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Has the West been won? A field survey and a species distribution model of *Iberolacerta horvathi* in the Alps

Giuseppe De Marchi[1,*], Giovanni Bombieri[1], Bruno Boz[1], Fausto Leandri[2], Jacopo Richard[3]

[1] *Associazione Faunisti Veneti, Venezia (VE), Italy*
[2] *World Biodiversity Association onlus, c/o Museo Civico di Storia Naturale, Verona (VR), Italy*
[3] *Veneto Agricoltura, Agenzia Veneta per l'Innovazione nel Settore Primario, Legnaro (PD), Italy*
* *Corresponding author*. Email: dromasardeola@gmail.com

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Abstract. The Horvath's rock lizard (*Iberolacerta horvathi*) is a rupicolous mountain species endemic of the eastern Alps and northern Dinaric range. The species has its known western limit of the distribution in the Veneto region of Italy. It is not known whether the species is really rare in Veneto or whether the area has been insufficiently surveyed. In addition, it is not known whether the westward distribution of the species is limited by a physiographic or by a climatic barrier. During the period 2016-2018, 118 sites were surveyed in the Veneto and Trentino-Alto Adige regions. Four new occurrences of *Iberolacerta horvathi* were discovered in Veneto that: 1) largely fill the gap between the westernmost known site and the closest site to the east; 2) extend further west the known distribution by 9 km. In addition the species was confirmed in three already known sites. A species distribution model was developed with the software MaxEnt, using 100 occurrences from Italy, Austria and Slovenia. The best model shows that the distribution is explained by the asperity of their habitat, the sedimentary bedrock, the aspect, the average temperature of the coldest quarter, the rainfall seasonality and the average summer rainfall. The last variable appears as the most likely responsible for the rarefaction of the species at its western limit. In addition, the species distribution model suggest that the Horvath's rock lizard might be present in some additional mountain groups where it has so far not been found yet.

Keywords. Horvath's rock lizard, Maxent, rainfall, temperature, roughness, aspect, Bedrock, Veneto.

INTRODUCTION

The present distribution of reptiles in Europe is much dependent on its climatic history, in particular to the Pleistocene oscillations. After the climate improvement following the last glacial maximum (18,000 BP) many species spread from southern refugia and have colonized very large areas (Joger et al., 2007). Some species were able to spread from their refugia in a more limited way due to ecological constraints or to the presence of geographical barriers like the Alps for species from the Apennines peninsula and the Pyrenees for species from the Iberian peninsula (Joger et al., 2007). The opposite happened to some cold adapted species, like the *Dinolacerta* mountain lizards of the southern Dinaric chain and the species of *Iberolacerta* of the Iberian Peninsula: they have likely reduced their range and have become restricted to high altitude isolated mountain peaks (Ortega et al., 2016). The conservation prospect of these high altitude species is likely going to worsen due to the ongoing climate change (Le Galliard et al., 2012).

A different case is the distribution of the Horvath's Rock Lizard (*Iberolacerta horvathi*), an endemic species of the northern Dinaric chain and eastern Alps (north-

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west Croatia, Slovenia and adjoining northeastern Italy and southern Austria) (Speybroeck et al., 2016), a species phylogenetically related to a group of mountain dwelling lizards of the Iberian Peninsula (Carranza et al., 2004, Crochet et al., 2004). As a matter of facts, the known presence localities in Italy and Austria are in areas that were glaciated during the last glacial maximum (Ivy-Ochs et al., 2009). So, the species should have colonized the eastern Alps from refugia in the southeastern Alps or from the Dinaric chain. Unfortunately, it is difficult to study how this colonization happened due to insufficient knowledge of the distribution of this species, as suggested by the recurrent discoveries of its presence in new mountain groups (e.g., Žagar et al., 2014). This lack of data is likely the result of the difficult accessibility of the rocky cliffs inhabited by the species and by the possible misidentification with the similarly looking (Žagar et al., 2012) and frequently syntopic common wall lizard, *Podarcis muralis* (Cabela et al., 2007). In Italy, Horvath's rock lizard is well distributed in the Friuli region (Lapini et al., 2004; Rassati, 2010; Rassati, 2012) but its presence appears to be particularly scattered west of the Piave River in the Veneto region. The westernmost site was discovered in 1993 close to the village of Listolade (Lapini and Dal Farra, 1994; Lapini et al., 2004), a site that was about 70 km away from the nearest known site. In spite of subsequent discoveries (Rassati, 2010; Rassati, 2012; Lapini, 2016) and quite extensive surveys (Tormen et al., 1998; Bonato et al., 2007; Bonato, 2011; Cassol et al., 2017) there is still a gap of around 30 km between the site of Listolade and the closest one to the east. Therefore, it is not known whether the species is present in this large gap and even west of Listolade. Moreover, it would be interesting to discover whether the species has reached its potential distribution or whether its westward post glacial expansion is still lagging behind its potential distribution, as it still happens for some plants (Svenning and Skov, 2007; Willner et al., 2009; Dullinger et al., 2012) and animals (Araújo et al 2008; Pinkert et al., 2018). In addition it is not known which factors might limit or have limited the westward spread of the species.

In order to fill these gaps in the knowledge of the species, the research has the following aims:

1) to improve the known distribution by surveying mountain groups west of the Piave River in the Trentino-Alto Adige and Veneto regions of Italy;

2) to correlate the presence of the species in Italy, Austria and Slovenia to climatic, geological, physiographic and ecological parameters in order to estimate, through a species distribution model, whether the western limit of the distribution has likely been fixed or whether new sightings further west should be expected.

MATERIAL AND METHODS

Field survey

Surveys were conducted during 94 days in the period April 2016 - September 2018 in 118 sites by one to three researchers per site. 20% (n = 24) of the sites were visited more than once. Surveyed areas were concentrated west of the Piave River but a few sites were investigated also just east of it. Due to the inaccessibility of many cliffs, investigated sites were not randomly distributed but were inevitably concentrated close to roads and mountain paths.

Species identification was rarely performed by catching the specimens with a long stick with a cotton loop. More commonly, species identification was performed by analysing pictures taken with a telephoto lens, an efficient technique also when lizards are on inaccessible rocky cliffs (De Marchi et al., 2019). Identification characters from the frequently syntopic common wall lizards are as in Corti et al. (2010).

The coordinates and altitude of the sites were obtained by hand held GPS devices. In addition, the sites where Horvath's rock lizards were found were characterized by the bedrock obtained from the geological map of Italy viewed on the Geoportale Nazionale (http://www.pcn.minambiente.it) and by the habitat classification obtained from the "Carta della Natura" of Veneto and "Carta della Natura" of Friuli-Venezia Giulia (1:50.000) (http://www.geoviewer.isprambiente.it/).

Species distribution model (SDM)

In order to elaborate the potential distribution of the species in Italy and in neighbouring Austria and Slovenia, a presence only modeling approach was chosen due to the lack of reliable absence points particularly outside our study area. A maximum entropy approach was developed with the software Maxent (Phillips et al., 2006; Merow et al., 2013; Phillips et al., 2017), which proved to be quite successful even when occurrence data were few and in presence of somehow biased samples (Elith et al., 2006). As occurrence data of Veneto are few and restricted to a too small area for statistical analyses, published data related to Italy (Lapini et al., 2004; Rassati, 2010; Rassati, 2012; Lapini, 2016; Lapini, 2017; Rassati, 2017), Austria (Tiedeman, 1992; Ortner, 2006; Cabela et al., 2002; Cabela et al., 2007) and Slovenia (Žagar, 2008a; Žagar, 2008b; Krofel, 2009; Cafuta, 2010; Žagar et al., 2011; Žagar et al., 2012; Osojnik et al., 2013; Žagar, 2016; Zauner, 2018) were collated. Such a wider area helps to reduce the risk that some local climatic conditions might wrongly highlight the importance of an environmental variable that in fact is not a relevant one (Phillips, 2006). Unfortunately, some published occurrences lacked coordinates but have only the altitude and a general description of the collecting site: only when the description was considered sufficiently detailed to be confidently associated to a single 300 m × 300 m pixel (see later) the occurrences were used by extracting the coordinated from Google-Earth. As some occurrences are aggregated due to sampling bias, some occurrence localities were manually removed so that the remaining ones are at least one km from the closest ones. Eventually, the 100 occurrences of the Horvath's lizard were joined together with a background dataset of 10,000 points to randomly sample the analysed area (lat 45.35°N to 47.00°N, lon 11.20°E to 15.00°E).

The environmental layers (all at European scale) were as follows. 19 bioclimatic variables at 30-arc seconds (about 1km) resolution derived from the monthly temperature and rainfall values for the period 1970-2000 (http://www.worldclim.org/bioclim). Slope, Roughness (the degree of irregularity of the surface, calculated by the largest inter-cell difference of a central pixel and its surrounding cell, as suggested by Wilson et al., 2007) and Aspect (the compass direction that a slope faces with values ranging 0-360°) layers calculated with the GIS software QGIS (version 2.8.6) from a 25m digital elevation model (Layer: DEM-v1.1-E40N20) downloaded from the Copernicus Land Monitoring Service (https://land.copernicus.eu/). A 250m vegetation layer, Corine Land Cover clc_12 (version 18_5), again downloaded from the Copernicus Land Monitoring Service. A geological layer from the 1 : 5 Million International Geological Map of Europe and Adjacent Areas (IGME5000, Asch, 2003) with bedrock types reclassified in the following five categories: crystalline (all igneous and metamorphic rocks), carbonates (limestone, dolomite or carbonates as predominant bedrocks), secondary carbonates (limestone, dolomite or carbonates locally present but not as predominant bedrocks), other sedimentary rocks (like sandstone, conglomerate et clay) and undifferentiated bedrock. All environmental layers were resampled to a resolution of 300 m using the package "raster" in R (Hijmans and van Etten, 2016).

While Maxent is partly able to balance between model fitting and model simplicity, an information approach was adopted to check whether simpler models with fewer variables performed better (Warren and Seifert, 2011; Zeng et al., 2016). First, a reduced set of environmental variables was pre-selected, based on ecological or biological knowledge. Out of the 19 available bioclimatic variables, BIO1 (Annual Mean Temperature), BIO4 (Temperature Seasonality), BIO5 (Max Temperature of Warmest Month), BIO6 (Min Temperature of Coldest Month), BIO10 (Mean Temperature of Warmest Quarter), BIO11 (Mean Temperature of Coldest Quarter) BIO12 (Annual Precipitation), BIO 15 (Precipitation seasonality), BIO18 (Precipitation of Warmest Quarter) and BIO19 (Precipitation of Coldest Quarter) were selected. Then, a reiterative process of model formation and stepwise removal of the least contributing variables was utilized (Zeng et al., 2016). Unfortunately, most temperature related variables (BIO1, BIO5, BIO6, BIO10, BIO11) were highly correlated (pearson coefficient >0.7). In a similar way most rainfall related variables (BIO12, BIO18, BIO19) were highly correlated. Therefore, Maxent models were run in order to select the single most predictive temperature variable and the single most predictive rainfall variable. This was done (Table 2) by running Maxent models (regularization multiplier was set at 1 and regularization values were linear-quadratic-product) alternatively containing only one of the correlated variables for temperature (BIO1, BIO5, BIO6, BIO10, BIO11) and only one of the correlated variables for rainfall (BIO12, BIO18, BIO19). Among the alternative models the one with the lowest Akaike information criterion corrected for low sample size (AICc) calculatd with the software ENMTOOLS version 1.4.4 (Warren and Seifert, 2011; Shcheglovitova and Anderson, 2013) was selected. The AICc is an estimator of the relative quality of statistical models for a given set of data, trading-off between the simplicity of the model and the goodness of fit of the model (Warren and Seifert, 2011). Then, simpler models were constructed by stepwise removal of the variable with the lowest permutation importance (Zeng et al., 2016) and the AICc of the resulting models was calculated in order to select the final set of variables. As "feature class" and "regularization multiplier" affect the performance of the model (Morales et al., 2017) the model was fine tuned by constructing models with 7 levels of the regularization multiplier (0.05, 0.1, 0.5, 1, 2, 4, 10) and three regularization values (Linear-Quadratic, Linear-Quadratic-Product and Hinge). Finally, the best model (Regularization value = Linear-Quadratic; Regularization multiplier = 0.1) was run 100 times with bootstrap resampling and the average model was calculated. The quality of this final model was tested by calculating the area under the curve (AUC) of the receiver operated characteristic (ROC) plots in order to discriminate a species' model from a random model. Finally, the percent contribution and permutation importance of the environmental variables to the final Maxent model were measured (Phillips, 2006).

RESULTS

The Horvath's Lizard was found in four new sites (Valle di San Lucano, Val del Grisol, Casoni and Forra del Piave) and its presence was confirmed in three sites (Monte Tudaio, Val Zemola and Listolade) already known in literature (Fig. 1). Fig. 2 shows the habitat of the four new occurrences for Horvath's Lizard and Table 1 reports some characteristics of all the seven sites.

The common wall lizard was observed in 60% of the investigated sites (n = 71, Fig. 1) and was frequently syntopic with the Horvath's rock Lizard, where this last species occurred (Table 1).

Species distribution model.

The Mean Temperature of Coldest Quarter (BIO11) turned out to be a better predictor of the distribution of the Horvath's rock lizard (Table 2) compared to other highly correlated temperature variables: Annual Mean Temperature (BIO1), Max. Temperature of Warmest Month (BIO5), Min. Temperature of Coldest Month (BIO6) and Mean Temperature of Warmest Quarter (BIO10). The Precipitation of Warmest Quarter (BIO 18) turned out to be a better predictor of the distribution (Table 2) compared to other highly correlated precipitation variables: Annual Precipitation (BIO12) and Precipitation of Coldest Quarter (BIO19).

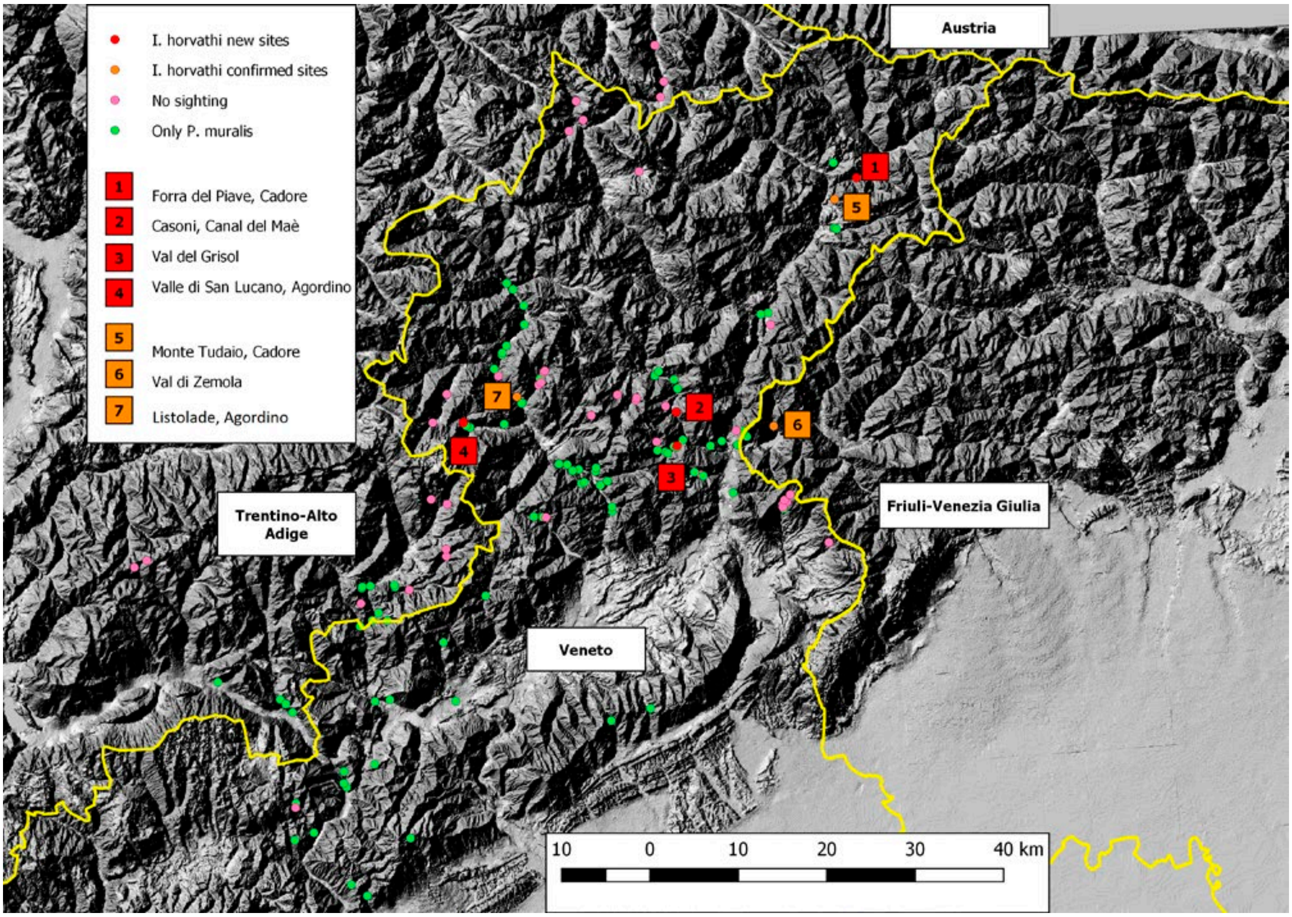

Fig. 1. Sites surveyed in 2016-2018. Red dots show the newly discovered occurrences of *Iberolacerta horvathi*, while orange dots show some confirmed occurrences.

The balancing between the simplicity of the model and goodness of fit to the known distribution resulted in a model that did not include Slope, Temperature Seasonality (BIO4) and Vegetation type (Corine Land Cover), the variables with the lowest permutation importance. As a result, the best model was explained only by Mean Temperature of Coldest Quarter (BIO11), Rainfall Seasonality (BIO15), Precipitation of Warmest Quarter (BIO18), Aspect, Roughness and Bedrocks (Table 2).

The best distribution model obtained after fine tuning (see methods and table 2) is shown in Fig. 3 (with cloglog output, which is the easiest to conceptualize as it gives an estimate between 0 and 1 of probability of presence). The model fits the distribution (average training AUC for the 100 bootstrap replicate runs is 0.922, standard deviation is 0.009) much better than a random model (AUC = 0.5). The variables that explain the distribution of the species are in order of percent contribution (Table 3): Roughness (33%), Bedrocks (26.5%), Mean Temperature of Coldest Quarter (19.5), Aspect (8.9), Rainfall of the Warmest Quarter (8.5%) and Rainfall seasonality (3.3).

Rainfall of the Warmest quarter decreases westward in the Italian Alps (Fig. 4): the 13 westernmost occurrences are in areas with a rainfall (Average±SD = 338 ± 37mm, n = 13) that is significantly lower (Welch Test = -9.67, $P < 0.001$) than the remaining occurrences (Average ± SD = 452 ± 53mm, n = 87).

DISCUSSION

Our field survey has discovered four new sites of Horvath's rock lizard in Veneto (Table 1 and Fig. 1 and 2): Forra del Piave is close to already known sites; Casoni (in the Bosconero mountain group) and Val Grisol (in the Schiara mountain group) fill the gap between the known westernmost site of Horvath's lizard and the previously known sites to the east; San Lucano Valley (in

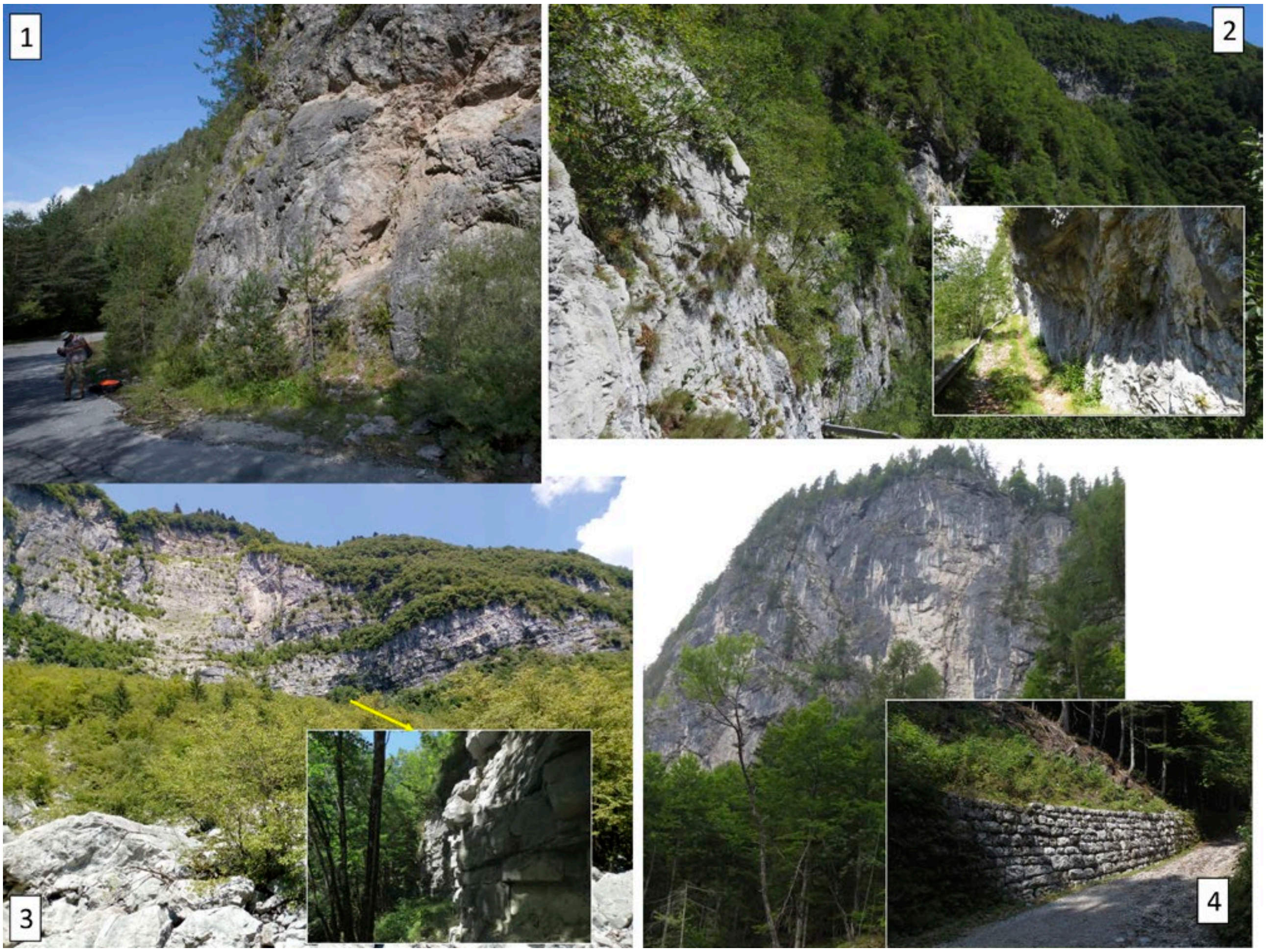

Fig. 2. Pictures showing the habitats of the newly discovered sites of Horvath's rock lizard. 1. Forra del Piave, Cadore; 2. Casoni, Canal del Maè; 3. Val del Grisol; 4. Valle di San Lucano, Agordino. In the last site, the first single individual was observed on the rock wall along the road; later, the presence of a more numerous population was documented in the neighbouring rocky cliffs (around 200 m away).

Pale di San Martino mountains) extends further west the known distribution by 9 km. Our extensive research in apparently suitable sites west of San Lucano Valley, in particular in the Vette Feltrine mountains and in the Valsugana Valley (Fig. 1 and Fig. 4), has been unable to discover additional sites. This lack of positive results suggests that the western limit of the distribution has been discovered. Interestingly, the San Lucano Valley is also the western limit in the southern Dolomite mountains of another reptile of eastern origin, the Nose-horned viper (*Vipera ammodytes*) (Sindaco et al., 2006), a species that has been found to have a close habitat similarity with Horvath's rock lizard also in another part of its distribution (Žagar et al., 2013). There is apparently no physiographic barrier to the spread of the lizards further to the west. As a matter of fact, a gravel bed mountain river like the Cordevole river (Fig. 4) should have not been a barrier to the westward spread of the species as proved by our discovery of the species just west of this river in the San Lucano Valley. In the past, gravel bed mountain rivers such as the Piave and the Cordevole (Fig. 4) should have been an even less effective barrier to the spread of the species during the phase of great sedimentation in the valleys that followed the deglaciation (Cordier et al., 2017) and continued up to 7000 BC in the Piave Valley (Carton et al., 2009): in this condition, water mostly flowed deep inside the gravel bed (Arscott et al., 2001) and could not stop the spread of lizards. Therefore, the lack of any apparent physiographic barrier lets us suggest that an environmental gradient should make the species less abundant in Veneto, where it is definitely rare, until it disappears. In general, an environmental variable might affect directly the species physiology (e.g., temperature) or might act in an indirect way by influencing

Table 1. Characteristics of the new and confirmed occurrences of Horvath's lizard surveyed in 2016-2018. The number associated to each site is the same as in Fig.1 and Fig. 2.

Site * new + confirmed	Date (day, month, year)	Coord. (°N, °E)	Altitude (m)	Aspect	Bedrock (from Geoportale nazionale italiano)	Vegetation (CNAT of Veneto and Friuli-Venezia Giulia)	Observed specimens	Syntopic Common Wall Lizard
1. Old road in Forra Piave, Santo Stefano di Cadore (BL), Veneto *	13.08.16 08.08.17	46.53516, 12.50901. 46.53258, 12.49400	825-870	S	R67: Neritic and platform dolomites (medium Triassic)	Scots pine oriental forest	Up to 3	Yes
2. Casoni, Canal del Maè, Forno di Zoldo (BL), Veneto *	25.08.17 27.08.17 01.07.18 08.07.18	46.30444, 12.22972	750-850	SO	R58: Pelagic limestones, marly limestone and marl (Jurassic)	Thermophilic calciphile beech forest of the Alps	Up to 8	Yes
3. Grisol de Entro, Val del Grisol, Longarone (BL), Veneto *	25.07.18	46.27017, 12.22878	825	SE	R58: Pelagic limestones, marly limestone and marl (Jurassic)	Ostrya carpinifolia thicket	1	Yes
4. Pont, San Lucano Valley, Taibon Agordino (BL), Veneto *	6.8.2018 9.8.2018 17.8.2018	46.30201, 11.91715. 46.30200, 11.91658. 46.30113, 11.91685.	1200-1250	NE-E	R67: Neritic and platform Dolomites (medium Triassic)	Calciphile fir forest of the Alps and central-northern Apennines	4	No
5. Monte Tudaio, Vigo di Cadore (BL), Veneto +	12.08.16	46.51413 12.47563	886	S	R67: Neritic and platform dolomites (medium Triassic)	Scots pine oriental forest	1	Yes
6. Val Zemola, Erto and Casso (PN), Friuli Venezia Giulia +	18.06.17 08.07.18	46.28607, 12.37178	1020	NE	R56: Neritic and platform limestones and sometimes dolomites (Jurassic)	Thermophilic calciphile beech forest of the Alps	Up to 2	No
7. Climbing rock, Listolade, (BL), Veneto +	22.05.16 25.09.16 13.04.17 09.09.18	46.32622, 11.99672	720	SO	R67: Neritic and platform Dolomites (medium Triassic)	Acidophile scots pine forest	Up to 11	Yes

the availability of food (e.g., rainfall) or the presence of parasites, predators or competitors (Austin, 2002). An important factor that might limit the abundance and the distribution of the Horvath's rock lizard may be the strong competition with the common wall lizard (*Podarcis muralis*) (Carranza et al., 2004). The two species have a similar overall body plan (Žagar et al., 2012) and similar ecological preferences, for example they eat similar food (Richard and Lapini, 1993). However, Horvath's rock lizards appear more adapted to rocky habitats due to their flat head and body (Corti et al., 2010), which might favour hiding in small crevices. They are more adapted to relatively cold habitats due to a higher potential metabolic activity (Žagar et al., 2015b), even if they do not exhibit the partial development of the egg inside the female body that is found in some other small mountain lizards (Ljubisavljević et al., 2012). On the contrary, common wall lizards are favoured in agonistic interactions with Horvath's rock lizards because of their larger head and consequent stronger biting force (Žagar et al., 2017), for example when competing for thermoregulation spots (Žagar et al., 2015a). Common wall lizards may be favoured as well for their higher reproductive potential (Amat, 2008). As a result, Horvath's rock lizards are confined to rocky habitats in low altitude shady gorges, at mid altitude in beech forest and to higher altitudes compared to the common wall lizards (Žagar, 2016). Vegetation type has not turned out to be important in our analysis for predicting the distribution of the Horvath's rock lizards likely because the Corine Land Cover classification that is currently available for our study area has been developed only to the "third level". This means, for example, that forests are classified only to the level of "coniferous forests" or "mixed forests", a level that is likely not enough for a proper classification.

Apart from the land cover classification, our analysis of the importance of the variables that constrain the distribution of the Horvath's lizard (Table 3) largely agrees with the previous results (Cabela et al., 2007; Žagar, 2016).

Table 2. AICc scores of different Maxent species distribution models varying in number of variables, features and regularization multipliers (see methods for details). The best model (in bold) is the one with the lowest AICc

Model #	Variables	Features	Reg.mult	AICc
1	BIO1,BIO4, BIO12, BIO15, Aspect, Asperity, Slope, Corine, Bedrock	LQP	1	2459.82
2	BIO5,BIO4, BIO12, BIO15, Aspect, Asperity, Slope, Corine, Bedrock	LQP	1	2468.09
3	BIO6,BIO4, BIO12, BIO15, Aspect, Asperity, Slope, Corine, Bedrock	LQP	1	2472.79
4	BIO10,BIO4, BIO12, BIO15, Aspect, Asperity, Slope, Corine, Bedrock	LQP	1	2465.77
5	BIO11,BIO4, BIO12, BIO15, Aspect, Asperity, Slope, Corine, Bedrock	LQP	1	2453.00
6	BIO11,BIO4, BIO18, BIO15, Aspect, Asperity, Slope, Corine, Bedrock	LQP	1	2447.56
7	BIO11,BIO4, BIO19, BIO15, Aspect, Asperity, Slope, Corine, Bedrock	LQP	1	2463.85
8	BIO11,BIO4, BIO18, BIO15, Aspect, Asperity, Corine, Bedrock	LQP	1	2452.31
9	BIO11, BIO18, BIO15, Aspect, Asperity, Corine, Bedrock	LQP	1	2447.72
10	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQP	1	2429.10
11	BIO11, BIO15, Aspect, Asperity, Bedrock	LQP	1	2430.33
12	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQP	0.05	2424.50
13	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQP	0.1	2431.21
14	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQP	0.5	2424.09
15	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQP	2	2442.47
16	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQP	4	2462.02
17	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQP	10	2529.97
18	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQ	0.05	2423.22
19	**BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock**	**LQ**	**0.1**	**2422.58**
20	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQ	0.5	2424.63
21	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQ	1	2431.17
22	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQ	2	2447.09
23	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQ	4	2459.09
24	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	LQ	10	2530.51
25	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	H	0.5	2795.60
26	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	H	1	2602.81
27	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	H	2	2529.67
28	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	H	4	2532.34
29	BIO11, BIO18, BIO15, Aspect, Asperity, Bedrock	H	10	2571.21

Table 3. Relative contributions of the environmental variables to the best Maxent model (see methods for details) for the distribution of Horvath's rock lizard.

Variable	Percent contribution (%)	Permutation importance (%)
Roughness	33.3	26.7
Bedrock	26.5	16.6
Temperature of the coldest quarter	19.5	38
Aspect	8.9	6
Rainfall of the warmest quarter	8.5	3.5
Rainfall seasonality	3.3	9.2

Roughness turns out to be important certainly due the preference of the Horvath's lizard for steep rocky areas. However, the pixel resolution of our analyses (300 m), constrained by the imprecision of the coordinates of the occurrences, is not enough to discriminate between rocky and simply steep slopes. That's why some areas that are likely unsuitable, like Visentin Mountain just south of Belluno, are predicted as suitable (Fig. 3 and 4).

The categorical variable Bedrock confirmed the importance of sedimentary rocks for the presence of the species with the highest suitability (more than 70%) in areas with the dominant bedrocks consisting of carbon-

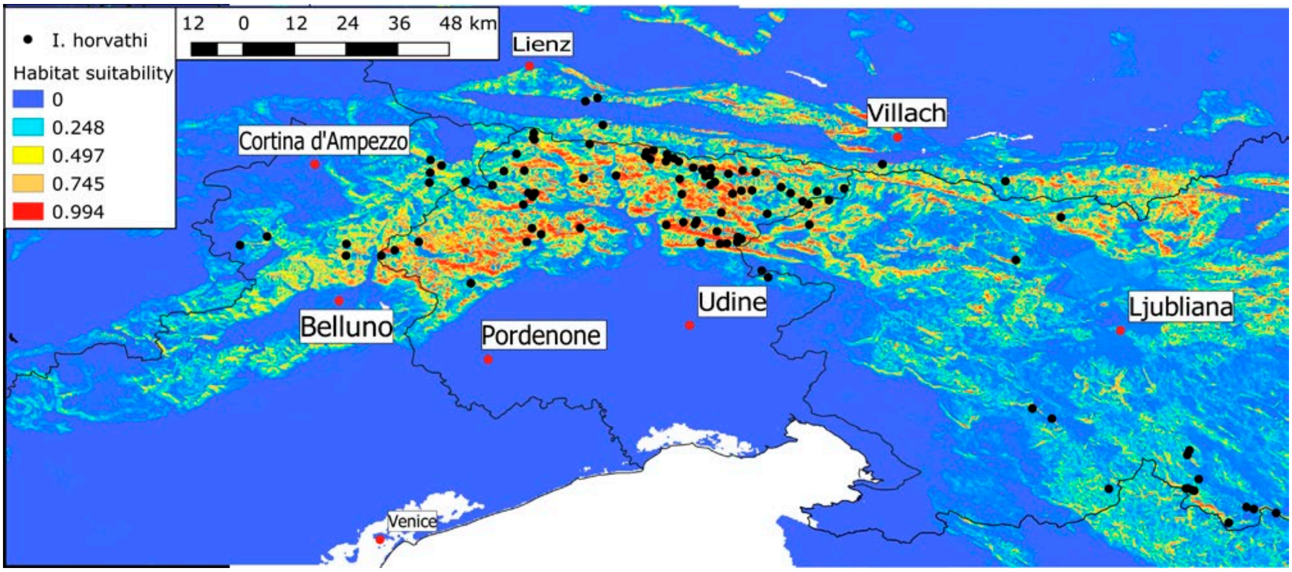

Fig. 3. The best species distribution model of Horvath's rock lizard in the Alps and neighbouring Dinaric Chain based on 100 occurrences (black dots) in Italy, Austria and Slovenia. The output is "cloglog", which gives an estimate between 0 and 1 of the probability of presence.

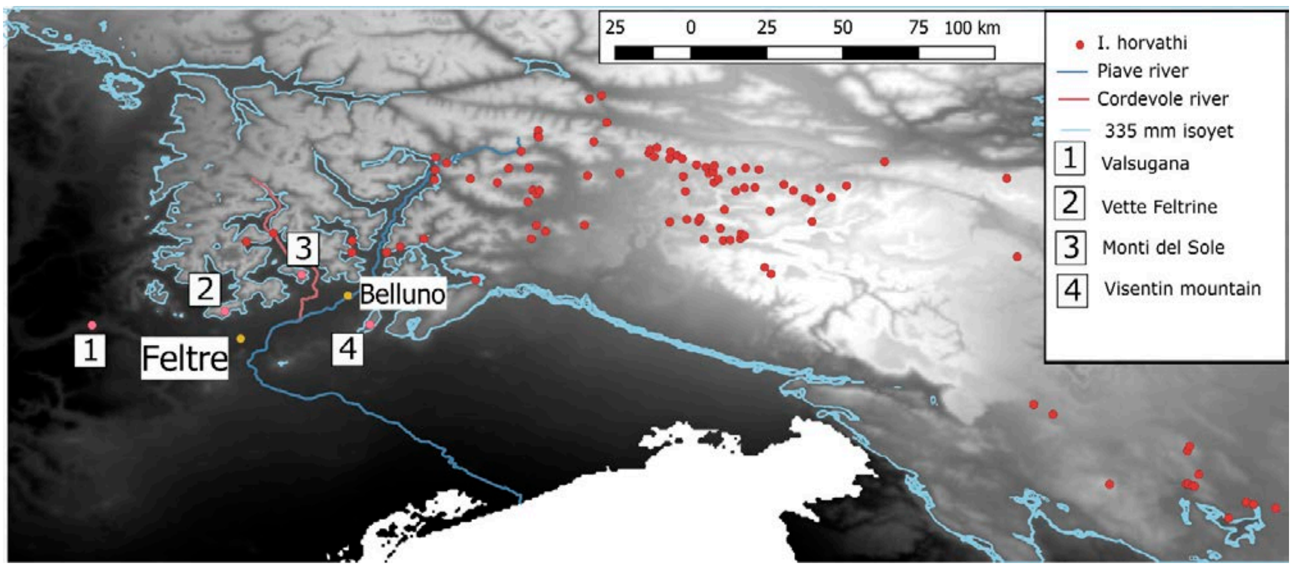

Fig. 4. Rainfall (the lighter areas the higher rainfall) during the warmest quarter. Yellow dots show the 100 occurrences of Horvath's rock lizard. The light blue line is the 335 mm isohyet. The location of some areas mentioned in the Discussion are added.

ates, dolomite and limestone, and with an intermediate suitability (40%) for areas where these three types of rocks are present, even if they are not dominant. A lower suitability (about 28%) was found for other types of sedimentary bedrocks. The remaining two types of bedrocks (metamorphic-magmatic and undifferentiated) were predicted as unsuitable. This result likely stems from the need of the lizard for fissured rocks where they can hide from predators and where rock dwelling plants (important for attracting the invertebrate food) can take root.

The inclusion of temperature as an important variable was similarly expected as the species is generally considered cold-adapted and able to live at higher altitudes and in shadier places compared to the frequently syntopic common wall lizard (Žagar, 2016). Why the temperature of the coldest quarter turned out to be the most important temperature related variable is not clear. It might be related to the duration of the snow cover and a too brief warm season for the species to thrive. Instead, the importance of a physiological limit for survival at low temperatures would have probably resulted in a higher importance of the minimum winter temperature.

Aspect is of course important as the lizards need direct sunlight for warming up and the north aspect is unsuitable (Žagar, 2008a). So, in spite of the low resolution of the occurrences that might mask the exact aspect of the cliff, this variable is a significant percent contribution (8.9%) in explaining the best model of distribution.

Our model shows the importance of two rainfall related variables, rainfall seasonality and average rainfall during the warmest quarter. Rainfall seasonality increases westward in the Eastern Alps (data not shown) but why rainfall seasonality might be important for the ecology of the species is not clear yet. Its ability to explain the distribution is, at any rate, very low (3.3%). The higher percent contribution of summer rainfall (8.5%) might stem from its likely importance to the growth of rupicolous plants where the Horvath's rock lizards look for food. Common wall lizards are comparatively less dependent on this hunting ground as they are much more euryecious (Sindaco et al., 2006). In addition, summer rainfall might be directly important as a source of drinking water as we have observed Horvath's lizards drinking in wet, dripping parts of the cliffs. Interestingly summer rainfall decreases westwards in the eastern Alps and the 13 westernmost occurrences (almost all in Veneto) are all close to the 335 mm isohyet (Fig. 4). So, the rarity of the species west of the Piave river and its disappearance further west might effectively depend upon a reduced rainfall during the warmest quarter. Two mountain groups, the Monti del Sole and the Vette Feltrine, appear suitable (Fig. 3) and are not separated by any significant physiograghic barrier from the four westernmost occurrences (Fig. 4); they should deserve additional field surveys even if a recent research (Cassol et al., 2017) and our data have so far failed to confirm the species in those areas.

The major limitation of our study comes from the low precision of the occurrences that did not allow a deeper analysis of the roughness and the inclusion of other factors that can be important, such as solar radiation, which can change radically within a few meters in rocky areas and is certainly important in the context of the competition with the common wall lizard. Future species distribution models based on more precise occurrences (Ernst, 2017) and on finer scaled climatic variables (now at 1 km resolution) can improve our understanding of the ecological niche of the species. Hopefully, phylogeographic studies (Cocca et al., 2016) will soon shed light on the glacial refugia where the Horvath's lizards survived before colonizing the deglaciating Alps.

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