Estimating abundance and habitat suitability in a micro-endemic snake: the Walser viper

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Abstract. Recently described species suffer lack of information that hampers setting up appropriate conservation strategies. The situation is particularly complex with micro-endemic snakes, for which detection and monitoring are particularly challenging. The Walser viper *Vipera walser* is a recently described snake inhabiting a small area of the SW Italian alps. We combined information on species distribution with repeated monitoring to identify the areas most suitable for the species, and to obtain estimates of species abundance. Species distribution models were used to identify the topographical, climatic, and land-cover features related to the occurrence of vipers. Furthermore, repeated transects and *N*-mixture models were used to estimate abundance and to identify factors related to the variation of abundance. The available data suggested that the species has a disjunct range, with a Northern range of ~45 km², and a southern range of ~225 km². Distribution models suggested that vipers are associated with areas with open vegetation, altitude between 1300 and 2300 m, high precipitation, low forest cover, low slope, and southern aspect. *N*-mixture models confirmed very low detection probability of these vipers, and suggested that the species has a low abundance, with the highest abundance in south-facing plots. We provide the first quantitative information on habitats and abundance variation for Walser vipers. The broad confidence intervals of abundance estimates exemplify the complexity of providing range-wide measures of abundance for secretive species. Given the narrow range of these vipers, continuous monitoring is required to understand how they respond to ongoing environmental changes in mountainous areas.

Keywords. Alpha-hulls, detectability, endemism, habitat suitability models, land cover, *Vipera walser*.

INTRODUCTION

Italy is among the European countries with the highest endemism of amphibians and reptiles (Sillero et al.,

2014). In the last decades, the integration of new genetic and morphological data has greatly expanded our knowledge of Italian biodiversity, with the identification of several reproductively isolated lineages, that have been pro-

posed as new candidate species (e.g., Cornetti et al., 2015; Dufresnes et al., 2018; Senczuk et al., 2019).

The Walser viper has been a striking addition to the Italian herpetofauna. In NE Piedmont, the occurrence of vipers morphologically assumed to be adders (*Vipera berus*) has long been recognized (Andreone and Sindaco, 1998; Sindaco et al., 2006). However, recent genetic data revealed strong genetic differences between these "adder-like" vipers and true adders; the closest relatives of these vipers belong to the cluster regrouping *V. dinniki*, *V. kaznakovi* and *V. darevskii*, in the Caucasus area. As a consequence, these adder-like vipers have been described as a new species, the Walser viper (*Vipera walser*, Ghielmi et al., 2016), a species endemic of a small area from the mountains between Biella and the Ossola valley, with a possible range < 500 km^2 (Fig. 1).

Recently described, micro-endemic species often suffer a tremendous lack of biological data. This is particularly problematic, because the small range inherently exposes these species to a high risk of extinction. Therefore, sound biological and ecological information is required to set up appropriate monitoring and conservation programs. Habitat suitability and spatial variation of abundance represent critical information to assess the conservation status of species. In the last years, advances in analytical tools have greatly improved our ability to provide sound biological information even in species for which only a limited amount of data is available (e.g., Raxworthy et al., 2003; Peterson et al., 2011; Mazerolle, 2015).

In this paper, we combine modelling and field data to improve our knowledge of the ecology of the Walser viper. First, we used habitat suitability models to evaluate the relationships between viper distribution, land cover, and topographical features at a fine spatial scale. Correlative species distribution models (SDM) allow to identify relationships between localities of presences and spatial variation of environmental variables, and can provide multiple key information (Peterson et al., 2011). SDM can reveal how the species respond to broad-scale variation of environmental features, thus providing first information on the habitats that are more suitable for the target species (Guisan and Thuiller, 2005; Peterson et al., 2011). These models often have a coarse spatial scale and sometimes lack accurate information on species microhabitat or on habitat features that can only be measured in the field (Beck et al., 2012; Potter et al., 2013; Ficetola et al., 2018b). Still, if reliable maps of habitats or land cover are available, it is possible to obtain relatively detailed information on species responses to major land cover categories. Furthermore, SDM can produce spatially-explicit maps, that can refine information

on species range. For instance, Raxworthy et al. (2003) developed SDM for chameleons in Madagascar, and then performed targeted surveys in areas suggested to be suitable by models. In several cases, these targeted surveys revealed new localities of occurrence, suggesting that SDM can greatly improve our knowledge on species living in remote areas, or for which information on the distribution is limited.

Second, we performed repeated visits in a large number of patches within the species range, to assess spatial variation of abundance. Variation of abundance is a key parameter to assess the threat status of species, still, accurate measurement of abundance can require extremely extensive workload (Pollock et al., 2002; Dodd, 2010). In the last years, approaches have been proposed to obtain estimates of abundance from repeated counts, without marking or capturing individuals (Royle and Nichols, 2003; Royle, 2004). The number of individuals counted at fixed sites on multiple occasions can be used to estimate the detection probability, and the size of populations can be estimated on the basis of *N*-mixture models (Royle and Nichols, 2003; Royle, 2004; Kéry et al., 2009; Dail and Madsen, 2011). Despite several limitations (Barker et al., 2018; Link et al., 2018), such models can provide cost-effective estimates of abundance while accounting for imperfect detection (Ficetola et al., 2018a; Kéry, 2018), as detection probability is typically low in snakes. In addition, *N*-mixture models can provide insights on the factors determining spatial variation of population abundance and, if monitoring is repeated through time, they can provide reliable estimates of population trends (Ficetola et al., 2018c). These data are particularly critical for recently described species, for which information on abundance is nearly absent.

METHODS

Species range and distribution models

In March 2019, we combined bibliographic data (Ghielmi et al., 2006; Ghielmi et al., 2016) with new field observations performed in 2016-2018 by the authors, and personal communications by local naturalists, to gather an exhaustive dataset of *V. walser* occurrences. We used the alpha-hull approach for an accurate definition of the species range. The alpha-hull approach is a procedure based on Delauney triangulation that uses presence points to estimate species ranges, and can allow for the exclusion of unoccupied areas within a species range (Burgman and Fox, 2003). Simulations showed that the alpha-hulls provide better approximations of species ranges compared to minimum convex polygons, particularly when the ranges have discontinuities (Burgman and Fox, 2003). Alpha-hulls were built using the alphahull package in R (Pateiro-Lopez and

Rodrjguez-Casal, 2010), following the procedure detailed in Ficetola et al. (2014).

Land cover data were obtained from the geoportal of the Piedmont region (http://www.geoportale.piemonte.it/) at the resolution of 2 m. We considered four land cover categories: agricultural, pasture, natural open vegetation, and forest. As a measure of land cover, we calculated the percentage of each land cover category in 100×100 m cells. Furthermore, we considered three topography variables: altitude (m a.s.l.), aspect (northness), and slope. As a climatic parameter, we considered summed annual precipitation, obtained through the Chelsa-clim dataset (Karger et al., 2017). This dataset is available at a coarser resolution than the other predictors (30 arc-seconds, approx. 650×900 m in the study area). We therefore used the *B*-spline interpolation to downscale it at the 100-m resolution (see Karger et al., 2017). Temperature variables were not included because they were strongly collinear with altitude ($r > 0.9$). The pairwise correlation between the remaining environmental variables was always $|r| < 0.65$, suggesting limited collinearity issues (Dormann et al., 2013).

We used maximum entropy modelling (MaxEnt) (Phillips et al., 2006; Elith et al., 2011) to build species distribution models relating the occurrence of vipers to land cover and topographical data. MaxEnt is a presence-background approach that evaluates the suitability of a given cell on the basis of environmental features (habitat, climate, topography…) in that cell. Comparative studies showed that MaxEnt is among the most efficient approaches to build SDM (Elith et al., 2006; Elith et al., 2011). MaxEnt is well suited to evaluate complex or non-linear relationships between species and environmental features, and produces an output representing the suitability of a specific area. We run models with linear, quadratic, and hinge features. To identify the best regularization parameter (b), we build five models with increasing values of b: 1, 2, 5, and 10 (Warren and Seifert, 2011). The model with b = 2 showed the highest cross-validation performance (see below), and was selected as model with highest generality (Warren and Seifert, 2011).

We used two approaches for the validation of species distribution model. First, the model was tested using a 5-fold cross-validation. Presence records were split into five sub-sets; the model was built using 80% of data (calibration data), and we tested predictive performance on the remaining 20% (test data). We repeated this procedure five times, each time using a different test dataset (Nogués-Bravo, 2009). As a measure of model performance, we calculated the area under the curve of the receiver operator plot (AUC), averaged over the five runs. AUC is an imperfect measure of the performance of SDM (Lobo et al., 2008), thus we also used a binomial test to evaluate if our models predict presence records better than expected under randomness, comparing the observed frequencies of correct and incorrect predictions. In this test, we assumed that a cell is suitable for vipers if it has suitability larger than 10th percentile training test threshold (Pearson et al., 2007). Second, the model was developed in late winter 2019. Therefore, we used data collected during the 2019 field activities to confirm the reliability of model predictions. Specifically, we used a likelihood ratio test to assess whether viper observations are more frequent in areas with high SDM suitability, compared to areas with low suitability. Since we have a-priori expectation on the frequency of observations (i.e., we expect more observations in high-suitability areas), we used a one-tailed test (Warren and Seifert, 2011).

Field activities

In the period 2016-2019, we established 71 fixed plots using visual encounter surveys (Crump and Scott, 1994). Each plot was visited during one year only (range: 5-26 plots per year); plots were visited multiple times (average: 5.7 surveys per plot; range: 3-12 surveys) from late May to early October, i.e., during the period of highest activity of vipers. The size of plots ranged between 600 and 23,000 m² (mean: 7600 m²), because of logistic and accessibility constraints. Visits were performed from 7 am to 17 pm (solar time), but most of them (69%) were performed in late morning (between 8.30 and 12.00 am). Plots were placed across the whole range of the species, mostly nearby areas with previous records of Walser vipers. In 2019, the location of plots was selected after the development of species distribution models, in order to validate the SDM and identify eventual new locations of the viper. Out of the 17 plots surveyed in 2019, three were in areas with low SDM suitability (suitability below the 10th percentile training presence threshold; range: 0.06-0.22) but nearby areas with high suitability. Ten were in areas with high SDM suitability (> 0.45) and nearby localities where the species is known to be present, and four were in areas with high suitability but out of the known species range (Mombarone; roughly 3 km SE of the southern limit of the species range, see Fig. 1b). During surveys, one to four observers carefully patrolled the plots, searching for active vipers. In other areas, the search under artificial shelters greatly improved the detection of reptiles (De Leo et al., 2006; Joppa et al., 2010; Sewell et al., 2012). Therefore, in 2019, visual encounters were integrated with the use of artificial cover objects (shelters). In each plot, we placed three corrugated bitumen 70×90 cm shelters that were checked during each survey.

Assessment of species abundance

We used *N*-mixture models to estimate the abundance of vipers on the basis of repeated counts at plots, and to identify environmental variables related to variation of abundance. *N*-mixture models allow the joint estimation of animal abundance and detection probability on the basis of repeated surveys at fixed sites, without the need of capturing and marking individuals for identification (Royle, 2004). Some analyses highlighted that jointly estimating detection probability and abundance could be problematic, and these models are sensitive to violations of their assumptions (Barker et al., 2018; Duarte et al., 2018), still analyses of real-world data showed that *N*-mixture models can provide reliable estimates of the abundance of wild vertebrates (Ficetola et al., 2018a; Kéry, 2018; Costa et al., 2019). We assumed that each plot, sampled during one single season, represented a closed population. We thus used a static (i.e., non-dynamic) *N*-mixture model formulation. The average distance between each plot and the closest one was 170 m (SE

= 19.6), a distance much longer than the typical movements of related species (e.g., Zuffi et al., 1999; Nash and Griffiths, 2018). *N*-mixture models were fitted using a Poisson error distribution, as in preliminary analyses Poisson models showed a lower Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002) than the corresponding zero-inflated Poisson models. In *N*-mixture models, we set the upper bound to approximate the infinite summation of the likelihood (K) at the maximum observed species abundance +100, since simulations suggested that this value provides stable and robust estimates (Ficetola et al., 2018c).

We considered four variables potentially influencing the detection of vipers: date (day of the year), hour, length of the survey (in minutes, log transformed), and the number of people participating in the survey. For date and hour, we also tested quadratic terms to take into account potential non-linear relationships. To identify the model best explaining variation of viper detection, we built models including all the potential combinations of independent variables, and ranked them on the basis of their AIC values. The model with lowest AIC value explains more variation with a limited number of parameters, and was selected as the minimum adequate model (Burnham and Anderson, 2002). First, we performed model selection on variables affecting detectability, then we performed model selection on variables affecting abundance.

We considered six variables potentially affecting the abundance of vipers at plots: plot surface, aspect, altitude, slope, and suitability predicted by the species distribution model. SDM suitability was included because previous studies suggested that environmental suitability models also help to predict parameters such as population density and fitness-related traits (Brambilla and Ficetola, 2012; Weber et al., 2017; Lunghi et al., 2018). Variables representing land cover were not included because 85% of plots were in areas with open natural vegetation, which is the most important land cover variables determining viper distribution (see results). We built models with all the possible combination of variables potentially affecting abundance, and ranked them using AIC, while keeping constant the observational component of the model (i.e., including the variables best explaining variation in detection probability). The correlation coefficient between site covariates was weak ($r < 0.4$ for all the considered variables).

N-mixture models were run with the package Unmarked in R (Fiske and Chandler, 2011). Before analyses, independent variables were scaled at mean = 0 and SD = 1 to improve model convergence. A goodness-of-fit test showed limited overdispersion and confirmed that the model was appropriate to the data ($\chi^2 = 432.6$, permutation $P = 0.12$, c-hat = 1.1).

RESULTS

Distribution data, species range, and distribution model

Overall, we gathered 117 distribution records (Fig. 1a). Localities from the literature (Ghielmi et al., 2006; Ghielmi et al., 2016) accounted for 50% of records, while 47% of records were obtained through recent surveys by the authors; we also obtained some personal communications by local naturalists (3% of records). Species records were clustered in two main areas: a northern group between the Strona and the upper Sesia Valley, and a southern group between the lower Sesia Valley and the Biella Alps. The lack of known records between these two areas suggests the possibility of a disjunct distribution, with a northern range of approx. 45 km^2, and a southern range of approx. 225 km^2.

The species distribution model suggested that vipers were associated to areas with open natural vegetation, altitude between 1300 and 2300 m, high annual precipitation, low forest cover, low slope, and with a southern aspect (Fig. 2). The presence of agricultural land cover and pastures showed very limited importance (relative importance < 1%). The cross-validation procedure suggested excellent performance, with average AUC on test data = 0.924 (SD = 0.038). Using the 10th percentile training presence threshold (suitability threshold = 0.36), the model correctly predicted occurrence at 86.3% of test data, a performance significantly better than expected by chance (binomial test: $P << 0.001$; success rate expected under randomness = 13.5%).

The model identified several patches of highly suitable habitats through the whole species range, in mountainous areas at altitude of 1300-2200 m, with gentle, south-facing slopes and covered by open vegetation. Within the species range, the total suitable surface (i.e., with suitability higher than the 10th percentile threshold) was 81.9 km^2. Several areas with good suitability were detected outside the known range of the species, for instance, in the SW of the study area (e.g., the Mombarone area) (Fig. 1b). Potentially suitable areas were also detected between the northern and southern populations.

Model validation with the 2019 data

Four plots surveyed in 2019 were outside the known range of *V. walser*, but in areas showing high suitability according to the SDM (Mombarone area; Fig. 1b). Each of them received six surveys; we never detected vipers at these plots. Thirteen plots surveyed in 2019 were inside the known range of *V. walser*; four were in areas with low suitability (suitability ≤ 0.2) and nine in areas with high suitability (> 0.45). Vipers were never detected in the plots with low suitability, while they were detected in 56% of plots with high suitability. The possibility to obtain at least one detection was significantly higher in plots with high suitability (likelihood ratio test: $\chi^2_1 = 4.96$, $P = 0.013$), confirming that the SDM can successfully predict viper occurrences.
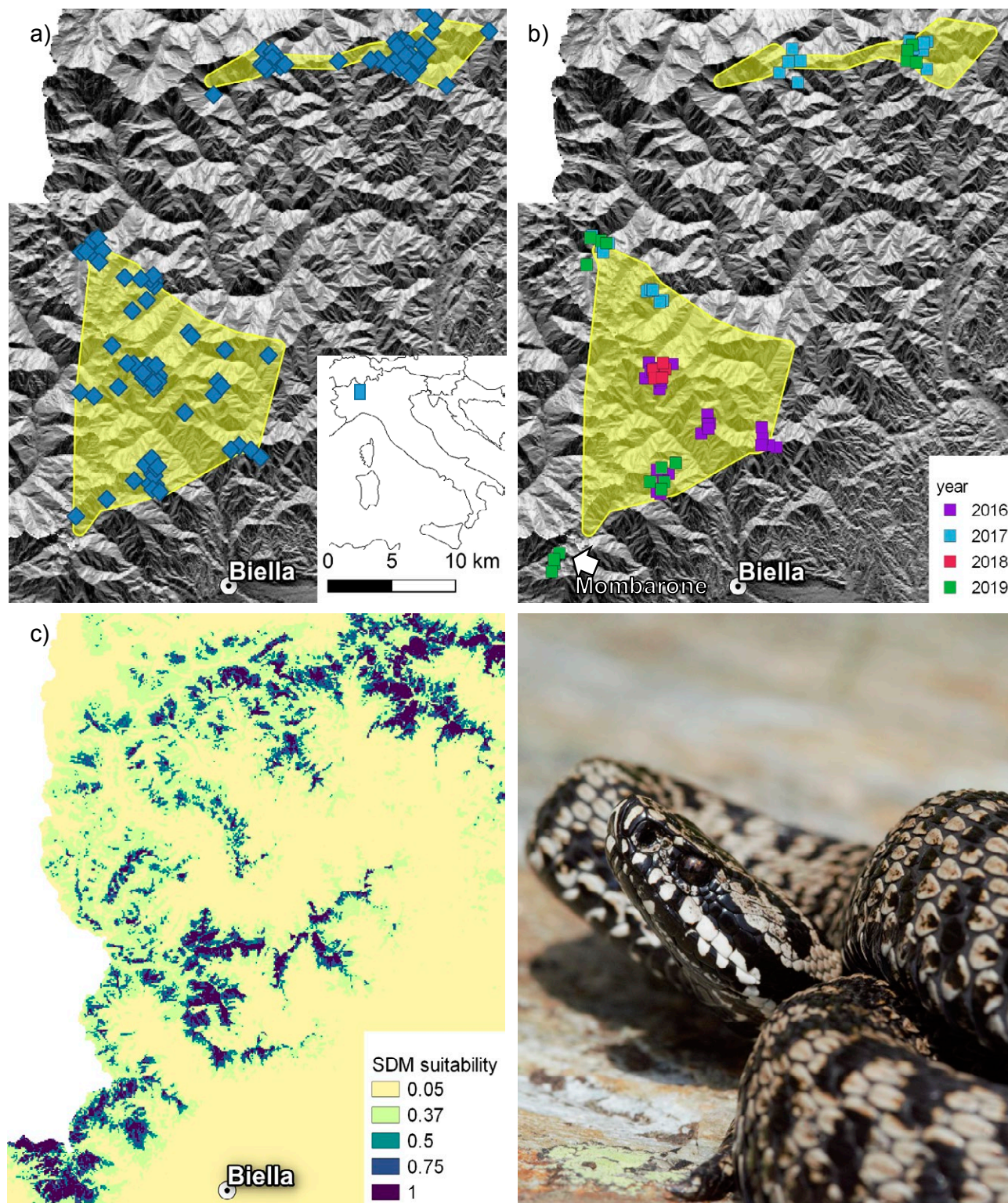
Fig. 1. a) Distribution records used to build species distribution models, and species range estimated using alpha-hulls. b) Location of fixed plots where we performed repeated counts. The arrow indicates the plots located in possibly suitable sites outside the known range of the species (Mombarone). c) Suitability map, estimated using species distribution models. 0.37 is the 10th training presence threshold. To limit the risk of poaching, points plotted on the maps have a random spatial error of up to 2 km (Lunghi et al., 2019). d) An adult male of *V. walser* (photo by GFF).

Repeated counts and abundance estimations

Overall, we obtained 39 viper detections from 24 out of the 67 plots within the species range. Vipers were detected across the whole study period (from June to early October). The best-AIC model suggested that the number of detection was only affected by the length of surveys, longer surveys allowing a higher probability of detecting vipers ($B \pm SE = 0.73 \pm 0.16$, $z = 4.45$, $P < 0.001$). Conversely, the detection rate was unrelated to date or hour of the survey, nor to the number of observers (Table 1). The detection probability of vipers was approx. 0.036 in 35-min. surveys (35 min. was the average length of surveys), but the incertitude of these estimates was large (95% CI of detection probability after 35 min: 0.007-0.16).

The abundance of vipers was negatively related to the northness of plots, with higher abundances in south-facing plots ($B = -0.70 \pm 0.30$, $z = -2.35$, $P = 0.019$). We did not detect any relationship between the remaining variables and the abundance of vipers (Table 1). The estimated abundance per plot ranged between zero and five individuals; the best estimate of total abundance across the 67 plots was 175 vipers, but confidence intervals were wide (95% CI: 38-383 vipers). Therefore, at the surveyed plots, the average density was 3.4 individuals / ha.

Table 1. a) Relationships between detections of *Vipera walser* and variables potentially influencing detection. The table reports the outcome of univariable *N*-mixture models, in which only each of these variables was related to the viper detections. All the models with more than one variable showed higher AICc values than the one with length of survey only. b) Relationships between detections of *Vipera walser*, and variables potentially influencing abundance. The table reports the outcome of *N*-mixture models, in which viper detection probability was related to length of survey, and viper abundance was related to each of these variables. All the models with more than one variable showed higher AICc values than the model with aspect only (Appendix 1).

	AICc	z	P
a) variables potentially influencing detection			
Date*	262.9	-0.321	0.749
Hour*	261.6	-1.14	0.256
N observers	262.8	0.51	0.610
Length of survey	244.4	4.48	**<0.001**
b) variables potentially influencing abundance			
Altitude*	246.7	0.13	0.895
Aspect	238.6	-2.35	**0.019**
Slope	245.2	1.24	0.217
Plot area	246.7	-0.22	0.830
Precipitation	245.7	1.03	0.302
SDM suitability	243.5	1.66	0.097

* Preliminary tests did not show any effect also for quadratic terms.

DISCUSSION

For recently described species, rapid biological and ecological studies are pivotal for a prompt assessment of the species status. By combining distribution records with ecological modelling and repeated surveys we provide key ecological data on the endemic, poorly known, Walser viper.

The application of alpha-hulls to species distribution data suggested that this viper has a disjunct range, with a northern range comprising the Strona and the upper Sesia Valley, and a southern range between the Biella Alps and the lower Sesia Valley. Alpha-hulls have an excellent capacity to reveal discontinuities in the specie range (Burgman and Fox, 2003), still they can be affected by the lack of biological records caused, for instance, by limited surveys. The available genetic data did not detect strong differences among Walser vipers (Ghielmi et al., 2016), still additional genetic or genomic studies, using highly variable or fast-evolving markers, are needed to understand the fine-scale genetic variation among the different populations.

Habitat suitability

Species distribution models showed that viper distribution is related to the interplay between topographic, climatic, and habitat parameters. First, vipers are associated with gentle, south-exposed slopes at altitudes between 1500 and 2300 m. This study was performed on a rather small geographical extent, and at this scale, the correlation between altitude and the available temperature data is almost perfect ($r > 0.9$), therefore altitude can be considered as a proxy of temperature. The narrow altitudinal range suggests a very narrow thermal niche, which is typical of many micro-endemic species (Quintero and Wiens, 2013; Slatyer et al., 2013; Cunningham et al., 2016). This inherently exposes micro-endemic species to a high risk of extinction, and is particularly alarming under scenarios of climate change (Botts et al., 2013; Slatyer et al., 2013; Böhm et al., 2016). Until recently, Walsers vipers were assumed to be adders *Vipera berus* (Andreone and Sindaco, 1998; Sindaco et al., 2006). However, it should be remarked that the altitudinal range of Walser's vipers does not match the one observed for adders in the Southern Alps. Present-day adder populations living in Lombardy (approx. 80 km E of the study area) have a broad altitudinal range (550-2500 m) and 26% of records are above 2000 m (Bernini et al., 2004). Conversely, all available Walser viper data are restricted at altitudes of 1300-2300 m, with just 4% of records above 2000 m. This suggests that Walser vipers have a
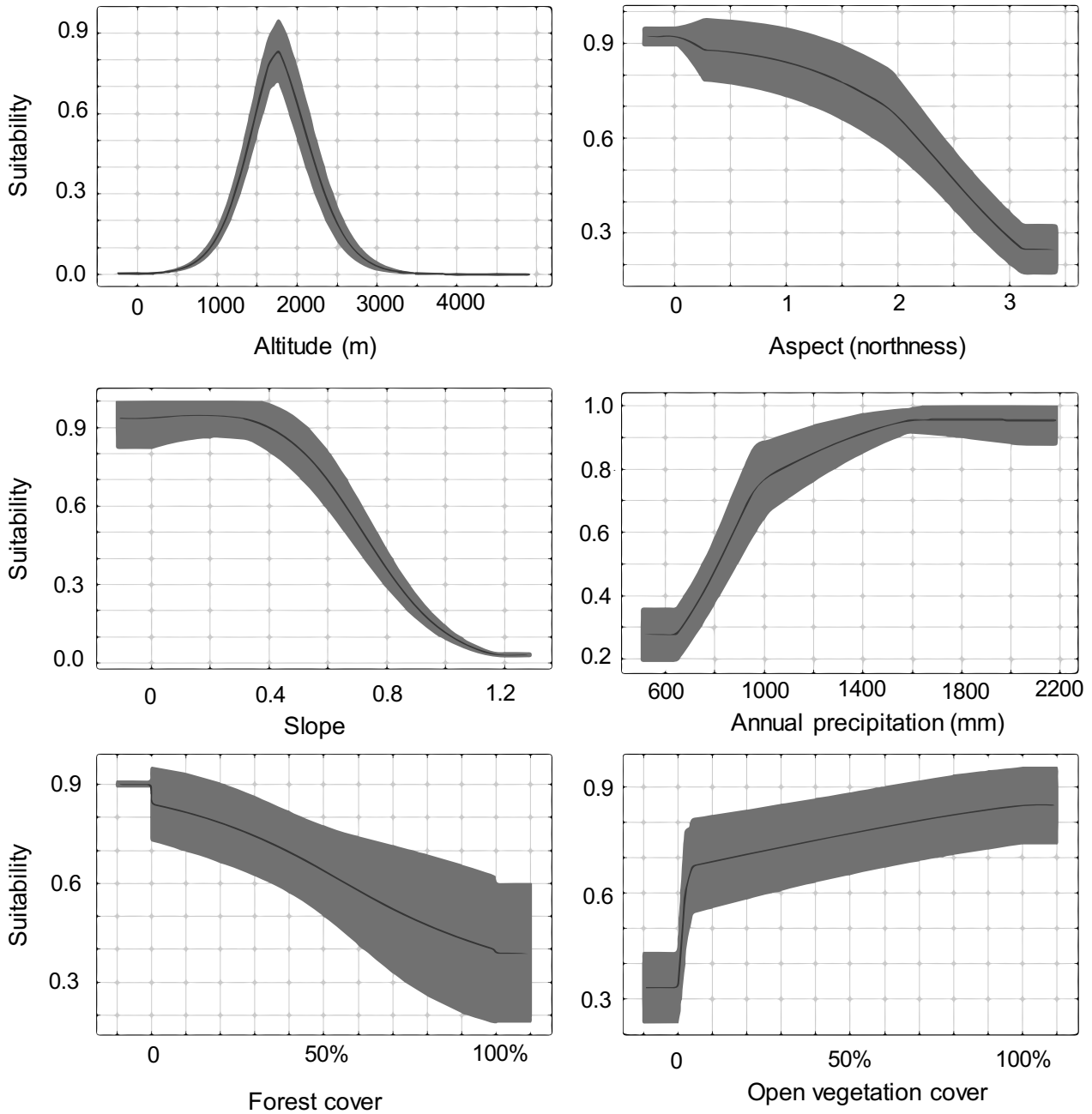
Fig. 2. Relationship between environmental variables and suitability, as estimated by species distribution models. The dark lines are the average response across the cross-validated runs; the confidence bands indicate ± one standard deviation.

narrower niche than adders, still, additional studies are required to compare the niches of the two species.

Second, vipers were associated to areas with relatively high precipitation levels and high cover of natural, open vegetation. The Walser viper range includes some of the valleys with the highest rainfall in the Alps (Mercalli et al., 2008). High precipitation levels can allow the exist-ence of a relatively humid environment with open vegeta-tion, which is the main habitat of this species (Ghielmi et al., 2016). Given the very small surface of suitable habi-tats, ensuring the long-term persistence of these environ-ments will be essential for the long-term survival of Wal-ser vipers.
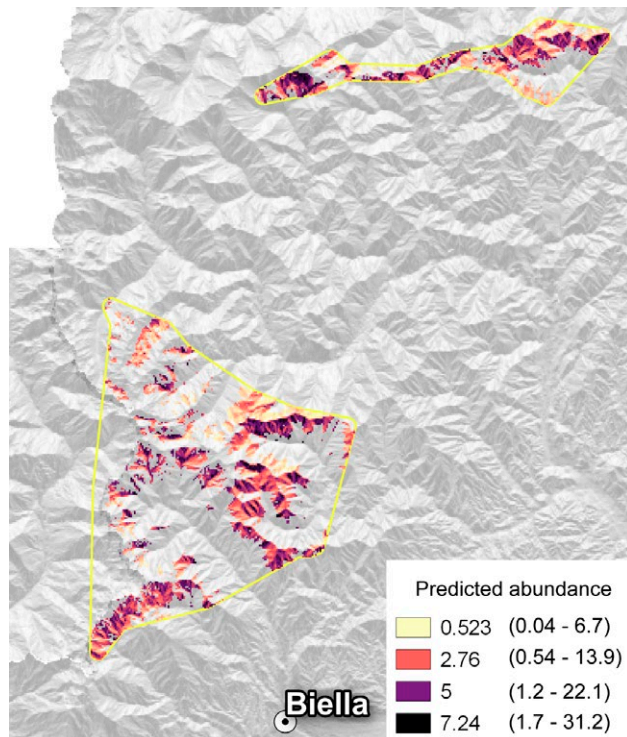
Fig. 3. Spatial variation of the density of *Vipera walser*: best predictions of the *N*-mixture model, assuming that abundance is affected by slope. The map indicates the averaged density (individuals / ha); 95% confidence intervals of the estimates are available in the legend. Projections have only been performed for the most suitable areas within the species range, according to the results of the species distribution model.

Variation in abundance

Repeated counts and *N*-mixture models can provide estimates of the absolute abundance of individuals, and are particularly useful when no data from other sources are available. Our models showed that, for individuals of Walser viper, detection probability is low (around 4% in standard surveys), and the species generally has a limited abundance (average: 3.4 individuals / ha). A low detection probability has been often observed in snakes (Luiselli et al., 2011; Rodda, 2012), and density estimates are comparable to the values observed in other studies (reviewed in Santini et al., 2018a). For instance, Neumeyer (1987) used capture-mark-recapture to assess the abundance of *Vipera berus* in subalpine environments, and found a density of approx. 3 individuals / ha. Translating modelled abundance in density estimates is often complex. Nevertheless, the home range size of the study species is likely small compared to plot size, thus the derived density probably does not suffer by temporary emigration (Kery and Royle, 2016).

Our plots covered well the whole range of the species (Fig. 1b), still performing extrapolations of abundance across a species range is extremely complex (Santini et al., 2018b). If we assume that the relationship between viper density and plot aspect is constant across the whole range, we can perform projections of the spatial variation of potential density (Fig. 3) that, in turn, could be used to obtain rough estimates of abundance across the species range. Such a projection would lead to a best unbiased prediction of 26,000 vipers, but the associated confidence intervals are extremely wide (95% intervals: 5500-130,000 vipers). These figures can be useful to obtain a first approximation of abundance when no other data are available, but must be taken with extreme caution. First, model extrapolation outside the sampled areas is always challenging, because we cannot be sure that the relationship between habitat and abundance is constant across the range. Importantly, species distribution models often overestimate species distribution (Guisan and Rahbek, 2011). This occurs because additional factors can influence species abundance, for instance, when a given patch is unsuitable because of the presence of a limiting factor not considered in this analysis. Second, the reliability of estimates obtained through *N*-mixture heavily depends on the verification of model assumptions (Barker et al., 2018; Link et al., 2018). For instance, unmodelled heterogeneity of detection probability can heavily bias total estimates of abundance (Link et al., 2018), and it is unlikely that our model took into account all the potential factors affecting viper detections. Third, the reliability of abundance estimates is sensitive to variation of detection probability, and low values of detection probability always challenge models that rely on unmarked individuals (Ficetola et al., 2018c). Unfortunately, the detection probability of vipers was extremely low.

Many conservation agencies require quantitative measures of abundance (e.g., IUCN, 2001; Stoch and Genovesi, 2016), but obtaining reliable estimates, with high accuracy and limited uncertainty, can be challenging. Our study showed that uncertainty can be large even for micro-endemic species for which a very large number of surveys is performed. Given the low detectability, an alternative approach for the monitoring of Walser vipers could rely on occupancy modelling (MacKenzie et al., 2017). Modelling co-occurrence in an occupancy framework or in a joint SDM framework may help improving inference on species occupancy when data for other species are available (e.g., common lizard). In addition, distribution may be better inferred using spatially and temporally replicated data in an occupancy framework, instead of presence-only data alone in a SDM framework.

One solution would be integrating opportunistic information (i.e., presence-only data, probably the most abundant and widely distributed source of information for the species) with detection-non detection data from an occupancy design (Dorazio, 2014).

Recommendation for monitoring and conservation

For data deficient species, a key goal for the near future is certainly improving knowledge on distribution, abundance, and threats. Walser vipers are rare and elusive, thus improving information on total abundance and population trends will be essential. Repeated counts at fixed sites are an excellent strategy for a consistent assessment of temporal variation in abundance, and have been recommended for the monitoring of many reptiles (Stoch and Genovesi, 2016). However, a large number of sites and surveys are required for a correct estimate of trends in elusive species. For instance, several tens of sites, each surveyed multiple times per year, are required if we want to obtain reliable estimates of species trends with dynamic *N*-mixture models (Ficetola et al., 2018c). The plots surveyed in this study can provide the needed baseline for the development of a long-term monitoring program. Alternatively, approaches involving the capture of individuals can be used to collect individual longitudinal data simultaneously to occupancy data. Capture-mark-recapture information would allow estimating population growth rate, the factors affecting it and its temporal variability. This can be done without the need to estimate population size and with the freedom to simultaneously test effects on drivers of demographic rates (e.g., survival, recruitment, and fecundity) (Tenan et al., 2014).

Despite the importance of future monitoring, conservation biologists must identify priorities and plan management actions even if information is incomplete (Soulé, 1985). Our data can already be useful for the conservation planning of Walser vipers. Distribution data and species distribution models suggest a very restricted distribution, with a total extent of occurrence < 300 km^2, and an estimated area of occupancy = 86.5 km^2. A limited geographic range is a key criterion for redlist assessment. For instance, the IUCN (2001) classifies as Threatened under the criterion B species that have small geographic range (extent of occurrence < 5000 km^2 and / or area of occupancy < 500 km^2), and also satisfy at least two of these three conditions: a) severely fragmented or restricted number of locations; b) continuing decline of the species or his habitat; c) extreme demographic fluctuations. The Walser viper has a very small range and is known from a limited number of locations. Until now, no

information is available on the decline of his habitat, and unrecorded habitat loss is possible. Remote sensing data are an efficient approach to assess habitat trends through time, when ground information is lacking (Tracewski et al., 2016). Data from Corine land cover suggest that the cover of suitable habitats within the species range has remained stable during the last decade, with approx. 124.6 km^2 of natural open vegetation in 2006, and 125.6 km^2 in 2018. However, during the last decades, the cover of open vegetation has decreased in several areas of the Alps because of the abandonment of traditional livestock farming (Falcucci et al., 2007), and this could cause habitat loss for Walser vipers in the future. If future monitoring will identify declines of abundance, occupancy, or of suitable habitat, Walser vipers can be classified as Endangered according to the IUCN redlist criteria.

Climatic change and the loss of open natural vegetation are the strongest threats to the biodiversity of montane environments of Europe (Brambilla et al., 2010; Brambilla et al., 2017), and will likely also affect Walser vipers in the next future. Despite only recently described, these vipers already are one of the most iconic animals of the Alps, and could serve as a flagship species for the prioritization of conservation management in these increasingly threatened environments.

REFERENCES

Andreone, F., Sindaco, R., editors. (1998): Erpetologia del Piemonte e della Valle d'Aosta, Atlante degli Anfibi e dei Rettili. Museo Regionale di Scienze Naturali, Torino.

Barker, R.J., Schofield, M.R., Link, W.A., Sauer, J.R. (2018): On the reliability of N-mixture models for count data. Biometrics **74**: 369-377.

Beck, J., Ballesteros-Mejia, L., Buchmann, C.M., Dengler, J., Fritz, S.A., Gruber, B., Hof, C., Jansen, F., Knapp, S., Kreft, H., Schneider, A.K., Winter, M., Dormann,

C.F. (2012): What's on the horizon for macroecology? Ecography **35**: 673-683.

Bernini, F., Bonini, L., Ferri, V., Gentilli, A., Razzetti, E., Scali, S., editors. (2004): Atlante degli Anfibi e dei Rettili della Lombardia. Provincia di Cremona, Cremona.

Böhm, M., Williams, R., Bramhall, H.R., McMillan, K.M., Davidson, A.D., Garcia, A., Bland, L.M., Bielby, J., Collen, B. (2016): Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. Global Ecol. Biogeogr. **25**: 391-405.

Botts, E.A., Erasmus, B.F.N., Alexander, G.J. (2013): Small range size and narrow niche breadth predict range contractions in South African frogs. Global Ecol. Biogeogr. **22**: 567-576.

Brambilla, M., Caprio, E., Assandri, G., Scridel, D., Bassi, E., Bionda, R., Celada, C., Falco, R., Bogliani, G., Pedrini, P., Rolando, A., Chamberlain, D. (2017): A spatially explicit definition of conservation priorities according to population resistance and resilience, species importance and level of threat in a changing climate. Divers. Distrib. **23**: 727-738.

Brambilla, M., Casale, F., Bergero, V., Bogliani, G., Crovetto, G.M., Falco, R., Roati, M., Negri, I. (2010): Glorious past, uncertain present, bad future? Assessing effects of land-use changes on habitat suitability for a threatened farmland bird species. Biol. Conserv. **143**: 2770-2778.

Brambilla, M., Ficetola, G.F. (2012): Species distribution models as a tool to estimate reproductive parameters: a case study with a passerine bird species. J. Anim. Ecol. **81**: 781-787.

Burgman, M.A., Fox, C.W. (2003): Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. Anim. Conserv. **6**: 19-28.

Burnham, K.P., Anderson, D.R. (2002): Model selection and multimodel inference: a practical information-theoretic approach. Springer Verlag, New York.

Cornetti, L., Ficetola, G.F., Hoban, S., Vernesi, C. (2015): Genetic and ecological data reveal species boundaries between viviparous and oviparous lizard lineages. Heredity **115**: 517-526.

Costa, A., Oneto, F., Salvidio, S. (2019): Time-for-space substitution in N-mixture modeling and population monitoring. J. Wildlife Manage. **83**: 737-741.

Crump, M.L., Scott, N.J. (1994): Visual encounter surveys. In: Measuring and monitoring biological diversity: standard methods for Amphibians, pp. 84-92. Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.C., Foster, M.S., Eds, Smithsonian Institution Press, Washington.

Cunningham, H.R., Rissler, L.J., Buckley, L.B., Urban, M.C. (2016): Abiotic and biotic constraints across reptile and amphibian ranges. Ecography **39**: 1-8.

Dail, D., Madsen, L. (2011): Models for estimating abundance from repeated counts of an open metapopulation. Biometrics **67**: 577-587.

De Leo, F., Donelli, O., Scali, S. (2006): Use of natural and artificial shelters in a snake community of northern Italy. In: Atti del V convegno nazionale Societas Herpetologica Italica, pp. 25-31. Zuffi, M.A.L., Ed, Firenze University Press, Firenze.

Dodd, C.K.J., editor. (2010): Amphibian ecology and conservation. A handbook of techniques. Oxford University Press, Oxford.

Dorazio, R.M. (2014): Accounting for imperfect detection and survey bias in statistical analysis of presence-only data. Global Ecol. Biogeogr. **23**: 1472-1484.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G., Marquez, J.R.G., Gruber, B., Lafourcade, B., Leitao, P.J., Munkemuller, T., McClean, C., Osborne, P.E., Reineking, B., Schroder, B., Skidmore, A.K., Zurell, D., Lautenbach, S. (2013): Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography **36**: 27-46.

Duarte, A., Adams, M.J., Peterson, J.T. (2018): Fitting N-mixture models to count data with unmodeled heterogeneity: Bias, diagnostics, and alternative approaches. Ecol. Model. **374**: 51-59.

Dufresnes, C., Mazepa, G.O., Rodriguez, N., Brelsford, A., Litvinchuk, S.N., Sermier, R., Betto-Colliard, C., Blaser, O., Borzée, O., Cavoto, E., Fabre, G., Ghali, K., Grossen, C., Horn, A., Lavanchy, G., Leuenberger, J., Phillips, B.C., Saunders, P.A., Savary, R., Maddalena, T., Stöck, M., Dubey, S., Canestrelli, D., Jeffries, D.L. (2018): Genomic evidence for cryptic speciation in tree frogs from the Apennine Peninsula, with description of *Hyla perrini* sp. nov. . Frontiers in Ecology and Evolution doi: 10.3389/fevo.2018.00144

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S., Zimmermann, N.E. (2006): Novel methods improve prediction of species' distributions from occurrence data. Ecography **29**: 129-151.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J. (2011): A statistical explanation of MaxEnt for ecologists. Divers. Distrib. **17**: 43-57.

Falcucci, A., Maiorano, L., Boitani, L. (2007): Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. Landscape Ecol. **22**: 617-631.

Ficetola, G.F., Barzaghi, B., Melotto, A., Muraro, M., Lunghi, E., Canedoli, C., Lo Parrino, E., Nanni, V., Silva-Rocha, I., Urso, A., Carretero, M.A., Salvi, D., Scali, S., Pennati, R., Andreone, F., Manenti, R. (2018a): N-mixture models reliably estimate the abundance of small vertebrates. Sci. Rep. **8**: 10357.

Ficetola, G.F., Lunghi, E., Canedoli, C., Padoa-Schioppa, E., Pennati, R., Manenti, R. (2018b): Differences between microhabitat and broad-scale patterns of niche evolution in terrestrial salamanders. Sci. Rep. **8**: 10575.

Ficetola, G.F., Romano, A., Salvidio, S., Sindaco, R. (2018c): Optimizing monitoring schemes to detect trends in abundance over broad scales. Anim. Conserv. **21**: 221-231.

Ficetola, G.F., Rondinini, C., Bonardi, A., Katariya, V., Padoa-Schioppa, E., Angulo, A. (2014): An evaluation of the robustness of global amphibian range maps. J. Biogeogr. **41**: 211-221.

Fiske, I., Chandler, R. (2011): unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. **43**: 1-23.

Ghielmi, S., Bergò, P.E., Andreone, F. (2006): Nuove segnalazioni di *Zootoca vivipara* Jaquin e di *Vipera berus* Linnaeus, in Piemonte, Italia nord-occidentale (Novitates Herpetologicae Pedemontanae II). Acta Herpetol. **1**: 29-36.

Ghielmi, S., Menegon, M., Marsden, S.J., Laddaga, L., Ursenbacher, S. (2016): A new vertebrate for Europe: the discovery of a range-restricted relict viper in the western Italian Alps. J. Zool. Syst. Evol. Res. **54**: 161-173.

Guisan, A., Rahbek, C. (2011): SESAM - a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. J. Biogeogr. **38**: 1433-1444.

Guisan, A., Thuiller, W. (2005): Predicting species distribution: offering more than simple habitat models. Ecol. Lett. **8**: 993-1009.

IUCN. (2001): IUCN Red List Categories and Criteria: Version 3.1. IUCN, Gland, Switzerland and Cambridge, UK.

Joppa, L.N., Williams, C.K., Temple, S.A., Casper, G.S. (2010): Environmental Factors Affecting Sampling Success of Artificial Cover Objects. Herpetol. Conserv. Biol. **5**: 143-148.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M. (2017): Climatologies at high resolution for the earth's land surface areas. Sci. Data **4**: 170122.

Kéry, M. (2018): Identifiability in N-mixture models: a large-scale screening test with bird data. Ecology **99**: 281-288.

Kéry, M., Dorazio, R.M., Soldaat, L., Van Strien, A., Zuiderwijk, A., Royle, J.A. (2009): Trend estimation in populations with imperfect detection. J. Appl. Ecol. **46**: 1163-1172.

Kery, M., Royle, J.A. (2016): Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1:Prelude and Static Models. Academic Press, Burlington, MA.

Link, W.A., Schofield, M.R., Barker, R.J., Sauer, J.R. (2018): On the Robustness of N-mixture models. Ecology **99**: 1547-1551.

Lobo, J.M., Jiménez-Valverde, A., Real, R. (2008): AUC: a misleading measure of the perfromance of predictive distribution models. Global Ecol. Biogeogr. **17**: 145-151.

Luiselli, L., Rugiero, L., Capula, M. (2011): Are communal nesting counts as useful as mark-recapture data for estimating population size in snakes? Herpetol. J. **21**: 73-81.

Lunghi, E., Corti, C., Manenti, R., Ficetola, G.F. (2019): Consider species specialism when publishing datasets. Nature Ecol. Evol. **3**: 19.

Lunghi, E., Manenti, R., Mulargia, M., Veith, M., Corti, C., Ficetola, G.F. (2018): Environmental suitability models predict population density, performance and body condition for microendemic salamanders. Sci. Rep. **8**: 7527.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.A., Hines, J.E. (2017): Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. 2nd edition. Academic Press, Burlington, MA.

Mazerolle, M.J. (2015): Estimating detectability and biological parameters of interest with the use of the R environment. J. Herpetol. **49**: 541-559.

Mercalli, L., Cat Berro, D., Acordon, V., Di Napoli, G. (2008): Cambiamenti climatici sulla montagna piemontese. Rapporto tecnico realizzato da Società meteorologica Subalpina per conto di Regione Piemonte. Società Meteorologica Subalpina Castello Borello, Bussoleno (TO), Italy.

Nash, D.J., Griffiths, R.A. (2018): Ranging behaviour of adders (*Vipera berus*) translocated from a development site. Herpetol. J. **28**: 155-159.

Neumeyer, R. (1987): Density and seasonal movements of the adder (*Vipera berus* L. 1758) in a subalpine environment. Amphibia-Reptilia **8**: 259-275.

Nogués-Bravo, D. (2009): Predicting the past distribution of species climatic niche. Global Ecol. Biogeogr. **18**: 521-531.

Pateiro-López, B., Rodrjguez-Casal, A. (2010): Generalizing the convex hull of a sample: The R package alphahull J. Stat. Softw. **34**: 1-28.

Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, A.T. (2007): Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. **34**: 102-117.

Peterson, A.T., Soberon, J., Pearson, R.G., Anderson, R.P., Martinez-Meyer, E., Nakamura, M., Araujo, M.B. (2011): Ecological niches and geographic distributions. Princeton University Press, Princeton.

Phillips, S.J., Anderson, R.P., Schapire, R.E. (2006): Maximum entropy modeling of species geographic distributions. Ecol. Model. **190**: 231-259.

Pollock, K.H., Nichols, J.D., Simons, T.R., Farnsworth, G.L., Bailey, L.L., Sauer, J.R. (2002): Large scale wildlife monitoring studies: statistical methods for design and analysis. Environmetrics **13**: 105-119.

Potter, K.A., Arthur, W.H., Pincebourde, S. (2013): Microclimatic challenges in global change biology. Global Change Biol. **19**: 2932-2939.

Quintero, I., Wiens, J.J. (2013): What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. Global Ecol. Biogeogr. **22**: 422-432.

Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A., Peterson, A.T. (2003): Predicting distributions of known and unknown reptile species in Madagascar. Nature **426**: 837-841.

Rodda, G.H. (2012): Population size and demographics. In: Reptile biodiversity. Standard methods for inventory and monitoring, pp. 283-300. McDiarmid, R.W., Foster, M.S., Guyer, C., Gibbons, J.W., Chernoff, N., Eds, University of California Press, Berkley and Los Angeles, CA.

Royle, J.A. (2004): *N*-mixture models for estimating population size from spatially replicated counts. Biometrics **60**: 108-115.

Royle, J.A., Nichols, J.D. (2003): Estimating abundance from repeated presence-absence data or point counts. Ecology **84**: 777-790.

Santini, L., Isaac, N.J.B., Ficetola, G.F. (2018a): TetraDENSITY: A database of population density estimates in terrestrial vertebrates. Global Ecol. Biogeogr. **27**: 787-791.

Santini, L., Isaac, N.J.B., Maiorano, L., Ficetola, G.F., Huijbregts, M.A.J., Carbone, C., Thuiller, W. (2018b):

Global drivers of population abundance in terrestrial vertebrates. Global Ecol. Biogeogr. **27**: 968-979.

Senczuk, G., Castiglia, R., Böhme, W., Corti, C. (2019): *Podarcis siculus latastei* (Bedriaga, 1879) of the western Pontine islands (Italy) raised to the species rank, and a brief taxonomic overview of *Podarcis* lizards. Acta Herpetol.: doi: 10.13128/Acta_Herpetol-25159.

Sewell, D., Guillera-Arroita, G., Griffiths, R.A., Beebee, T.J.C. (2012): When is a species declining? Optimizing survey effort to detect population changes in reptiles. Plos One **7**: e43387.

Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P.A., Isailović, J.C., Denoël, M., Ficetola, G.F., Gonçalves, J., Kuzmin, S., Lymberakis, P., de Pous, P., Rodríguez, A., Sindaco, R., Speybroeck, J., Toxopeus, B., Vieites, D.R., Vences, M. (2014): Updated distribution and biogeography of amphibians and reptiles of Europe based on a compilation of country-wide mapping studies. Amphibia-Reptilia **35**: 1-31.

Sindaco, R., Doria, G., Razzetti, E., Bernini, F., editors. (2006): Atlas of Italian Amphibians and Reptiles. Polistampa, Firenze.

Slatyer, R.A., Hirst, M., Sexton, J.P. (2013): Niche breadth predicts geographical range size: a general ecological pattern. Ecol. Lett. **16**: 1104-1114.

Soulé, M.E. (1985): What is conservation biology? Bioscience **35**: 727-734.

Stoch, F., Genovesi, P. (2016): Manuali per il monitoraggio di specie e habitat di interesse comunitario (Direttiva 92/43/CEE) in Italia: specie animali. ISPRA, Roma.

Tenan, S., Pradel, R., Tavecchia, G., Igual, J.M., Sanz-Aguilar, A., Genovart, M., Oro, D. (2014): Hierarchical modelling of population growth rate from individual capture–recapture data. Methods Ecol. Evol. **5**: 606-614.

Tracewski, L., Butchart, S., Di Marco, M., Ficetola, G.F., Rondinini, C., Symes, A., Wheatley, H., Beresford, A., Buchanan, G. (2016): Toward quantification of the impact of 21st century deforestation on the extinction risk of terrestrial vertebrates. Conserv. Biol. **30**: 1070-1079.

Warren, D.L., Seifert, S.N. (2011): Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol. Appl. **21**: 335-342.

Weber, M.M., Stevens, R.D., Diniz-Filho, J.A.F., Grelle, C.E.V. (2017): Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. Ecography **40**: 817-828.

Zuffi, M.A.L., Macchia, M., Ioale, P., Giudici, F. (1999): Winter activity in a coastal population of *Vipera aspis* (Reptilia, Viperidae). Revue d'Ecologie-La Terre Et La Vie **54**: 365-374.

APPENDIX

Appendix S1. N-mixture models relating the detections of *Vipera walser* to variables potentially influencing abundance. The table reports the regression coefficient of each variable included in each model; models are ranked on the basis of the corrected Akaike's information criterion. Only models with weight >0.001 are shown. k: *N* of parameters in the model.

Model	Length of survey	Aspect	Altitude	Plot area	Precipitation	Slope	k	AICc	weight
1	0.69	-0.70	-	-	-	-	4	238.6	0.312
2	0.69	-0.68	-	-	0.06	-	5	240.8	0.103
3	0.70	-0.70	-	-0.02	-	-	5	240.9	0.098
4	0.69	-0.70	-0.01	-	-	-	5	240.9	0.097
5	0.69	-0.70	-	-	-	0.00	5	240.9	0.097
6	0.70	-0.71	-	-	0.10	-0.07	6	243.2	0.032
7	0.70	-0.68	-	-0.02	0.06	-	6	243.2	0.031
8	0.69	-0.68	-0.01	-	0.06	-	6	243.2	0.031
9	0.70	-0.70	-0.01	-0.02	-	-	6	243.3	0.029
10	0.70	-0.70	-	-0.02	-	0.00	6	243.3	0.029
11	0.69	-0.70	-0.01	-	-	0.00	6	243.4	0.029
12	0.73	-	-	-	-	-	3	244.4	0.017
13	0.72	-	-	-	-	0.21	4	245.2	0.012
14	0.71	-0.71	-	-0.02	0.10	-0.07	7	245.7	0.009
15	0.74	-	-	-	0.17	-	4	245.7	0.009
16	0.70	-0.71	0.00	-	0.10	-0.07	7	245.7	0.009
17	0.70	-0.68	0.00	-0.02	0.06	-	7	245.7	0.009
18	0.70	-0.70	-0.01	-0.02	-	0.00	7	245.8	0.008
19	0.74	-	-	-0.04	-	-	4	246.7	0.006
20	0.72	-	0.03	-	-	-	4	246.7	0.006
21	0.72	-	-	-	0.06	0.17	5	247.4	0.004
22	0.73	-	-	-0.04	-	0.21	5	247.5	0.004
23	0.72	-	0.00	-	-	0.21	5	247.5	0.004
24	0.75	-	-	-0.03	0.16	-	5	248	0.003
25	0.74	-	0.02	-	0.17	-	5	248	0.003
26	0.71	-0.71	0.00	-0.02	0.10	-0.07	8	248.2	0.003
27	0.74	-	0.03	-0.04	-	-	5	249	0.002
28	0.73	-	-	-0.03	0.06	0.17	6	249.8	0.001
29	0.72	-	0.01	-	0.06	0.17	6	249.8	0.001
30	0.73	-	0.00	-0.04	-	0.21	6	249.9	0.001
31	0.75	-	0.03	-0.03	0.17	-	6	250.4	0.001