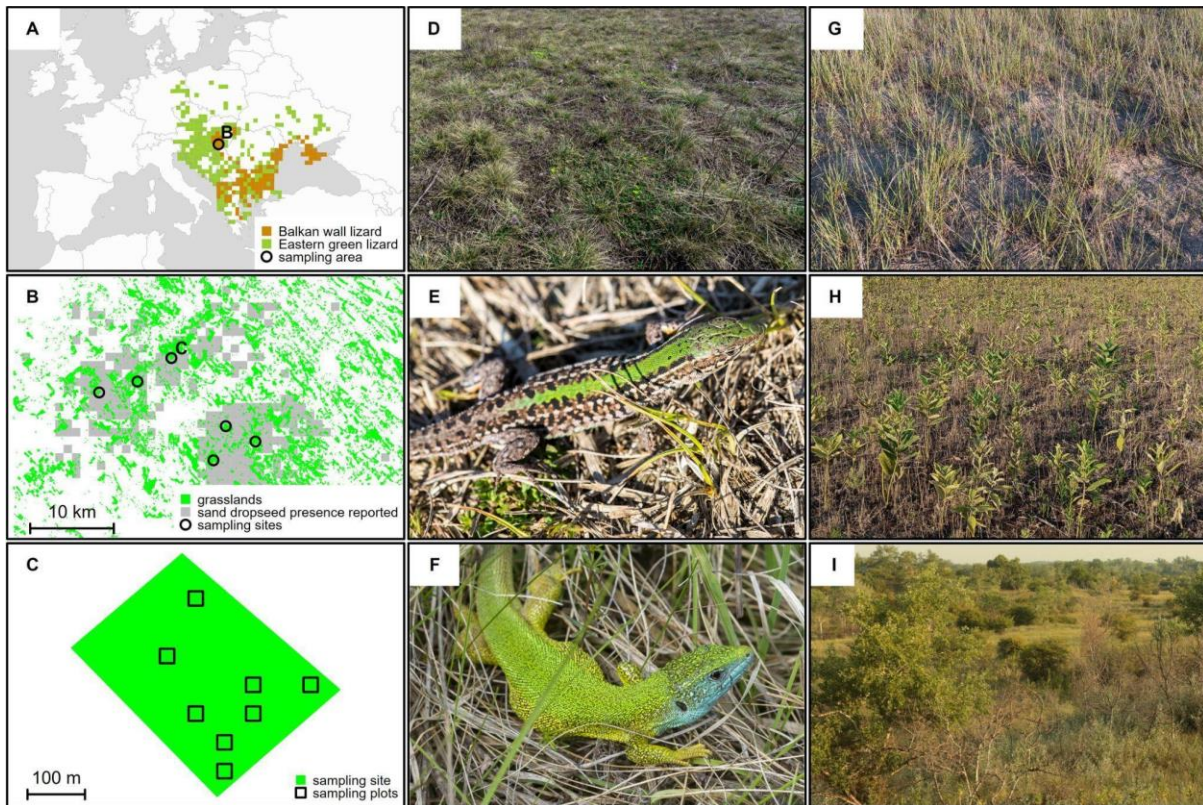
608 Tables

609 **Table 1.** Coefficient estimates for detectability (logit link) and abundance (log link) of the
 610 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 Common milkweed cover	-0.5828	0.2176	-2.6789	0.0074
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 naturalness	0.4979	0.153	3.2541	0.0011

611

612 Figures

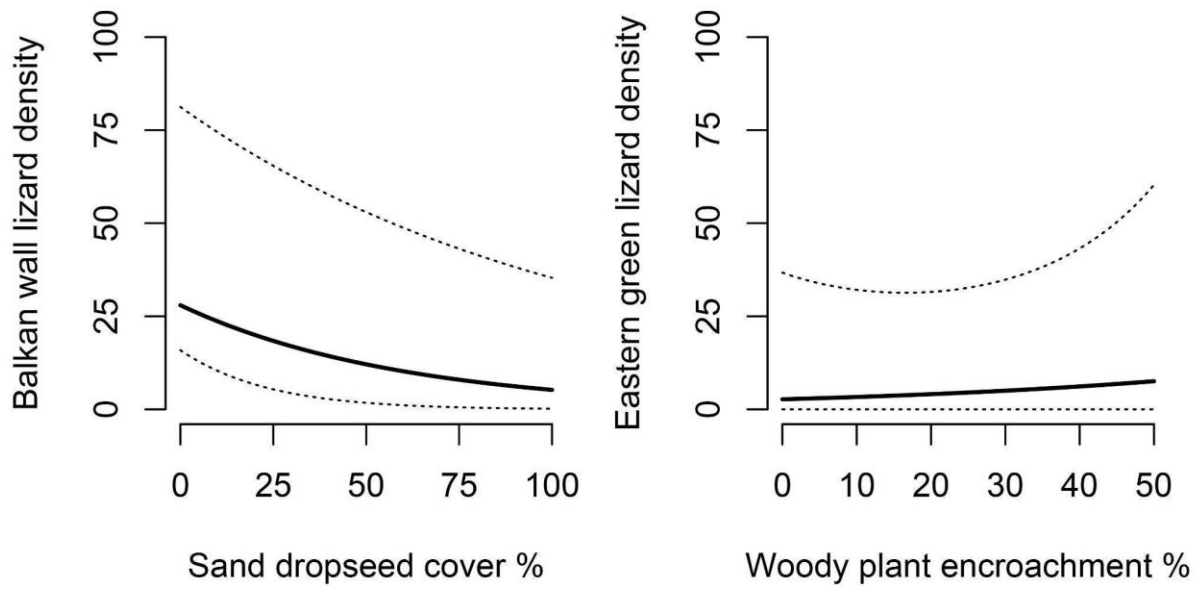


613

614 **Figure 1.** Distribution of the studied lizard species (modified from Sillero et al. 2014) and the
 615 location of the sampling area (panel A), location of the sampling sites (panel B) and an
 616 example of random sampling plots at one of the sampling sites (panel C). Examples for the
 617 surveyed grassland habitats, D: high nature value open sand steppe without invasive plant
 618 species, G: Sand dropseed dominated grassland, H: Common milkweed dominated grassland,
 619 I: encroachment of woody vegetation. Representative individuals of the studied lizard
 620 species: Balkan wall lizard (panel E), Eastern green lizard (panel F). Pictures D-H by E.
 621 Mizsei, I by B. Bancsik.

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624

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