

Automated image processing for quantitative characterization of grassland vegetation structure: microhabitat selection in threatened meadow and steppe vipers

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Abstract

1. Understanding animals' selection of microhabitats is important in both ecology and biodiversity conservation. However, there is no generally accepted methodology for the characterisation of microhabitats, especially for vegetation structure. 2. Here we present a method that objectively characterises vegetation structure by using automated processing of images taken of the vegetation against a whiteboard under standardised conditions. We developed an R script for automatic calculation of four vegetation structure variables derived from raster data stored in the images: leaf area (LA), height of closed vegetation (HCV), maximum height of vegetation (MHC), and foliage height diversity (FHD). 3. We demonstrate the applicability of this method by testing the influence of vegetation structure on the occurrence of three viperid snakes in three grassland ecosystems: *Vipera graeca* in mountain meadows in Albania, *V. renardi* in loess steppes in Ukraine and *V. ursinii* in sand grasslands in Hungary. 4. We found that the variables followed normal distribution and there was minimal correlation between those. Generalized linear mixed models revealed that snake occurrence was positively related to HCV in *V. graeca*, to LA in *V. renardi* and to LA and MHC in *V. ursinii*, and negatively to FHD in *V. renardi*, and to HCV in *V. ursinii*. 5. Our results demonstrate that biologically meaningful vegetation structure variables can be derived from automated image processing. Our method minimises the risk of subjectivity in measuring vegetation structure, allows upscaling if neighbouring pixels are combined, and is suitable for comparison of or extrapolation across different grasslands, vegetation types or ecosystems.

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ABSTRACT

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2. Here we present a method that objectively characterises vegetation structure by using automated processing of images taken of the vegetation against a whiteboard under standardised conditions. We developed an R script for automatic calculation of four vegetation structure variables derived from raster data stored in the images: leaf area (LA), height of closed vegetation (HCV), maximum height of vegetation (MHC), and foliage height diversity (FHD).
3. We demonstrate the applicability of this method by testing the influence of vegetation structure on the occurrence of three viperid snakes in three grassland ecosystems: *Vipera graeca* in mountain meadows in Albania, *V. renardi* in loess steppes in Ukraine and *V. ursinii* in sand grasslands in Hungary.
4. We found that the variables followed normal distribution and there was minimal correlation between those. Generalized linear mixed models revealed that snake occurrence was positively related to HCV in *V. graeca*, to LA in *V. renardi* and to LA and MHC in *V. ursinii*, and negatively to FHD in *V. renardi*, and to HCV in *V. ursinii*.
5. Our results demonstrate that biologically meaningful vegetation structure variables can be derived from automated image processing. Our method minimises the risk of subjectivity in measuring vegetation structure, allows upscaling if neighbouring pixels are combined, and is suitable for comparison of or extrapolation across different grasslands, vegetation types or ecosystems.

KEYWORDS

biodiversity monitoring, ecological complexity, habitat diversity, habitat selection, reptile, Viperidae, visual obstruction reading

INTRODUCTION

Predicting the occurrence or abundance of animals hiding in the vegetation has been one of the earliest challenges for mankind and remains so for many ecologists. Understanding how animals choose microhabitats is a central aim in ecology and is fundamental for evidence-based conservation (Johnson et al., 2014). Habitat selection is a key evolutionary strategy because it both depends on and is influenced by resource availability and interactions with conspecifics and other species. Thus it has inevitable influence on individual fitness, and accordingly the evolution of life-history traits is associated with habitat properties (Morris, 2003). Habitat selection can thus be interpreted to reflect an adaptive strategy on evolutionary time scale optimization (MacArthur et al., 1962; Pianka, 1973), although intraspecific competition and population density may also influence the choice of the individuals (Fretwell & Lucas, 1970; Lawlor & Smith, 1976), and these costs of a particular choice are rarely considered (Rosenzweig, 1981).

The characterisation of microhabitats, however, has proven to be difficult and there is no generally accepted methodology applicable across ecosystems, habitat types and animal groups (Stein et al., 2014). More complex habitats, i.e., those characterized by higher microhabitat diversity, are supposed to sustain a higher

number of ecological niches and species occupying them compared to habitats with decreased structural diversity (MacArthur & MacArthur, 1961; Loke et al., 2015). Habitat or microhabitat diversity is often divided into two components: compositional diversity arises from the identity of different elements, whereas structural diversity arises from the two- or three-dimensional physical arrangement of the elements (Tews et al., 2004; Lengyel et al., 2016). Both aspects can be further subdivided into abiotic components (e.g., composition: soil types, hydrology; structure: elevation, topography) and biotic components (e.g., composition: plant species identity; structure: vegetation complexity). The quantification of abiotic elements and biotic compositional elements is usually straightforward via objective measurements (e.g., for soil types, hydrology: qualitative list of soil types, maps, measurement of groundwater table; for elevation, topography: GPS readings, landform diversity; plant species/association identity: list of species or plant associations). In contrast, a plethora of context-dependent methods have been used to measure vegetation structure (Mushinsky & McCoy, 2016). Several terms have been used for vegetation structure, such as structural complexity/diversity, canopy/foilage height/diversity, vegetation complexity/heterogeneity, architectural complexity (Tews et al., 2004). In studies of animal habitat selection, vegetation structure is often quantified by estimates of phytomass or by cover estimates. Additional methods include quantifying the presence or cover of structures formed by plants, e.g. tussocks, shrubs, dead phytomass such as leaves, height of shoots, leaf area, cover at various heights (Benkobi et al., 2000; Vermeire & Gillen, 2001; Pringle et al., 2003; Garden et al., 2007; Faria & Silva, 2010; Stumpel & van der Werf, 2012; Mizsei et al., 2020a). Many of these methods depend on subjective eyeball estimates made in the field confounded by observer bias and measurement error (Milber et al., 2008; Bergstedt et al., 2009), e.g. on plant cover, or return one value, e.g. vegetation height or phytomass, which, at most, is a proxy for the 3-D physical arrangement or distribution of vegetation elements. All these drawbacks prevent generalisations of animal-vegetation structure relationships across habitats, ecosystems and spatial scales. There is thus a clear need for objective methods that provide balanced measurements on multiple variables including both the horizontal and vertical distribution of vegetation elements and the one-value characteristics that succinctly summarise important aspects of vegetation structure.

Reptiles are among the most threatened vertebrates and decline globally due to habitat loss and degradation, introduced invasive species, environmental pollution, diseases, unsustainable use of natural/seminatural habitats and climate change (Gibbons et al., 2000). By now, one out of five reptile species has become threatened by global extinction, and local extinctions are becoming common. To cope with this, conservation priorities should be determined and actions should be implemented to reduce this rate (Böhm et al., 2013). In Europe, the meadow and steppe vipers (*Vipera ursinii* complex) are among the most threatened reptiles. Lowland populations of this complex (*V. renardi*, *V. u. rakosiensis*, *V. u. moldavica*) lost almost all their habitats due to transformation of grasslands to croplands, and populations in Austria, Bulgaria and Moldova have gone completely extinct (Krecsák et al., 2003; Tupikov & Zinenko, 2015; Mizsei et al., 2018a). Alpine populations are threatened by overgrazing and climate change (Mizsei et al., 2020b). Although habitat restoration is increasingly 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 due to lack of knowledge on vegetation characteristics preferred by target reptiles or due to lack of proper monitoring (Block et al., 2001; Ruiz-Jaen & Aide, 2005; Jellinek et al., 2014; Mizsei et al., 2020b).

Here we present an approach to explore animal-vegetation relationships by objectively characterising vegetation structure by using photography-based standardized field data recording followed by computer-based automated quantification of particular structural attributes of the vegetation. We demonstrate the applicability of this approach in a case study using data collected in grassland habitats of three populations of the threatened *V. ursinii* complex of meadow vipers. While the applied field photography, based on images taken from vegetation against a whiteboard under standard conditions, has been used before, the algorithm-based quantification of vegetation structure, to our knowledge, is novel in the literature. We show that the variables derived from this methodology explain a significant part of the variation in snake occurrence and that the approach can thus be an important part of the repertoire of methods to characterise vegetation structure in studies of animal habitat selection.

MATERIAL AND METHODS

Study species and questions

We studied snake-vegetation relationships in habitats of three species representing the three main phylogenetic lineages of the *V. ursinii* complex (Freitas et al., 2020). *V. graeca* (Nilson & Andr en, 1988) is an endangered species endemic to the Pindos mountains in Albania and Greece, inhabiting dry sub-alpine grasslands above the treeline between 1600 and 2200 m above sea level (Mizsei et al., 2018b). *V. renardi* (Christoph, 1861) is widely distributed in the steppe biome from Ukraine to China, from lowlands to high mountains, and shows high intraspecific genetic diversity (Zinenko et al., 2015). The nominal subspecies *V. r. renardi*, sometimes referred to as “western” or “lowland” *V. renardi* (Nilson & Andr en, 2001; Zinenko et al., 2015) was involved in our study. *V. ursinii* (Bonaparte, 1835) is a vulnerable species endemic to Europe, consisting of three phylogenetically divergent lineages in sub-alpine meadows and two on lowland grasslands (Ferchaud et al., 2012; Mizsei et al., 2017). *V. ursinii rakosiensis* (M ehely, 1893), also known as the Hungarian meadow viper, an endangered lowland subspecies (P echy et al., 2015) was involved in our study. In each study system, we addressed the same three questions: (1) Which variables describing vegetation structure explain the occurrence of particular snake species? (2) Are differences between influential vegetation structure variables related to differences in habitat selection between species? (3) Which variables can be recommended for use in studies of snake habitat selection in grasslands?

Field data collection

Sampling sites were selected in typical viper habitats in Albania (*V. graeca* : Kulmak and Tomorr mountains), Hungary (*V. ursinii* : Pesz radacs meadows) and Ukraine (*V. renardi* : Davydivka steppe) (Fig. 1). We searched for vipers by walking slowly in the designated habitat patches in weather conditions suitable for viper activity. When observing a viper, we recorded the coordinates of the location with standard GPS precision, the time of observation, and the age and sex of the individual. Spatial data on fine-scale location of recorded vipers (hereinafter: points of known viper presence) were collected for several days at each site (*V. graeca* : July 31 to August 12, 2019; *V. renardi* : September 25 to October 2, 2019; *V. ursinii* : September 10 to 15, 2019, and April 19 to May 18, 2020). The number of days spent with field data collection was adjusted to the density of snakes estimated in previous site visits. At the end of each search period, we recorded vegetation structure at all the points of known viper presence. To draw a distinction between the parts of habitats actually used by vipers and the surrounding parts not used by vipers, a minimum convex polygon (MCP) covering the points of known viper presence with a 10 m buffer was drawn. Outside the MCP covering the parts of habitats actually used by vipers randomly selected points were placed (i.e., at least 10 m far from the closest point of known viper presence (hereinafter: random points). The randomly selected points were not in the analyses in case of being placed in areas inaccessible to the surveyor or apparently unsuitable for snakes such as rocky cliffs, water bodies or arable fields. The number of random points was set at five times the number of presence locations.

Quantifying vegetation structure

Vegetation structure was recorded in the field by taking photographs of the vegetation against a whiteboard applying standardised settings. The whiteboard was made of plexiglass of size 0.25 m (width) \times 1 m (height), installed in a vertical position on its shorter edge at all viper presence and random locations. The vegetation against the whiteboard was photographed with a digital SLR camera (55 mm focal length and maximum f/11 aperture) fixed at a height of 0.5 m in a distance of 4 m from the whiteboard (Fig. 2) as in Volesky et al. (1999).

The resulting photographs were pre-processed (cropping, white adjustment, retouching) with the GIMP 2.8.18. image editing software. Next, we applied image processing using an automated *for loop* written in the R statistical environment (version 3.6.1., R Core Team, 2019). The script is available in Supplementary Material (SM). The script first retrieved the images by the ‘load.image’ function of the ‘imager’ package (Barthelme, 2019), converted it to a black and white image by the ‘grayscale’ function, and then to a binary (0-1) image by the ‘threshold’ function of the ‘imager’ package. The resulting image was converted to a data frame using the ‘as.data.frame’ function and the coordinates of every image pixel covering the whiteboard

were calculated (0.25×1 m, average resolution: 1 to 1.5 megapixels image⁻¹). The resulting data frame had three columns for each image, the x and y pixel coordinates (in cm) and the pixel value (0 = white, 1 = black).

We used the data frame to calculate four variables to quantify particular attributes of the vegetation structure. At first, leaf area, referred to as LA hereafter, a frequently used quantity in vegetation characterisation (Volesky, 1999), was calculated as the count of black pixels rescaled to cm² units. At second, we calculated visual obstruction readings (VOR), developed primarily for prairie vegetation based on the Robel pole method (Benkobi et al., 2000; Vermeire & Gillen, 2001). This method takes two readings by eye at a height of 1 m from a distance of 4 m from the pole with height tick-marks: (i) the height at which the pole is first visible, i.e., not obstructed by vegetation (low reading) and (ii) the maximum height reached by the vegetation (high reading). The average of the two readings strongly correlates with prairie phytomass (Benkobi et al., 2000; Vermeire & Gillen, 2001). In our study, we modified the lower reading by calculating the maximum height at which 95% of the whiteboard is mantled by the vegetation, and we refer to this as the height of closed vegetation (HCV) (Fig. 2) to avoid confusion with the VOR reading terminology. We chose 95% as a threshold because glint on some leaves in the image could return white cells and could thus reduce the true coverage. At third, the high reading was calculated as the maximum height of the vegetation (MHV) regardless of its width, cover, or surface area (Fig. 2). Finally, to characterise the vertical distribution of vegetation, we calculated foliage height diversity (FHD) (Karr & Roth, 1971) as the Shannon diversity of the number of black cells in each pixel row using the ‘diversity’ function of the ‘vegan’ package (Oksanen et al., 2019). Calculating FHD from values in each pixel row circumvents the problem of arbitrarily choosing counting intervals, e.g. ten 10-cm height intervals in each of which cover is estimated or measured for the calculation of FHD (MacArthur et al., 1962; Karr & Roth, 1971).

Other variables

We applied further variables that may influence the occurrence of snakes at each site. In *V. graeca* habitats, we estimated the cover of bare rock, grass and shrub surfaces in a circle of 1-m radius around points of viper presence and random points. In *V. renardi* habitats, we recorded the number of rodent burrows in a circle of 1-m radius around points of viper presence and random points as these snakes often use rodent burrows for hiding. In *V. ursinii* habitats, there were no rocks or shrubs, and rodent burrows were rare and not recorded.

Statistical analyses

We analysed whether and how vegetation structure and other characteristics of grassland habitats affect the fine-scale occurrence of snakes by building Generalized Linear Mixed Models (GLMM) separately for each study species. In GLMMs, presence/absence of vipers was incorporated as a binary dependent variable, while the four variables characterising vegetation structure were applied as fixed explanatory variables, with grass/rock/shrub surface cover in *V. graeca* GLMMs and number of burrows in *V. renardi* GLMMs as additional fixed variables. The sampling site was incorporated in the GLMMs as a random factor to control for the spatial non-independence of the observations. We fitted the GLMMs specifying binomial error distribution using the ‘lme4’ package (Bates et al., 2014). We then used an information-theoretic framework and a model selection approach (Burnham & Anderson, 2002) to run all possible combinations of fixed effects to identify models with substantial empirical support based on Akaike differences ($\Delta_i = \text{AIC}_i - \text{AIC}_{\text{min}} < 2.0$) and to perform model averaging based on the relative importance of explanatory variables using the ‘MuMIn’ package in R (Bartoń, 2018).

RESULTS

The number of snakes found (presence locations) varied from 32 to 73 across the three species. *V. graeca* and *V. ursinii* were much rarer locally than *V. renardi*, and the search effort-corrected density was an order of magnitude higher in *V. renardi* than in the other two species (Table 1). Vegetation structure was recorded by white-board photography in a total of 141 presence locations and 726 random locations. Almost half of the pre-randomised locations in the alpine habitats of *V. graeca* were in inaccessible cliffs and 17% of pre-randomised locations fell on roads or water bodies in *V. renardi* habitats (Table 1).

Most of the vegetation structure variables followed a normal distribution, except for MHV in *V. ursinii* habitats, where vegetation was at some sampling points taller than 1 m, i.e., the height of the whiteboard (Fig. 1, 3). The correlations between vegetation structure variables were usually not significant, except between LA and HCV in *V. graeca* and in *V. ursinii* habitats and when data were pooled across species, and also between LA and FHD in *V. graeca* habitats (Fig. 3).

In *V. graeca*, the full GLMM returned no significant main effect, whereas HCV was included in all and shrub cover was included in five of the six best models ($\Delta\text{AICc} < 2$). The averaged parameter estimate was significant and positive only for HCV (Table 2), indicating a higher chance of occurrence of *V. graeca* in taller and closed vegetation.

In *V. renardi*, LA and the number of burrows had significant explanatory power in the full model and LA, FHD and number of burrows were included in both best models ($\Delta\text{AICc} < 2$). The effects of LA and number of burrows were positive, whereas that of FHD was negative (Table 2), indicating higher chances of *V. renardi* occurrence in microhabitats with higher, more homogeneous cover and more burrows.

In *V. ursinii*, the full model had the lowest AICc value, and in the two best models ($\Delta\text{AICc} < 2$), LA and MHV had significant positive effects, whereas HCV had a significant negative effect (Table 2), indicating higher chances of *V. ursinii* occurrence in tall, high-cover but more open vegetation.

DISCUSSION

Our study provided key results in the development of field data collection and data processing methodology for quantifying the role of vegetation structure in studies of animal microhabitat selection and in understanding how vegetation affects the occurrence of snakes in grasslands. Our results demonstrate that variables relevant in describing vegetation structure can be derived from the automated processing of images taken by standardised whiteboard photographs. In addition, at least one of the variables so derived influenced the occurrence of snakes in three species in three widely differing grassland ecosystems.

Our method decreases subjectivity in quantifying vegetation structure as it returns exact cover values along with the vertical range in pixel rows and does not rely on estimates by eye, and minimises observer bias and measurement error. Moreover, it does not require arbitrarily delimited measurement classes to characterise vertical variation in structure. Our method considers image pixels as the unit of analysis, however, specification of larger units, e.g. 4, 9 or 16 image pixels combined is also possible, which allows decreasing the resolution (upscaling) and computing time. Repeating the analyses at different unit sizes can provide further insight as it offers the possibility of studying scale-dependence in habitat selection, i.e., the identification of the environmental grain size at which animal-vegetation relationships are the strongest (Gunton et al., 2014; Lengyel et al., 2014). The objectivity of the method also allows comparisons made in two or more species or ecosystems and also allows local measurements to be extrapolated to larger areas, habitat types or ecosystems.

Our results support the role of vegetation structure in microhabitat selection of snakes. While compositional habitat diversity (plant species composition) and estimated cover of vegetation have been reported to influence the occurrence of reptiles (Nemes et al., 2006; Stumpel & van der Werf, 2012), our study confirmed that vertical aspects of vegetation structure can also be important in the habitat selection of reptiles (Mizsei et al., 2020b). For all three viper species studied, HCV and LA were the most important variables, indicating that vipers chose microhabitats where the vertical cover of the grass was higher than average, as measured in random locations. In the case of *V. ursinii*, a previous study (Máté & Vidéki, 2007) did not find a relationship between snake occurrence and plant species composition of the same study grassland. Our study thus also exemplifies that considering the structural aspects of vegetation can provide additional explanatory power in predicting the occurrence of snakes in microhabitats.

The role of vegetation structure in the microhabitat selection of snakes is probably determined by a trade-off between the need to hide from predators, for which the chances are better in higher or more dense vegetation (Wilgers & Home, 2007; Hansen et al., 2018), and the need to thermoregulate, for which the chances are

better in lower or sparser vegetation (Muri et al., 2015). This trade-off is probably the reason why HCV had opposite effects on the occurrence of *V. graeca* (positive) and *V. ursinii* (negative) because different species may find different optimum values along the continuum of vegetation height. Considering the latter negative relationship, it has to be noted that tall wetland plants were common in *V. ursinii* habitats, representing more dense cover and shading, which probably reduced the possibility of sunbathing for the vipers (Muri et al., 2015), which can explain why vipers appeared to avoid microhabitats with tall and dense vegetation. Further studies of other species with different needs for hiding vs. thermoregulation will certainly shed more light on this trade-off in habitat selection in snakes. Such knowledge will be fundamental for habitat restoration and conservation management actions for snakes.

Two limitations of this study need to be mentioned for the correct interpretation of our results. First, our study was limited by the small number of presence locations for *V. ursinii* and the high spatial scatter of *V. graeca* presence locations in the study area. Unfortunately, these rare endangered species have low detectability due to their low abundance, hidden lifestyle and camouflaged body pattern. Data collection requires huge sampling effort that represents significant challenges in logistics and person-power. A potential source of error common in such studies is the assumption of absence in random locations where the species is not found because absence cannot be deduced without uncertainty as the individuals of the study species may actually live at particular random locations (Olivier & Wotherspoon, 2006; Phillips et al., 2009). In our study, the possibility of this error was high in *V. renardi*, which species showed extreme abundance in the study habitat and several new presence locations were found during sampling “random” locations. Another practical limitation of our method is that placing the whiteboard on uneven ground or very dense vegetation may result in changes in the vegetation next to the whiteboard, which may distort the value of vegetation structure variables. To avoid this problem, we recommend a careful trimming of the vegetation in the plane and on the backside of the board to make sure that the board is standing firmly on the ground.

In conclusion, the supplementation of standardised whiteboard photography with automated image processing allows the calculation of simple measures of vegetation structure that can provide additional insight into animal-vegetation relationships beyond the role of plant species composition. The combined use of field recording and image processing and analysis offers several options that broaden the range of cost-effective ecological survey methods and can make a substantial contribution to the design and implementation of evidence-based conservation, including the conservation of endangered, grassland specialist vipers.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTION

E.M., M.B., G.R., G.D. and S.L. conceived the ideas and designed methodology; E.M., M.B., G.R., B.B., D.R., M.S. and A.M. collected data; E.M. programmed image processing and analysed the data, E.M. and S.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

This study was conducted via the implementation of an R script consisting automated image processing to measure leaf area (LA), height of closed vegetation (HCV), maximum height of vegetation (MHC), and foliage height diversity (FHD). The R script, example images and example data are available at Zenodo ([url](https://zenodo.org/record/7000000)).

TABLES

Table 1. Number of snakes found (presence locations), search effort, density of snakes and number of random locations studied in the three species.

Variable	V. graeca	V. renardi	V. ursinii
Number of presence locations	36	73	32
Search effort (person-days)	125	22	48
Effort-corrected density (individuals/person-day)	0.288	3.318	0.667
Number of random locations	157	249	320
% of random locations in inaccessible areas	47%	17%	0%

Table 2. Averaged parameter estimates of the best Generalized Linear Mixed Models testing the effects of vegetation structure and other relevant variables on presence-absence of vipers in grasslands. Significant

parameter estimates are highlighted in bold letters.

Species	Explanatory variable	Estimate	SE	Z	P
<i>Vipera graeca</i>	(Intercept)	-6.345	14.131	0.449	0.653
	Height of closed vegetation (HCV)	0.073	0.029	2.444	0.014
	Shrub surface cover	0.089	0.149	0.594	0.552
	Grass surface cover	0.081	0.200	0.409	0.682
	Rock surface cover	0.058	0.205	0.283	0.777
	Maximum height of vegetation (MHV)	-0.004	0.011	0.401	0.688
<i>Vipera renardi</i>	(Intercept)	0.315	1.360	0.232	0.816
	Burrow availability	0.184	0.078	2.358	0.018
	Foliage height diversity (FHD)	-0.442	0.240	1.842	0.065
	Leaf area (LA)	0.002	0.001	2.980	0.003
	Maximum height of vegetation (MHV)	-0.003	0.008	0.458	0.646
<i>Vipera ursinii</i>	(Intercept)	-1.261	2.893	0.436	0.663
	Foliage height diversity (FHD)	-0.779	0.475	1.641	0.101
	Maximum height of vegetation (MHV)	0.016	0.008	1.987	0.046
	Leaf area (LA)	0.003	0.001	2.266	0.023
	Height of closed vegetation (HCV)	-0.074	0.033	2.230	0.025

FIGURES

Figure 1. (a) Distribution of the study species in Europe according to Mizsei et al. (2018) and the location of study sites (dots), (b) example insets for presence (dots) and absence (crosses) points at the study sites, (c) grasslands at the study sites.

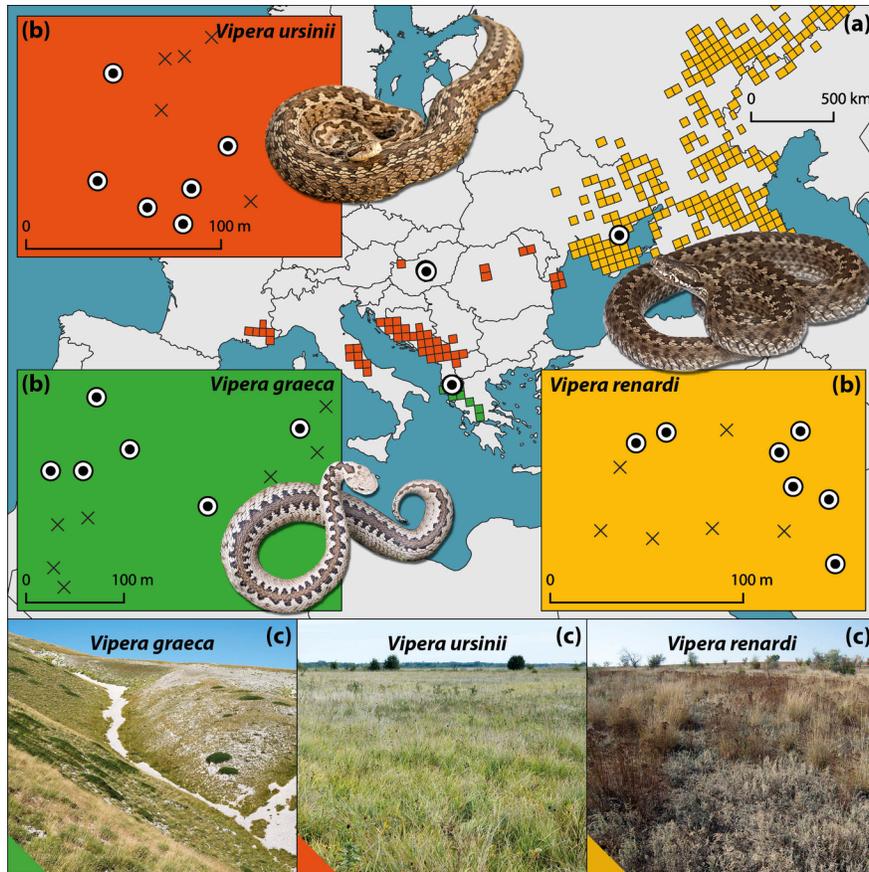


Figure 2. Main steps of processing the whiteboard images and example of the vegetation structure variables.

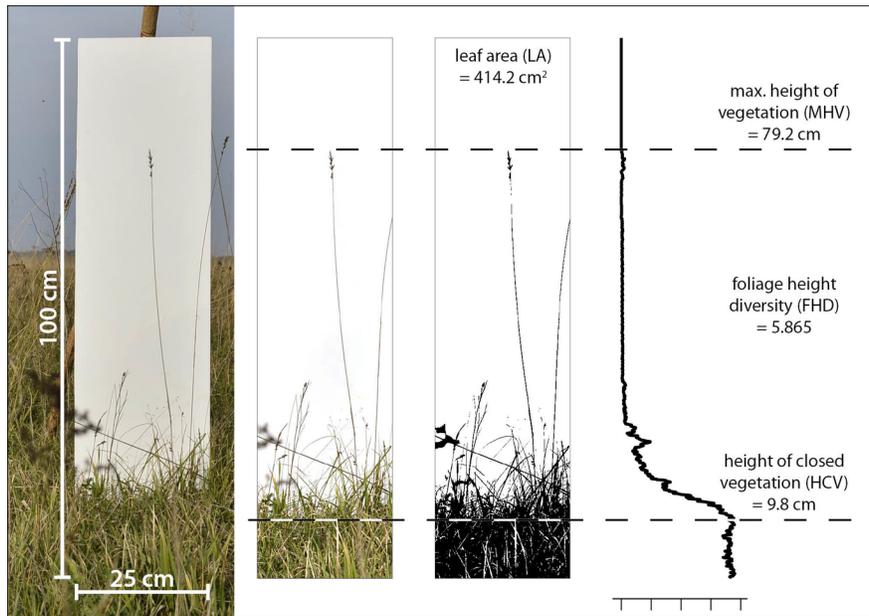


Figure 3. Vegetation structure variables: distributions (histograms in diagonal), correlations (lower left panels), Pearson’s correlation coefficients (upper right panels), and boxplots (right-hand column) of vegetation structure variables by species. Correlation coefficients in black are for data pooled for the three species, and coefficients in boldface type indicate significant correlations ($p < 0.05$).

