



Reptile responses to vegetation structure in a grassland restored for an endangered snake

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Received: 14 March 2020 / Accepted: 19 June 2020 / Published online: 9 July 2020
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Abstract

Grassland ecosystems are among the most threatened biomes, and their restoration has become common in nature conservation. Yet restoration is rarely applied specifically for reptiles, which are among the most threatened vertebrates. The Meadow Viper (*Vipera ursinii*) has become extinct in most of lowland Europe, and an endangered subspecies (*Vipera ursinii rakosiensis*) has been a target of habitat restoration and captive breeding in Hungary since 2004. We quantified vegetation properties and the density of reptiles that either spontaneously colonised (three species) or were reintroduced (*V. ursinii*) in a grassland restored specifically for this purpose. We used a fine-scale survey to estimate the cover, and compositional and vertical diversity of the vegetation. We characterised sampling units along three habitat gradients: wetness, openness and grass tussock size. Model selection based on data from replicated counts showed that Green Lizards (*Lacerta viridis*) responded positively to vegetation cover and negatively to tussock area and height, and number of burrows. The Sand Lizard (*Lacerta agilis*) responded positively to vegetation cover, vertical diversity and wetness, and negatively to openness. The Balkan Wall Lizard (*Podarcis tauricus*) responded positively to tussock height and negatively to vegetation cover. Finally, *V. ursinii* responded positively to vegetation cover and tussock height, and negatively to compositional diversity. Our results show the general importance of structural and compositional diversity of vegetation to reptiles. These results suggest that adaptive management should focus on increasing the total cover (for lizards) and the structural diversity of vegetation (for each species) to benefit reptiles in restored grasslands.

Keywords Habitat complexity · Habitat diversity · Habitat selection · Grassland reconstruction · Lacertidae · Viperidae · Latent variable · Conservation · Steppe

The Student Conference on Conservation Science (SCCS) is organized each year in several locations, Tihany at the Lake Balaton in Hungary being one of them. Since 2016, Community Ecology offers a prize at SCCS Tihany for the best presentation in the field of Community Ecology. An independent jury awards the prize that is an invitation to submit a manuscript to the journal. This is the paper of the third SCCS Tihany Awardee, Edvárd Mizsei, from 2018.

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Introduction

Grassland ecosystems are among the most endangered biomes (Habel et al. 2013); for instance, most of the grasslands in Europe have been converted to croplands, tree plantations or built-in areas (Wesche et al. 2016). Human-induced land conversion caused a significant loss, as well as fragmentation and degradation of grassland habitats in Europe, followed by an astounding decline in species diversity and abundance, including local and global extinctions

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(Thomas 1995; Wenzel et al. 2006; Habel et al. 2019). Restoration of altered habitats has recently become a central goal of nature conservation; however, grassland restoration could be in conflict with cropland cultivation because soils below grasslands are usually suitable for crop management (Hölzel et al. 2002; Konvicka et al. 2007). However, the target state aimed by grassland restoration is often defined based on the desired plant species or vegetation, and higher trophic levels are rarely targeted (Woodcock et al. 2008). Consequently, knowledge of the vegetation composition, structure or complexity required for habitat restoration for vertebrate wildlife is rather poor in most cases (Lengyel et al. 2016, 2020).

The success of habitat restoration strongly depends on how the targeted vegetation state is defined and on the availability of knowledge on habitat selection and/or preference of target species or functional groups (Török and Helm 2017). To assess habitat selection by target species, solid data are needed on vegetation. Several methods and variables have been developed and implemented to measure influential properties of the vegetation, which usually depend on the subject habitat or species (Mushinsky and McCoy 2016), e.g. phytomass, plant species cover and composition, number or cover of structure-forming plants (e.g. bushes, tussocks, etc.), leaf area, height of shoots, cover on different vertical levels (Garden et al. 2007; Stumpel and van der Werf 2012; Kacoliris et al. 2010; Benkobi et al. 2000). The most of habitat selection studies focus on vegetation composition, while some characteristics of vegetation structure could be more influential on habitat selection of species of higher trophic levels than composition. These are the characteristics of vegetation structure that can provide the preferred microclimate (e.g. shade), harbour individuals by enhancing camouflage of sit and wait predators, or provide hide cover from predators (e.g. Kacoliris et al. 2010).

Reptiles are among the most threatened vertebrates, with one in five species threatened with extinction. Reptiles are declining globally due to habitat loss and degradation, introduced invasive species, environmental pollution, diseases, unsustainable use and climate change (Gibbons et al. 2000). Local extinctions have become frequent and conservation priorities should be determined and actions should be implemented urgently to reduce extinction rates (Böhm et al. 2013). In Europe, the Meadow Viper (*Vipera ursinii*) is among the most threatened reptiles, because its lowland populations (*Vipera ursinii rakosiensis*, *Vipera ursinii moldavica*) lost almost all their habitats due either to the transformation of the grasslands to croplands or to non-suitable grassland management such as intensive pastures or mown hayfields. *Vipera ursinii rakosiensis* has become extinct in Austria and Bulgaria, and only a few populations remained in Hungary and Romania (Krecsák et al. 2003; Péchy et al. 2015; Mizsei et al. 2018). Since

2004, two nature conservation projects funded mostly by the LIFE-Nature programme of the European Union have been implemented to enhance the long-term conservation of *Vipera ursinii rakosiensis* in Hungary by means of habitat restoration, ex situ breeding, reintroduction of captive-bred individuals to reconstructed sites or restocking declining populations (Péchy et al. 2015). Although habitat restoration is used in reptile conservation (e.g. Péchy et al. 2015; Triska et al. 2016; Michael et al. 2018), little is known on the efficiency of these actions, because of lack of knowledge on preferred vegetation characteristics or due to the lack of effective monitoring (Block et al. 2001; Ruiz-Jaen and Aide 2005; Jellinek et al. 2014).

This study aimed to identify vegetation features that influence the presence–absence and abundance of reptiles in a grassland restored for *Vipera ursinii rakosiensis*. This area was afforested in the 1960s with Black Locust (*Robinia pseudoacacia*) and Black Pine (*Pinus nigra*) and was restored to grassland in the 2010s as a target site for the reintroduction of that endangered snake (Péchy et al. 2015). For a better understanding of habitat selection of reptiles, we conducted a fine-scale survey focusing on both reptile abundances and vegetation characteristics at the target restoration site. We then performed model selection based on generalised linear models to detect compositional and structural features of the vegetation that affect grassland-specialist reptile populations. With this study, we intend to provide information for future grassland restoration efforts in an evidence-based conservation approach.

Materials and methods

The study site is a 16.87-ha restored grassland dedicated for the conservation of *Vipera ursinii rakosiensis* in Kiskunság National Park (central Hungary), in the “Felső-kiskunsági turjánvidék” (HUKN20003) site of the Natura 2000 network, the network of areas protected under conservation directives of the European Union. Grassland restoration was started by the felling of all trees and the removal of stumps and was implemented by sowing the seeds of a limited set of native grass species (e.g. *Stipa capillata*, *Festuca rupicola*, *Dactylis glomerata*) in 2006. The site now hosts over 100 plant species (c. 20% of the regional species pool), most of which colonised the area spontaneously; however, most plant species with limited dispersal ability (e.g. *Iris arenaria*, *Ephedra distachya*) are still absent. Since the restoration, this grassland has been managed by low-intensity grazing by cattle (0.2–0.3 animal units/ha).

Four lizard and three snake species are known to occur at the study site; however, we focused our study on the Sand Lizard (*Lacerta agilis*), the Green Lizard (*Lacerta viridis*), the Balkan Wall Lizard (*Podarcis tauricus*) and the Meadow

Viper (*Vipera ursinii rakosiensis*). The abundance of the Viviparous Lizard (*Zootoca vivipara*) and the Smooth Snake (*Coronella austriaca*) was too low to obtain a meaningful sample size, and the Grass Snake (*Natrix natrix*) was excluded because this species is more typical in or near wetlands than in grasslands. The three included lizard species have spontaneously colonised the study site from the neighbouring primary grasslands after the restoration, while the viper population was established by reintroduction. In 2010, 31 captive-bred individuals were released at the site, and 141 captive-bred individuals were released in the following years between 2011 and 2015 (Péchy et al. 2015). Observations of older, unregistered vipers that could not possibly be the offspring of the released individuals suggested that vipers from the native population in neighbouring areas have also colonised the study site.

We estimated the abundance of the studied reptile species by a systematic survey replicated along a 4-km-long transect during April and May of 2018. All grid cells covering the study site (see below) were surveyed 17 times, between 0830 and 1130 AM and 1500–1800 PM. Due to the limits of visual detection, reptiles were detected and recorded in a belt covering 2 m on both sides of the central line of the transect (i.e. a 4-m-wide belt represented the transect). Surveys were done by a single observer (ZF) to minimise observer bias (Bailey et al. 2004; Fitzpatrick et al. 2009). Point occurrence data were recorded by a Spectra Mobile-apper 20 handheld GPS unit for each reptile observation. Occurrence data were summed up for each grid cell for each species, and total counts were used as a proxy of abundance, as counts are good predictors of abundance (Norvell et al. 2003; Kéry 2008). During the data collection, very few individuals of *Vipera ursinii rakosiensis* were observed due to its rarity; thus, we included further records of this species sampling times of other surveys conducted in 2018 (see acknowledgements).

For characterising the fine-scale vegetation structure, we split the whole study site into 25 × 25 m grid cells, resulting in 324 cells in total. Grid cells located at the border were cut according to the shape of the study site. Grid cells with small extent were omitted from further analyses; therefore, 274 cells were included in the study. We estimated the cover of 30 vegetation parameters on an ordinal scale for each grid cell between 22 March and 10 April 2018 (Table 1). We calculated *total vegetation cover* and *compositional diversity* of vegetation by the Shannon index of surveyed plant species' cover (Table 1) using the vegan R package (Oksanen et al. 2018). To assess *vertical diversity*, first, we summed up the vegetation cover on four vertical groups and calculated the Shannon index in each cell (Table 1). Furthermore, we searched for underlying factors by reducing 22 plant cover variables to four *latent variables* (inferred from the cover estimates) by a Bayesian ordination approach using the boral

package to reduce variance inflation arising from multicollinearity in the modelling (Hui 2018). Based on the relation of latent variables to the original vegetation variables, we interpreted the latent variables as gradients of “dry to wet vegetation” (LV1), “large to small tussocks” (LV2), “short to tall tussocks” (LV3) and “closed to open vegetation” (LV4) (Table 1). Finally, we counted the potential keystone structures in the surveyed cells (e.g. bare soil ground, logs, twig piles) and burrows made by animals (e.g. ground squirrels) (Table 1).

We assessed the effect of vegetation features on reptiles' fine-scale occurrence (presence–absence), by using generalised linear mixed-effect models (glmm) using the lme4 package (Bates et al. 2015). We built glmms separately for each species by specifying binomial error distribution, with presence–absence as a binary dependent variable, and vegetation variables as explanatory variables. Cell id was used as random factor to control for spatial non-independence. To find the best set of explanatory variables for each species, we used a model selection approach to identify models with substantial empirical support based on Akaike differences ($\Delta i = \text{AIC}_i - \text{AIC}_{\min} < 2.0$) in an information-theoretic framework (Burnham and Anderson 2002). We then performed model averaging of the best models for each reptile species using the MuMIn package (Bartoń 2019).

To assess the effect of vegetation features on reptiles' abundance, we built generalised linear models for multivariate abundance data (manyglm) for each species separately, specifying a negative-binomial error distribution and log link with unknown overdispersion parameter using the mvabund package (Wang et al. 2019). In manyglms, species abundance was the dependent variable and explanatory variables were the same set for each species as identified by the model selection of glmms.

All statistics presented here were calculated in R 3.6.1 (R Core Team 2019). R scripts are available upon request from the corresponding author.

Results

We counted 484 reptile individuals (279 *Lacerta viridis*, 99 *Lacerta agilis*, 89 *Podarcis tauricus*, 17 *Vipera ursinii*) during our sampling. *L. viridis* was present in 43.4% of cells ($N = 274$ cells), *L. agilis* in 17.1%, *P. tauricus* in 23% and *V. ursinii* in 4.7%. The maximum observed abundance of each reptile species was: 13 individuals of *L. viridis*, 8 of *L. agilis*, 4 of *P. tauricus* and 3 of *V. ursinii*. Based on the occupied cells only, the density of *L. viridis* was 37.6 ± 2.98 individual/hectare (mean \pm SE), *L. agilis* was 33.7 ± 3.52 , *P. tauricus* was 22.6 ± 1.56 and *V. ursinii* was 20.9 ± 2.79 .

Model selection results showed that the presence–absence and abundance of reptiles were influenced by different sets

Table 1 Fine-scale vegetation and habitat variables mapped in 25×25 m grid cells, and the use of original variables to derive variables for modelling

| Original variable | Subgroup | Type | Mean (range) | Derived variables | | | | | |
|-------------------------------|---------------|----------|---------------|--------------------------|---------------------------------|-------------------------|---------------------|-----------------------|-------------------|
| | | | | Veg- etation cover | Compo- sitional diversity | Structural diversity | Latent variables | Keystone structure | Animal burrows |
| Bare ground | Ground | Cover | 9.86 (0–25) | | | + | | | |
| Mosses | Ground | Cover | 9.91 (0–35) | | | + | | | |
| Plant rosettes | | Cover | 1.71 (0–10) | + | + | + | | | |
| Overall vegetation | Ground | Cover | 74.1 (50–100) | | | + | | | |
| <i>Onosis spinosa</i> | | Count | 4.05 (0–50) | + | + | + | | | |
| Bushes | Low height | Count | 5.28 (0–90) | | | + | | | |
| | Medium height | Count | 6.44 (0–100) | | | + | | | |
| | High height | Count | 0.29 (0–15) | | | + | | | |
| Non-tussocky vegetation | Low height | Cover | 18.0 (0–70) | + | + | + | + | | |
| | Medium height | Cover | 2.78 (0–50) | + | + | + | + | | |
| | High height | Cover | 1.23 (0–50) | + | + | + | + | | |
| <i>Cynodon dactylon</i> | Low height | Cover | 1.86 (0–25) | + | + | + | + | | |
| | Medium height | Cover | 6.64 (0–50) | + | + | + | + | | |
| | High height | Cover | 6.75 (0–50) | + | + | + | + | | |
| <i>Chrysopogon gryllus</i> | Low height | Cover | 0.12 (0–10) | + | + | + | + | | |
| | Medium height | Cover | 1.35 (0–25) | + | + | + | + | | |
| | High height | Cover | 2.97 (0–50) | + | + | + | + | | |
| <i>Deschampsia caespitosa</i> | Low height | Cover | 0 (0–0) | + | | | | | |
| | Medium height | Cover | 0.28 (0–30) | + | + | + | + | | |
| | High height | Cover | 0.59 (0–15) | + | + | + | + | | |
| <i>Stipa capillata</i> | Low height | Cover | 2.83 (0–15) | + | + | + | + | | |
| | Medium height | Cover | 0.13 (0–15) | + | + | + | + | | |
| | High height | Cover | 11.1 (0–60) | + | + | + | + | | |
| <i>Festuca</i> spp. | Low height | Cover | 2.11 (0–25) | + | + | + | + | | |
| | Medium height | Cover | 4.55 (0–50) | + | + | + | + | | |
| | High height | Cover | 0.15 (0–25) | + | + | + | + | | |
| <i>Calamagrostis epigeios</i> | Low height | Cover | 0 (0–0) | + | | | | | |
| | Medium height | Cover | 0.00 (0–1) | + | + | + | + | | |
| | High height | Cover | 1.84 (0–75) | + | + | + | + | | |
| <i>Bothriochloa ischaemum</i> | Low height | Cover | 0 (0–0) | + | | | | | |
| | Medium height | Cover | 0.71 (0–25) | + | + | + | + | | |
| | High height | Cover | 5.63 (0–50) | + | + | + | + | | |
| <i>Holoschoenus romanus</i> | Low height | Cover | 0 (0–0) | + | | | | | |
| | Medium height | Cover | 0 (0–0) | + | | | | | |
| | High height | Cover | 0.13 (0–5) | + | + | + | + | | |
| <i>Molinia caerulea</i> | Low height | Cover | 0 (0–0) | + | | | | | |
| | Medium height | Cover | 0 (0–0) | + | | | | | |
| | High height | Cover | 0.39 (0–20) | + | + | + | + | | |
| Arthropod burrows | | Count | 5.92 (0–40) | | | | | | + |
| Small rodent burrows | | Count | 4.73 (0–50) | | | | | | + |
| Ground squirrel burrows | | Count | 0.10 (0–3) | | | | | | + |
| Artificial burrows | | Count | 0.06 (0–3) | | | | | | + |
| Mole hills | | Count | 8.86 (0–100) | | | | | + | |
| Steppe mouse hills | | Count | 0.34 (0–3) | | | | | + | |
| Logs | | Count | 7.61 (0–95) | | | | | + | |
| | | Diameter | 4.47 (0–25) | | | | | + | |

Table 1 (continued)

| Original variable | Subgroup | Type | Mean (range) | Derived variables | | | | | |
|-------------------|----------|-------|--------------|--------------------------|---------------------------------|-------------------------|---------------------|-----------------------|-------------------|
| | | | | Veg- etation cover | Compo- sitional diversity | Structural diversity | Latent variables | Keystone structure | Animal burrows |
| Twig piles | | Count | 0.10 (0–2) | | | | | + | |
| Soil tussocks | | Count | 1.77 (0–40) | | | | | + | |
| Soil digging | | Count | 0.87 (0–25) | | | | | + | |
| | | Cover | 0.32 (0–20) | | | | | + | |

of explanatory variables (Table 2). The presence of *L. viridis* was positively influenced by vegetation cover and LV2 “large to small tussocks”, and its abundance was positively affected by LV2 “large to small tussocks”, and negatively by LV3 “short to tall tussocks” and burrows. The presence–absence of *L. agilis* was negatively influenced by LV4 “closed to open vegetation”, and its abundance was positively influenced by vegetation cover, vertical diversity, LV1 “dry to wet vegetation” and negatively by LV4 “close to open vegetation”. The presence–absence of *P. tauricus* was negatively affected by vegetation cover, and positively by LV3 “short to tall tussocks”, and its abundance was also positively affected by LV3 “short to tall tussocks”. Finally, the presence–absence of *V. ursinii* was positively affected by vertical diversity and negatively by compositional diversity, while its abundance was positively influenced by vertical diversity and LV3 “short to tall tussocks”, and negatively by compositional diversity (Table 2).

The predictions of presence–absence glmms and abundance manyglms were very similar, the values predicted by the two models strongly correlated in each species (*L. viridis* $r^2=0.74$, *L. agilis* $r^2=0.98$, *P. tauricus* $r^2=0.94$, *V. ursinii* $r^2=0.92$; $P<0.0001$ in each species; Fig. 1). The spatial pattern of predicted abundance fitted well to the point observations of the studied reptiles, except for the rare *V. ursinii* (Fig. 2).

Discussion

Our study of restored grasslands provided evidence that reptiles are able to spontaneously colonise the restored grassland if there is a spatial connection to potential source populations. Our previous observations show that the observed abundances of the species were not lower than in other sites in the region, including the reintroduced *V. ursinii*.

Our study revealed the importance of structural and compositional features of the vegetation to grassland-dwelling reptiles. Our results showed that the physical structure of the vegetation (height, cover, tussocks) was more important than floral composition in shaping the small-scale

spatial distribution of the studied reptile species. The presence–absence and abundance of reptiles mostly depended on total vegetation cover and several variables describing vegetation structure such as tussocks height. We found that the horizontal composition of vegetation was important only for *V. ursinii*. This information is central in habitat restorations, where the target state should be defined based on the habitat preference of each target species. Our study also shows that habitat restorations should target the vegetation structure that is most likely to benefit all species (Lengyel et al. 2020). Restoration of vegetation structure may be achieved in a more economic way compared to vegetation composition or plant species richness, which is usually expensive in case of target state of primary grasslands (cultivating/collecting seeds, producing high-diversity seed mixtures, soil preparation, sowing, etc.; Török et al. 2011).

Many studies showed that the studied *Lacerta* species are present in a wide range of habitats; however, there is surprisingly limited information about the fine-scale (microhabitat-level) requirements and preference of the studied species. The general view on the habitat of *L. viridis* is that it consists of grasslands interspersed with bushes, trees, particularly containing edges and ecotones between grassland and forest (Heltai et al. 2015). The thermal quality of the microhabitat is also known to influence habitat selection (Korsós 1982). Kovács and Kiss (2016) found that the number and availability of burrow play a more important role than the naturalness of habitats. Contrary to these studies, our results show that *L. viridis* was more abundant in cells characterised by less tussocky vegetation and low burrow numbers. Previous works on the habitat selection of *L. agilis* suggested the importance of soil type and wetness (Covaciu-Marcov et al. 2006), burrow availability (Török 2002), and a preference to open, bush- and treeless habitats (Nemes et al. 2006; Heltai et al. 2015). In our study, we found no evidence of the effect of burrow numbers on abundance on *L. agilis*, but we detected a preference to open and wet vegetation, characterised by high cover and vertical diversity. The few studies on habitat choice in *P. tauricus* showed a preference to open and short grass, and the species was also found in disturbed and polluted habitats (Kati et al. 2007; Covaciu-Marcov

Table 2 Parameter estimates of models. Significant ($P < 0.05$) parameter estimates are highlighted in bold letters

| | | Presence–absence | | Abundance | |
|--------------------------|---------------------------------|--------------------------------------|--------------|--------------------------------------|--------------|
| | | glmm | | manyglm | |
| | | Estimate \pm SE | P | Estimate \pm SE | P |
| <i>Lacerta viridis</i> | (Intercept) | -3.249 \pm 1.109 | 0.003 | -2.816 \pm 1.059 | 0.009 |
| | Total vegetation cover | 0.014 \pm 0.007 | 0.042 | -0.002 \pm 0.007 | 0.797 |
| | Compositional diversity | 0.466 \pm 0.443 | 0.294 | 0.362 \pm 0.492 | 0.435 |
| | Vertical diversity | 1.829 \pm 1.033 | 0.078 | 2.288 \pm 1.136 | 0.063 |
| | LV1 “dry to wet vegetation” | 0.241 \pm 0.163 | 0.142 | 0.192 \pm 0.175 | 0.262 |
| | LV2 “large to small tussocks” | 0.274 \pm 0.131 | 0.036 | 0.638 \pm 0.142 | 0.001 |
| | LV3 “short to tall tussocks” | -0.16 \pm 0.149 | 0.284 | -0.364 \pm 0.161 | 0.032 |
| | Key stone structures | 0.317 \pm 0.296 | 0.287 | 0.578 \pm 0.314 | 0.093 |
| | Burrow availability | -0.006 \pm 0.005 | 0.245 | -0.019 \pm 0.006 | 0.001 |
| <i>Lacerta agilis</i> | (Intercept) | -8.695 \pm 2.641 | 0.001 | -12.064 \pm 2.579 | 0.001 |
| | Total vegetation cover | 0.03 \pm 0.012 | 0.018 | 0.034 \pm 0.013 | 0.011 |
| | Vertical diversity | 3.874 \pm 2.075 | 0.063 | 6.089 \pm 2.135 | 0.007 |
| | LV1 “dry to wet vegetation” | 0.388 \pm 0.246 | 0.116 | 0.83 \pm 0.288 | 0.002 |
| | LV2 “large to small tussocks” | -0.144 \pm 0.233 | 0.541 | -0.269 \pm 0.244 | 0.311 |
| | LV4 “closed to open vegetation” | -0.73 \pm 0.254 | 0.004 | -1.052 \pm 0.271 | 0.002 |
| | Burrow availability | -0.011 \pm 0.009 | 0.301 | 0.005 \pm 0.009 | 0.631 |
| | (Intercept) | 1.983 \pm 1.534 | 0.198 | 2.859 \pm 1.617 | 0.081 |
| | Total vegetation cover | -0.023 \pm 0.011 | 0.043 | -0.02 \pm 0.013 | 0.135 |
| <i>Podarcis tauricus</i> | Compositional diversity | 0.759 \pm 0.674 | 0.262 | 0.541 \pm 0.669 | 0.432 |
| | Vertical diversity | -2.492 \pm 1.347 | 0.065 | -2.977 \pm 1.573 | 0.074 |
| | LV1 “dry to wet vegetation” | -0.234 \pm 0.252 | 0.355 | -0.297 \pm 0.242 | 0.229 |
| | LV2 “large to small tussocks” | -0.227 \pm 0.175 | 0.197 | -0.268 \pm 0.188 | 0.163 |
| | LV3 “short to tall tussocks” | 0.392 \pm 0.196 | 0.046 | 0.492 \pm 0.219 | 0.029 |
| | LV4 “closed to open vegetation” | 0.343 \pm 0.232 | 0.141 | 0.361 \pm 0.238 | 0.121 |
| | Key stone structures | -0.393 \pm 0.472 | 0.407 | -0.612 \pm 0.477 | 0.205 |
| | (Intercept) | -8.917 \pm 3.785 | 0.019 | -10.534 \pm 4.863 | 0.049 |
| | Total vegetation cover | 0.018 \pm 0.019 | 0.366 | -0.002 \pm 0.027 | 0.924 |
| <i>Vipera ursinii</i> | Compositional diversity | -2.984 \pm 1.366 | 0.031 | -4.467 \pm 1.664 | 0.013 |
| | Vertical diversity | 7.97 \pm 3.743 | 0.034 | 11.253 \pm 4.417 | 0.017 |
| | LV1 “dry to wet vegetation” | 0.169 \pm 0.449 | 0.709 | 0.27 \pm 0.557 | 0.676 |
| | LV2 “large to small tussocks” | 0.67 \pm 0.458 | 0.145 | 0.349 \pm 0.492 | 0.574 |
| | LV3 “short to tall tussocks” | 0.973 \pm 0.522 | 0.063 | 1.436 \pm 0.641 | 0.039 |
| | LV4 “closed to open vegetation” | -0.251 \pm 0.396 | 0.528 | -0.579 \pm 0.553 | 0.358 |
| | Key stone structures | -1.401 \pm 1.119 | 0.212 | -0.971 \pm 1.171 | 0.469 |
| | Burrow availability | 0.009 \pm 0.011 | 0.425 | 0.008 \pm 0.014 | 0.626 |

et al. 2006). Our results also showed the negative effect of vegetation cover on the presence of *P. tauricus*, and we also found a positive effect of high tussocks on both the presence and abundance of this lizard. The latter can be explained by the presence of tussocks of maidenhair (*Stipa* spp.) on generally open, sandy patches with low vegetation cover. Finally, a previous study on the habitat preference of *V. ursinii* failed to detect any compositional feature of the preferred vegetation (Máté and Vidéki 2007). Our results show that the abundance of this species increased with vertical diversity and presence of high tussocky vegetation, while

the compositional diversity of vegetation negatively affected both its presence and abundance.

A comparison of our results to previous studies shows a diverse set of variables that can influence reptile habitat suitability, including even opposite effects of similar variables. Differences among results for the same species can be explained by four main reasons: (i) use of different spatial scales (Jorgensen and Demarais 1999; Belmaker et al. 2015), (ii) study of different lineages or locally adapted populations of widespread species (Faulks et al. 2015), (iii) biased dataset or alternative ways of analysis (Merckx et al.

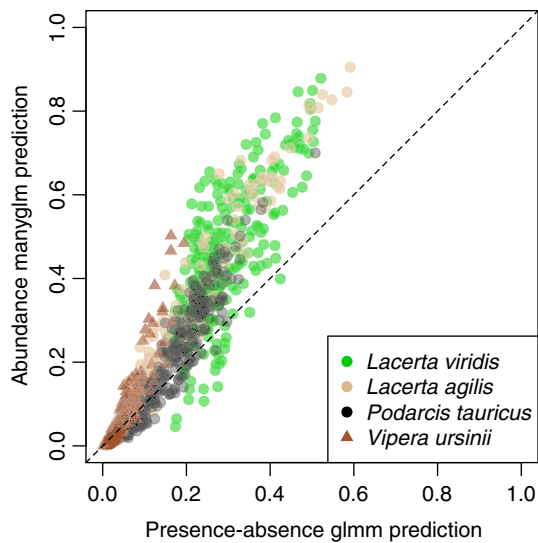
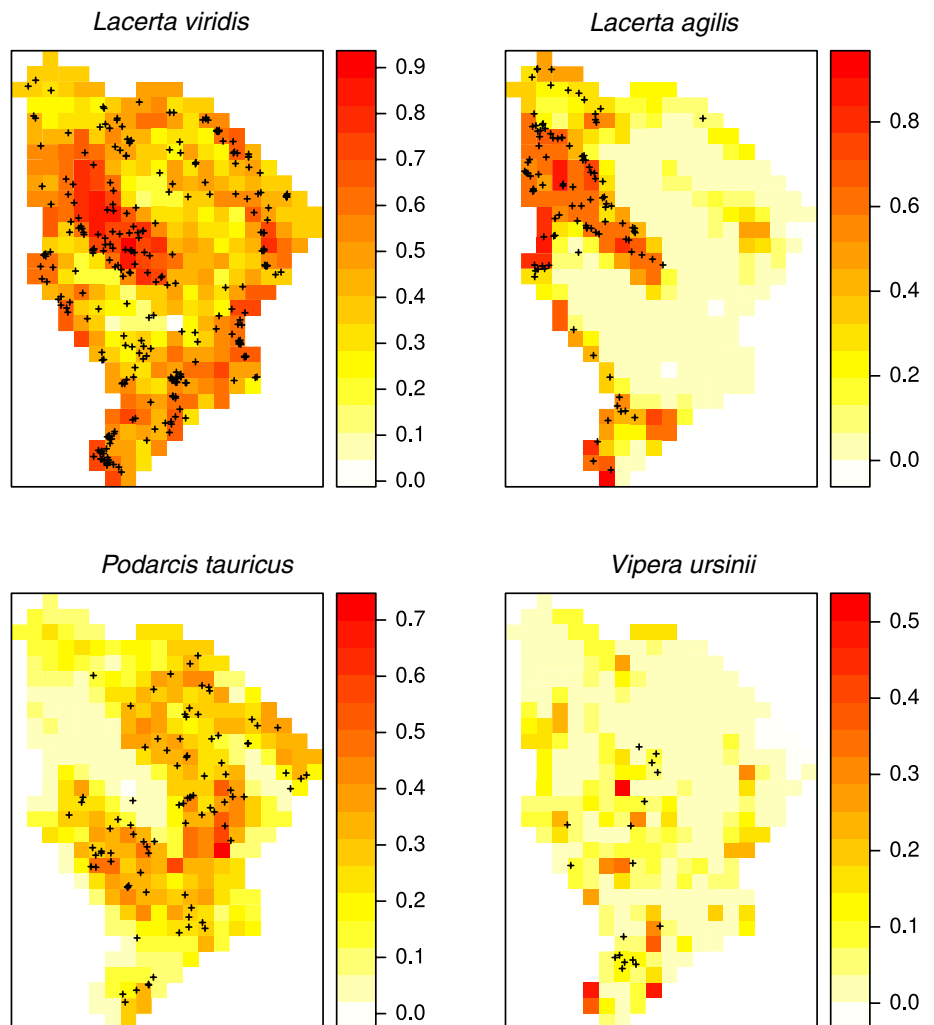


Fig. 1 Predictions of abundance manyglms as function of presence-absence glmms

2011; Bradley et al. 2012), and (iv) insufficient survey effort, including a low number of spatial or temporal replicates (Tyre et al. 2003). A limitation of our study is that *V. ursinii* is a cryptic species with low detectability, and studies based solely on visual observations may be biased as detection probability may be heavily affected by habitat structure. Another limitation of our study is that we surveyed only a single restoration site as this was the only restored site in the area. We thus had no alternative sites to survey to gain spatial replicates; however, we thoroughly sampled the site with a high survey effort to collect abundance data. Furthermore, this was a pilot study to determine the importance and usefulness of tussock-related structural features of the vegetation for planning further research and monitoring of habitat suitability of target-state and restored grasslands.

Our study provides several important inputs to conservation practice. One important lesson is that the floristic composition of the vegetation was much less important than the structure of the vegetation. Consequently, although most restorations aim at the re-establishment of selected target plant species, plant species composition

Fig. 2 Spatial prediction of abundance manyglms and observations made during the surveys



does not have to enjoy priority in restorations that specifically target reptiles. Habitat restoration for reptiles should be designed to facilitate the formation of vegetation structure adequate for the target reptile species. Some features (e.g. tussocks) that are of key importance to reptiles can be formed only by a limited number of plant species; therefore, the colonisation of these species needs to be ensured from neighbouring areas. If there is a barrier to the spontaneous dispersal of these species, colonisation should be assisted by active sowing or planting. In target-state or advanced restored grasslands, habitat management is of central importance to maintain the preferred vegetation structure. Management (by livestock grazing or mowing) should be planned and implemented to shape or to sustain vegetation structure preferred by the target reptile species. Mowing by machines is known to destroy the tussocks (Pech et al. 2015; Tognetti and Chaneton 2015); thus, mowing is not a recommended option for management of reptile habitats in sand grasslands.

In conclusion, vegetation structure variables (cover, vertical diversity) appeared to be better predictors of small-scale occurrence and abundance of grassland-specialist reptiles compared to variables describing vegetation species composition. Tussocks were also found to be important one way or another in three of the four studied species and can be thus considered as keystone structures for reptiles in grasslands. Grassland restoration for reptiles should thus focus mainly on mimicking the vegetation structure preferred by the target species. Grassland management by mowing, grazing and abandonment also influences the vertical structure of vegetation in the short term. Thus, management should also be implemented to enhance vegetation structural diversity. Further studies are necessary to determine the vegetation structure optimal for reptiles in target-state (reference) grasslands and to define appropriate management goals of restored grasslands for the re-establishment and long-term survival of the populations of the target reptile species.

Acknowledgements Open access funding provided by ELKH Centre for Ecological Research. We are grateful to the staff of Kiskunság National Park Directorate and MME BirdLife Hungary, especially to Tamás Péchy and Bálint Halpern for their efforts made to re-establish the Hungarian Meadow Viper at the study site, and to Tibor Somlai for providing additional data. The grassland restoration and the reintroduction programme were financially supported by the European Commission (LIFE04NAT/HU/000116). EM was supported by the ÚNKP-19-3-II-DE-46 New National Excellence Program of the Ministry for Innovation and Technology (Hungary). SL was funded by a Grant from the National Research, Development and Innovation Office of Hungary (GINOP 2.3.3-15-2016-00019).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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