

A step towards SDMs: A “couple-and-weigh” framework based on accessible data for biodiversity conservation and landscape planning

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Abstract

Aim: The ongoing global change makes landscape planning and management of ecological corridors crucial to preserve biodiversity. We propose a workflow optimizing the use of different data sources to convert ecological niche models (ENMs) into landscape-focused species distribution models (SDMs), using these latter to compute ecological corridors. We infer corridors connecting present occurrence localities to future climatic refugia as well as to localities where extinct populations occurred. Also, a continuous connectivity change index is proposed to assess current–future differences. Finally, we discuss possible applications of our workflow to conservation, assessing the capability of established protected areas to preserve ecological corridors.

Location: Europe.

Methods: As case study to illustrate our framework, we use a database comprising occurrence localities of *Vipera ursinii*, one of the most endangered European reptiles. We obtain weighted SDMs for each of the four *V. ursinii* subspecies by coupling climate-based ENMs with standardized occurrence frequencies along land use and altitude gradients through weighted averaging in GIS. We calculate current and future landscape connectivity for each subspecies based on the corresponding weighted SDM. We compare predictive performance of “traditional” ENMs, including climate, land use and topography as predictors and weighted SDMs.

Results: Weighted SDMs outperform ENMs, according to Boyce index. SDMs are used to infer connectivity, predicted to decrease in all future scenarios for *V. ursinii*, and assess where connections may favour movements of individuals to, for example, future suitable areas. Generally, protected areas are predicted to cover low-connectivity territories.

Main conclusions: The proposed “couple-and-weigh” approach could represent a helpful tool to investigate biogeography, conservation and landscape planning topics, as it permits to capitalize on occurrence records and accessible environmental

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predictors by narrowing the target species' potential distribution, estimated within "traditional" ENMs, to the realized one through post-modelling GIS analyses, which in turn improves estimation of friction maps used to infer connectivity.

KEYWORDS

Circuitscape, ecological corridors, landscape connectivity, open data capitalization, protected areas, species distribution models, *Vipera ursinii*, weighted suitability

1 | INTRODUCTION

Maintaining connections among natural areas through ecological corridors (Forman, 1995; Vos et al., 2002) represents a priority for biodiversity conservation. Ecological corridors facilitate the exchange of individuals among populations, essential to favour gene flow preserving genetic diversity. In the Anthropocene, ecological connectivity is fundamental to let individuals move through suitable natural areas included in a non-suitable matrix (e.g. highly human-impacted landscape patches; Beauguard et al., 2020; Ford et al., 2020). Consequently, several theoretical and technical studies were published to support ecological corridor planning, as well as to assess the efficacy of connectivity over time (e.g. Ford et al., 2020; Kremen & Merenlender, 2018; Lashari et al., 2020; Xiao et al., 2020).

Many software applications were developed to address corridors' location and design (for the most recent state of art, see Ribeiro, et al. (2017)). They take advantage of increasing computational power and efficient algorithms specifically developed to process massive data. One of such software packages, Circuitscape, uses circuit theory to classify the whole landscape in terms of connectivity value (McRae et al., 2008). As recently reviewed (Dickson et al., 2018), circuit theory gained more and more support among conservationists and landscape ecologists because it overcomes the many limitations of the other approaches, such as the "route selection" assumption (i.e. individuals' knowledge about the landscape they move through) (McClure et al., 2016; McRae et al., 2016).

A further core element of corridor modelling is the "friction map", representing the resistance (e.g. land use, topography, vegetation cover, urban-to-natural gradients) that the target landscape offers to the movement of individuals (Adriaensen et al., 2003). Predictions from ecological niche models (ENMs) can be used as friction maps (Di Febbraro et al., 2019; Rippa et al., 2011); nonetheless, converting an ENM into a species distribution model (SDM) (Peterson & Soberón, 2012) could maximize information that the derived friction map provides to the corridors modelling software.

ENMs can be converted to SDMs through post-modelling analysis; for instance, predictions from a climate-based ENM can be cut based on variables (e.g. urbanized areas) not included during model fitting (Costanza et al., 2020; Pearson & Dawson, 2003). As a potential flaw, this approach may lead to information loss by *a priori* removing from the model output some landscape patches which instead may be suitable for a part of the species' life cycle

(e.g. occasional or seasonal movements, see Barve et al. (2011) for the role of accessible areas in ecological modelling). Also, Mendes et al. (2020) clearly found that a posteriori methods perform better than a priori ones, especially to deal with over- and underpredictions which can derive from models fitted on many multicollinear variables (Dormann et al., 2013). In this paper, we take advantage of presence-only data (i.e. species' occurrences) and environmental predictors to model connectivity by integrating all the information about species' requirements within a weighted scheme, coupling ENM and GIS techniques.

We apply this "couple-and-weigh" approach to the meadow viper *Vipera ursinii* (Bonaparte, 1835), using the information and ENMs reported in Console et al. (2020) as a basis to devise the proposed workflow: starting from the ENMs, calibrated for each *V. ursinii* subspecies upon current climatic conditions, we forecast the modelled climate-occurrence relationships to two different future climatic scenarios. Moreover, information about habitats and altitude in which the meadow viper occurs is used to refine the ENMs and move towards SDMs; here, SDMs are intended sensu Peterson and Soberón (2012), who stated that SDMs "must include steps to transform areas estimated from potential to actual, so as to reconstruct distributions accurately.". The SDMs are further used to calculate landscape corridors, which are then processed in GIS environment to highlight possible conservation issues for *V. ursinii* populations and inform European protected areas management.

2 | METHODS

The "couple-and-weigh" approach we introduce is a multistep process integrating ENM outputs with frequency-based estimates of species' habitat use within "weighted SDMs", from which comprehensive friction maps can be derived. The whole process, as well as its applications, is reported in Figure 1, and each step is detailed in the next paragraphs.

2.1 | Target species and study area

The target species is the meadow viper *Vipera ursinii* (Bonaparte, 1835), classified as "Vulnerable-B2ab(III)" by the International Union for Conservation of Nature (IUCN) (Joger et al., 2009). Four subspecies, *V. u. macrops* (Méhely, 1911); *V. u. moldavica* Nilson, André

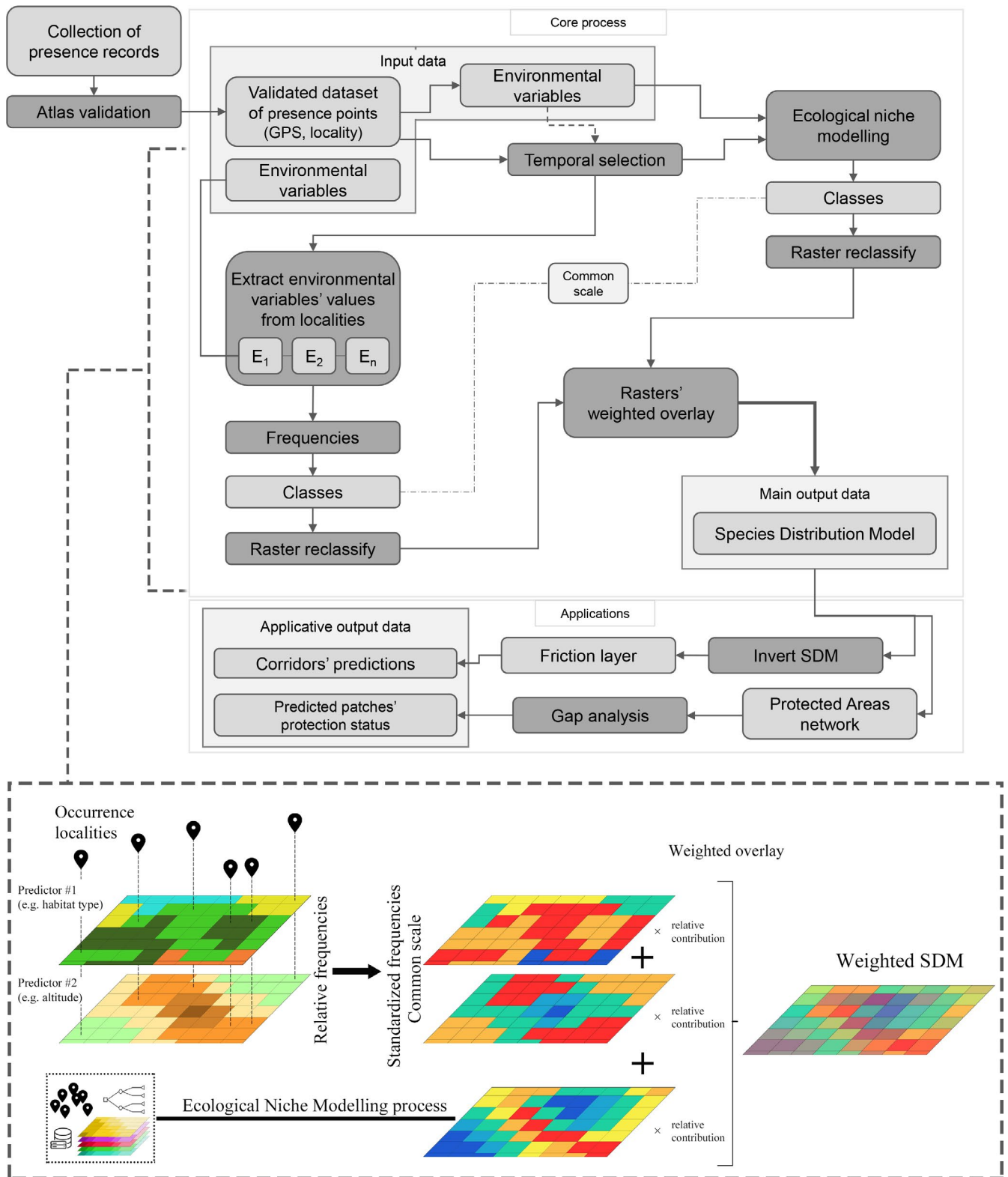


FIGURE 1 Overview of the proposed workflow and dataflow. Input data require occurrence localities of a target species at the highest geographical precision available and any environmental predictors considered useful. Ecological niche models (ENM) are calculated, and discrete suitability classes are defined from their outputs. Standardized frequencies across species' occurrence localities are calculated for each environmental variable not included in ENM. Reclassified ENM's output and standardized frequencies are merged through weighted averaging to obtain an SDM and then the corresponding friction map. Landscape corridors are inferred, and conservation-related analyses over these latter are applied

and Joger, 1993; *V. u. rakosiensis* Méhely, 1893; and *V. u. ursinii* (Bonaparte, 1835), are distributed in Europe within different disjunct regions (Ferchaud et al., 2011). Occurrence data for each subspecies were obtained from the validated data set of Console et al. (2020); study area is reported in Appendix S1. The data set was thinned to make it more suitable to provide practical conservation guidelines: we discarded all occurrences older than 1992, the establishment year of the Natura 2000 European network which permitted several structured field studies providing comparable occurrence data.

2.2 | Environmental variables

Three families of predictors were used to encompass the different types of environmental variables usually considered to fit ENMs (and obtain the corresponding friction maps): climatic, topographic and habitat-related.

The same set of uncorrelated variables from WorldClim 1.4 (Hijmans et al., 2005) that Console et al. (2020) selected to fit ENMs for current conditions (detailed in Appendix Note S1) was used here to project suitability under future climatic scenarios, at the same spatial resolution (30 arc-s).

Information about topography was obtained from a 25-m resolution digital elevation model (DEM) downloaded from the Copernicus repository (<https://land.copernicus.eu/imagery-in-situ/eu-dem>).

The raster map of the European Nature Information System (EUNIS), downloaded from the European Environment Agency website (<https://www.eea.europa.eu/data-and-maps/data/ecosystem-types-of-europe>), was used as a source of habitat types (100-m resolution). Information from EUNIS was integrated with a raster (adjusted at 100-m resolution) representing roadways within the study area and retrieved from the [openstreetmap.org](https://www.openstreetmap.org) database (OpenStreetMap). All the GIS processes detailed above were performed in ArcMAP 10.0 (ESRI, 2010).

2.3 | Species distribution modelling: workflow and friction map

After the temporal filtering of occurrence records, a GIS point sampling was performed, for each subspecies, upon the EUNIS and DEM raster maps to obtain the habitat type and altitude of each occurrence locality. Successively, the relative frequency of each habitat type and altitudinal class (100 m intervals) across occurrence localities was calculated, then divided by the highest value and finally converted to a 0-to-10 scale (lower to higher relative frequencies), obtaining standardized occurrence frequencies of each subspecies within each habitat type and altitudinal class. Thus, the value that will be given to each pixel in the “couple-and-weigh” phase (see below) corresponds to the standardized occurrence frequency of the subspecies within the habitat type/altitudinal class covering that pixel.

The ENMs used here for future projections are the ones which in Console et al. (2020) attained high discrimination performances (i.e. showing both AUC >0.8 and TSS >0.7, for all the reasons reported in Iannella et al. (2018)). The weighted mean of probabilities (“wmean”) algorithm from the “biomod2” R package was then used to derive ensemble models whose component ENMs are weighted based on their respective discrimination scores (Thuiller et al., 2016; Thuiller et al., 2009). Variability in the future climatic conditions predicted by different global climate models (GCM) has been shown as an important driver of uncertainty in model predictions (Stralberg et al., 2015). Thus, we used three different GCMs, namely CCSM4 (Gent et al., 2011), IPSL (Marti et al., 2010) and MIROC-CHEM (Watanabe et al., 2011), to project, using the “BIOMOD_EnsembleForecast” function from “biomod2”, the obtained ensemble models to 2050 under the 6.0 (2050_6.0) and 8.5 (2050_8.5) representative concentration pathways (RCPs).

For each subspecies and RCP, the ensemble forecasts to future climatic conditions undergone a weighted averaging through the MEDI (Multivariate Environmental Dissimilarity Index) algorithm (Iannella et al., 2017), which weighs the single projections based on the degree of univariate extrapolation (Elith et al., 2010) of the corresponding GCM (i.e. its environmental divergence compared with calibration conditions) and merges them into a single weighted forecast.

As “BIOMOD_EnsembleForecast” reports the climatic suitability in a 0-to-1000 “floating” (i.e. continuous) scale, the “Reclassify” tool was used to obtain an “integer” (i.e. discrete) raster map, with 0-to-10 classes, making ensemble projections of climate-based ENMs comparable to the above-mentioned standardized frequencies of EUNIS habitats and altitude classes. Subsequently, the ArcMap “Weighted Overlay” tool was used to merge these three predictors into a single map, to obtain a more reliable estimate of suitable areas by comprising different aspects of the target species’ ecological requirements. This tool merges a given set of rasters, sharing a common evaluation scale, through a weighted averaging in which each input raster is assigned a specific weight set by the operator (Figure 1). Here, equal weights were given to the single predictors (ENMs’ output, EUNIS habitats and altitude rasters); depending on literature or expert-based indications, one may give different weights to some predictors (e.g. weighting more climate than land use and altitude). This “couple-and-weigh” process was used to obtain both “current” and “future” weighted SDMs, starting from projections of the respective climate-based ENMs. It is important to highlight that the proposed workflow can narrow ENMs into SDMs by including several predictors in the “couple-and-weigh” step, possibly encompassing all the terms of the biotic–abiotic–mobility (BAM) framework (Soberón & Peterson, 2005) when available. In this case study, some abiotic (climate, altitude) and biotic (habitats) predictors were used, while migration/accessibility information was not considered as missing or not comprehensively available.

The predictive performance of the weighted SDMs obtained for current conditions was evaluated by computing the continuous Boyce index (B), which ranges from -1 (counter prediction) to $+1$ (optimal prediction) (Boyce et al., 2002; Hirzel et al., 2006), upon occurrence localities of each target subspecies. The ensemble of ENMs (ENMclim) used to generate the weighted SDMs was evaluated as well through B to assess possible performance differences between the “source” climatic models and the refined (weighted) ones.

Moreover, to deepen the performance assessment, three independent additional models were built for each subspecies using the “SDMtoolbox” version 2.4 implemented in ArcMAP (Brown, 2014), a tool which integrates the MAXENT algorithm (Phillips et al., 2006) with spatial jackknifing techniques applied to the iterative selection of training–test occurrence localities during model calibration (Brown, 2014). The first model ($wSDM_{MAXENT}$) was obtained implementing the “couple-and-weigh” approach described above (i.e. ENMs built in SDMtoolbox, then refined through the “Weighted overlay” tool), while the second one ($ENMclim_{MAXENT}$) was calibrated using climatic predictors only. The third model ($ENMtot_{MAXENT}$) included all the predictors (selected bioclimatic variables, altitude and EUNIS habitats) during model fitting. Three spatially jackknifed groups were set so that the Boyce index was computed upon three different sets of test data for each model type ($wSDM_{MAXENT}$, $ENMclim_{MAXENT}$ and $ENMtot_{MAXENT}$).

As modelling future changes in land use is still a highly uncertain task, as emerged for urban growth (Ellman, 1997; Forman, 2014; Liu et al., 2010), we used the raster representing present geographical arrangement of EUNIS habitats (for which European Union official future projections are ongoing nowadays (European Environmental Agency, 2020)) also to generate “future” SDMs. Thus, our predictions represent optimistic forecasts, as urban-modified territories are predicted to increase (Jiang & O’Neill, 2017; Riahi et al., 2017). Altitude was maintained fixed at its current values as well.

2.4 | Corridors modelling

We converted the weighted SDMs into friction maps (whose values are inversely proportional to suitability) through the “Raster calculator” tool to subsequently include them in Circuitscape (McRae et al., 2008), the software used to infer corridors connecting the “post-1992” populations (i.e. populations represented by occurrence data retained after the applied temporal filtering) of each target subspecies. Circuitscape is implemented in Java and applies both circuit and random walk theories to model ecological connectivity across a landscape (McRae et al., 2008, 2016). Starting from a friction map and some source/target locations (the nodes), the software produces a connectivity map representing the expected net probability of an organism moving from one node to another (McRae et al., 2008). Circuitscape outperformed least-cost corridors modelling when validated upon empirical case studies, where species are expected to move without previous knowledge of the landscape

(McClure et al., 2016), as in the case of *V. ursinii*. The Circuitscape “pairwise” approach was used: for each possible pair of populations, each term of the couple is iteratively both the source and the destination node (McRae et al., 2013).

2.5 | Corridors changes and conservation applications

Once obtained connectivity maps for both current and future scenarios, we assessed the areas where connectivity is predicted to change, that is where potential corridors are interrupted or enhanced due to climate change (with the other variables fixed at their current values, see above).

To make corridors change estimates comparable across different ranges, we calculated in ArcMap an appropriate standardized connectivity change index (SCCI) defined by the formula:

$$\frac{\text{corridor}_{\text{Future}} - \text{corridor}_{\text{Current}}}{\text{corridor}_{\text{Future}} + \text{corridor}_{\text{Current}}}$$

which returns values ranging from the loss (-1) to the gain ($+1$) of connectivity, with $SCCI = 0$ representing corridor stability. The resulting maps were cropped to the extent of a 15-km buffer minimum convex polygon calculated for each subspecies (two different ones for the Italian and French *V. ursinii* populations) to focus on the areas in which inter-populations connections are likely to occur, considering the highest inter-annual dispersal recorded for *V. ursinii* (Újvári & Korsos, 1987) and the possible movements of individuals across multiple years.

As future conditions may promote species’ distributional shifts towards areas which possibly show low or no suitability for them nowadays (Cerasoli et al., 2019; Di Musciano et al., 2020; Iannella et al., 2019), we assessed potential connectivity between current occurrence areas of the “post-1992” populations and future suitable patches. For each subspecies, future suitable patches were estimated by binarizing the continuous suitability map of the “future” weighted SDM according to the 10th percentile training presence threshold computed upon the “current” weighted SDM (Elith et al., 2011; Lahoz-Monfort et al., 2014; Phillips et al., 2006). Also, the suitability value maximizing the true skill statistics (TSS_{max}) for the “current” weighted SDM was considered as alternative binarizing threshold (Allouche et al., 2006; Brunetti et al., 2019; Iannella et al., 2019), to assess possible dependencies of future connectivity estimates upon the chosen thresholding method. Then, Circuitscape was set to the “Advanced: activate independent sources and grounds” mode, in which the current populations represented the sources and the binarized suitable areas represented the grounds (i.e. destinations).

Further, taking advantage of the whole data set of Console et al. (2020), which includes occurrence localities of likely extinct populations (i.e. not detected since 1992), we extracted from the “future” weighted SDMs the suitability predicted for the territories

where these “pre-1992” populations occurred. If such suitability value exceeded the chosen binarizing threshold, we inferred potential corridors from present occurrence areas to those of extinct populations (sources and grounds, respectively, within Circuitscape “Advanced mode”) to assess the potential of each subspecies to re-establish in formerly inhabited territories.

Values of raster maps representing potential connectivity among current populations, between current populations and former occurrence areas of extinct ones, as well as between current populations and future suitable areas, were normalized dividing them by their highest value (0–1 scale) so that comparable values among all the considered subspecies could be reported.

As the maps obtained from corridors modelling allow the evaluation of areas where the major changes in connectivity are likely to occur, we evaluated whether existing protected areas (PAs) (Natura 2000 sites and Nationally Designed Areas, NDAs) would sufficiently cover the territories potentially assuring proper inter-population connectivity. To perform this gap analysis, based upon predicted connectivity and areas covered by PAs, we applied a 15-km buffer around occurrence localities of “post-1992” populations to exclude areas that are not sufficiently contiguous to current presence areas.

3 | RESULTS

3.1 | Environmental occurrence patterns

The distribution of *Vipera ursinii macrops*, *V. u. moldavica*, *V. u. rakosiensis* and *V. u. ursinii*, hereafter indicated as *macrops*, *moldavica*, *rakosiensis* and *ursinii*, is shown in Appendix S1. The temporal filtering of records retrieved from the database of Console et al. (2020) resulted in 44 occurrence localities for *macrops*, 52 for *moldavica*, 28 for *rakosiensis* and 332 for *ursinii* (23 occurrences for the French range and 309 for the Italian range).

Relative occurrence frequencies along the altitudinal gradient show that both *macrops* and *ursinii* mostly occur between 1,600 and 1,800 m a.s.l. (Figure 2a). Differently, the two “lowland” subspecies, *moldavica* and *rakosiensis*, are most frequent within the 0–200 m a. s. l. and the 200–300 m a. s. l. ranges, respectively (Figure 2a). Considering EUNIS habitats, the highest relative occurrence frequencies are found, for all subspecies, within “Mesic grasslands” followed by “Arable land with unmixed crops grown by low-intensity agricultural methods” (coded as “E2” and “I1” by Janssen et al. (2016), respectively); *rakosiensis* is the only subspecies for which both these two habitats show comparably high frequencies (Figure 2b).

3.2 | Weighted suitability

For each subspecies, climatic suitability (future predictions reported in Appendix S2a–d) and relative occurrence frequencies along the

altitudinal gradient and across EUNIS habitats were reclassified to a common 0–10 scale, and resulting layers were merged through the “Weighted overlay” process, both for current (Figure 2c–f) and for future predictions (Appendix S3a–d).

Predictive performance of the obtained weighted SDMs was high, for both the main (“biomod2”-based) and the additional (“Maxent”-based) models, according to the attained Boyce index (B) values reported in Table 1.

Compared with the climate-based ENMs reported in Console et al. (2020) for current conditions, the “current” weighted SDMs obtained here generally depict narrower and more sparse suitable areas for all the subspecies (Figure 2c–f), with *rakosiensis* being the one with the widest suitable extents (Figure 2e).

Within the “future” weighted SDMs, a generalized decrease in suitable territories appears under the different scenarios for *macrops* (Appendix S3a), *rakosiensis* (Appendix S3c) and *ursinii* within both the French and the Italian range (Appendix S3d). Differently, future predictions for *moldavica* report more mixed patterns, with a decrease in suitability within southern coastal areas and eastern plains and a concurrent increase in suitability in the plains south-east from the Carpathians (Appendix S3b).

3.3 | Corridors modelling

The corridors network estimated upon the friction maps derived from “current” weighted SDMs show diffuse, high connectivity for *macrops* populations in central Dinarides, along with an isolated corridor system in south-eastern Balkans (Korab and Sar mountains) characterized by high connectivity among the local occurrences but scarce connections to the Dinaric patch (Figure 3a). Both the Danube delta and the Moldova region, up to Eastern Carpathians' foot, show high connectivity among all the local *moldavica* occurrence localities. Moreover, isolated populations occur in the westernmost portion of the Moldova region, while a central, unique population is connected, although with minor connectivity values, both to the northern and to the southern corridors systems (Figure 3b). A vast highly connected central corridor system is found for *rakosiensis* (Figure 3c): particularly, a small intra-connected network (i.e. a group of connected populations which are instead poorly connected with others) emerges within the eastern portion of this system, up to the foot of the Bihor Massif, while two occurrence localities falling at the borders between Austria and Hungary, in the western portion of the system, are relatively isolated. Within the French range of *ursinii*, two highly connected clusters emerge in the Maritime Alps, while three western occurrences appear to be isolated in the Vaucluse and Var areas (Figure 3d). Differently, the *ursinii* Italian range shows a northern (Laga, Sibillini and Duchessa mountains) and southern (Majella and Meta mountains) clusters of populations being intra-connected but isolated from the two interconnected central ones (Gran Sasso and Sirente Massifs) (Figure 3d).

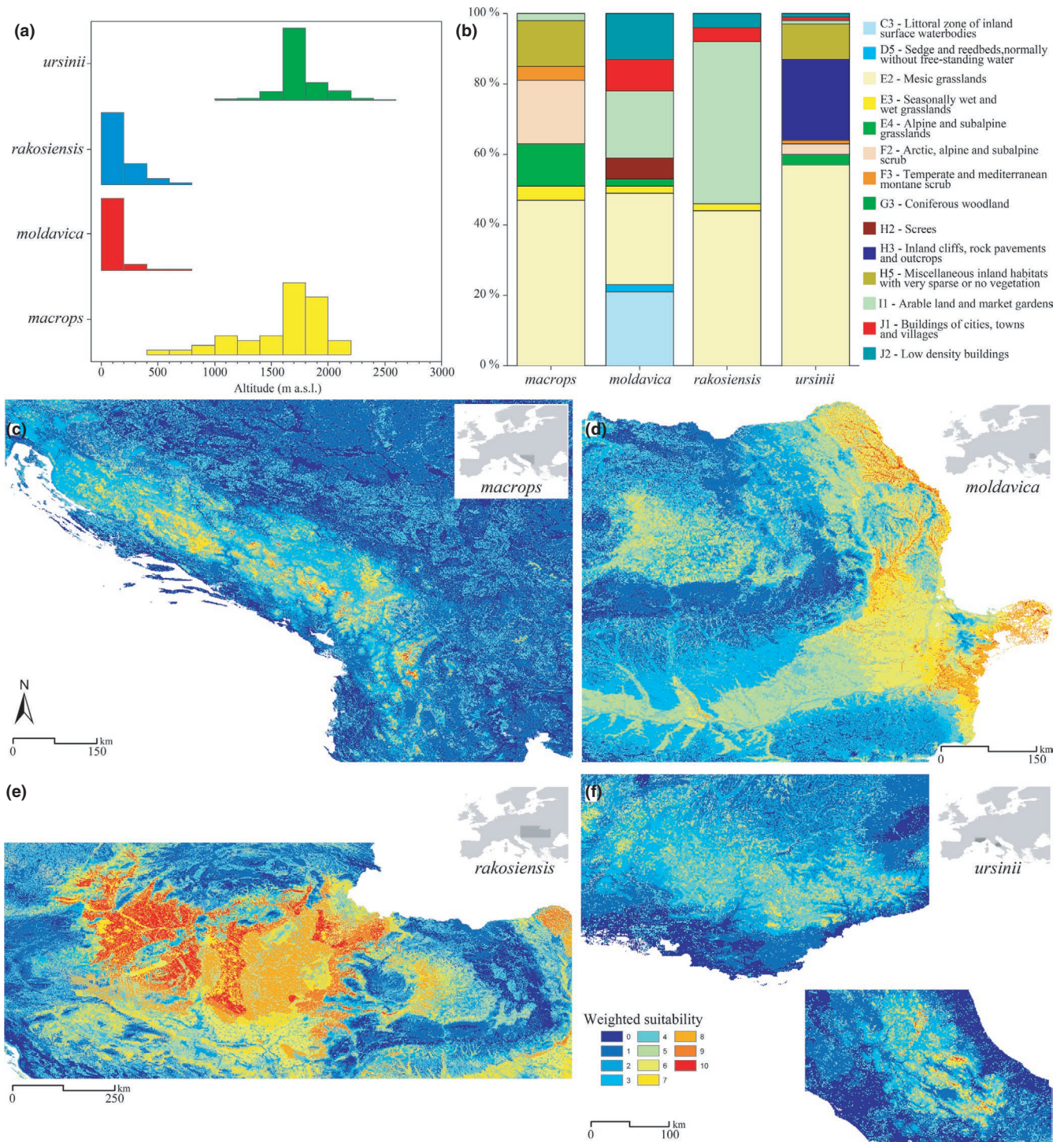


FIGURE 2 Elevation and habitat occurrence frequencies and weighted suitability for current scenario. Relative frequency of occurrence along (a) elevation gradient (200 m interval) and (b) EUNIS habitat types for the four *Vipera ursinii* subspecies. Weighted suitability maps for (c) *macrops*, (d) *moldavica*, (e) *rakosiensis* and (f) *ursinii* (upper: French, lower: Italian range) subspecies

3.4 | Future connectivity changes

According to the standardized connectivity change index (SCCI), noticeable connectivity loss (i.e. $SCCI < 0$) emerges for *macrops* in the 2050_6.0 scenario, with the major Dinaric network losing most of its present corridors (Figure 4a). The 2050_8.5 scenario

is even worse, predicting diffuse lowering of connectivity in the whole *macrops* range (Appendix S4a). The two sub-networks of *moldavica* (Moldova and Danube delta) are predicted to remain intra-connected, although a loss of connectivity in the Moldova valleys is reported. On the other hand, the negative SCCI values predicted in central Romania in both future scenarios suggest

TABLE 1 Predictive performance, in terms of Boyce index, of the considered model types validated upon test data selected through repeated split-sample within the 'biomod2' modelling platform ("Weighted SDM" and "ENMclim") or test data selected through spatial jackknifing within the SDMtoolbox platform ("wSDM_{MAXENT}", "ENMclim_{MAXENT}", "ENMtot_{MAXENT}")

	Weighted SDM	ENMclim	wSDM _{MAXENT}	ENMclim _{MAXENT}	ENMtot _{MAXENT}
<i>macrops</i>	0.952	0.436	0.882	0.703	0.814
<i>moldavica</i>	0.814	0.598	0.893	0.725	0.753
<i>rakosiensis</i>	0.777	0.749	0.766	0.735	0.751
<i>ursinii</i>	0.981	0.888	0.894	0.672	0.642

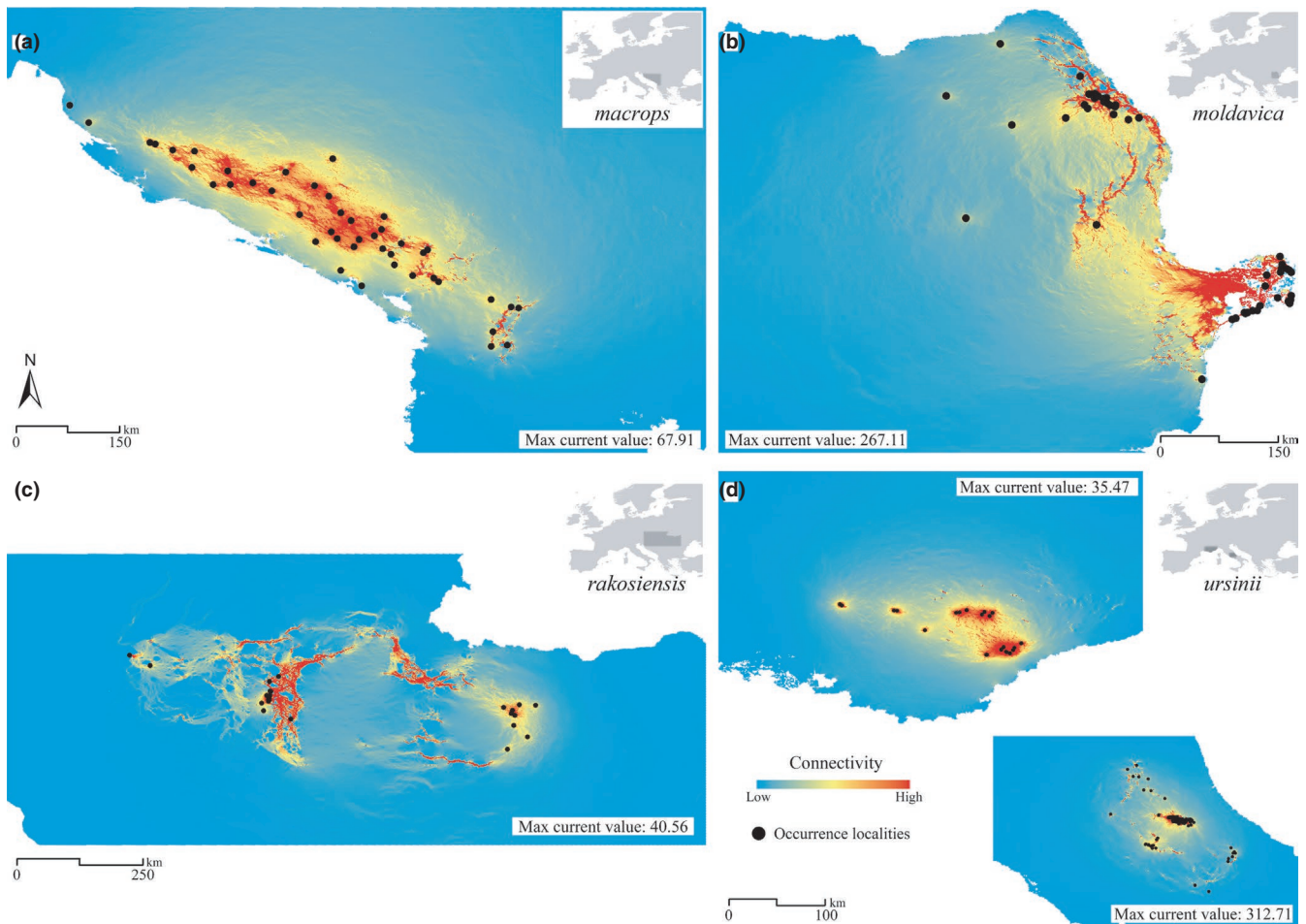


FIGURE 3 Corridors for *Vipera ursinii* under current climatic conditions. Connectivity among occurrence localities of (a) *macrops*, (b) *moldavica*, (c) *rakosiensis* and (d) *ursinii* (upper: French, lower: Italian range) subspecies. Each panel has a different full-scale value, considering the specificity of the area the subspecies occurs in

possible future isolation for the Danube and Moldova clusters as well as for the unique population inhabiting this area. Differently, medium SCCI values characterize the other north-western populations (i.e. no clear gains or losses in connectivity) (Figure 4b and Appendix S4b). A drop in connectivity is estimated for the central Hungarian corridors of *rakosiensis*, with populations from the central portion of its range losing their connections to the eastern and western ones. Moreover, while central populations are predicted to maintain local connections among each other, those in

the eastern and western portions would also lose their current intra-connectivity (Figure 4c, Appendix S4c). Diffuse connectivity loss is predicted for *ursinii* in Southern France under both the 2050_6.0 and 2050_8.5 scenarios, possibly resulting in the future isolation of the French *ursinii* populations as only some narrow corridors are predicted to persist in the Maritime Alps (Figure 4d, Appendix S4d). A very similar scenario of extensive connectivity loss is inferred for the Italian range of *ursinii*, especially under 2050_8.5 (Figure 4d, Appendix S4d).

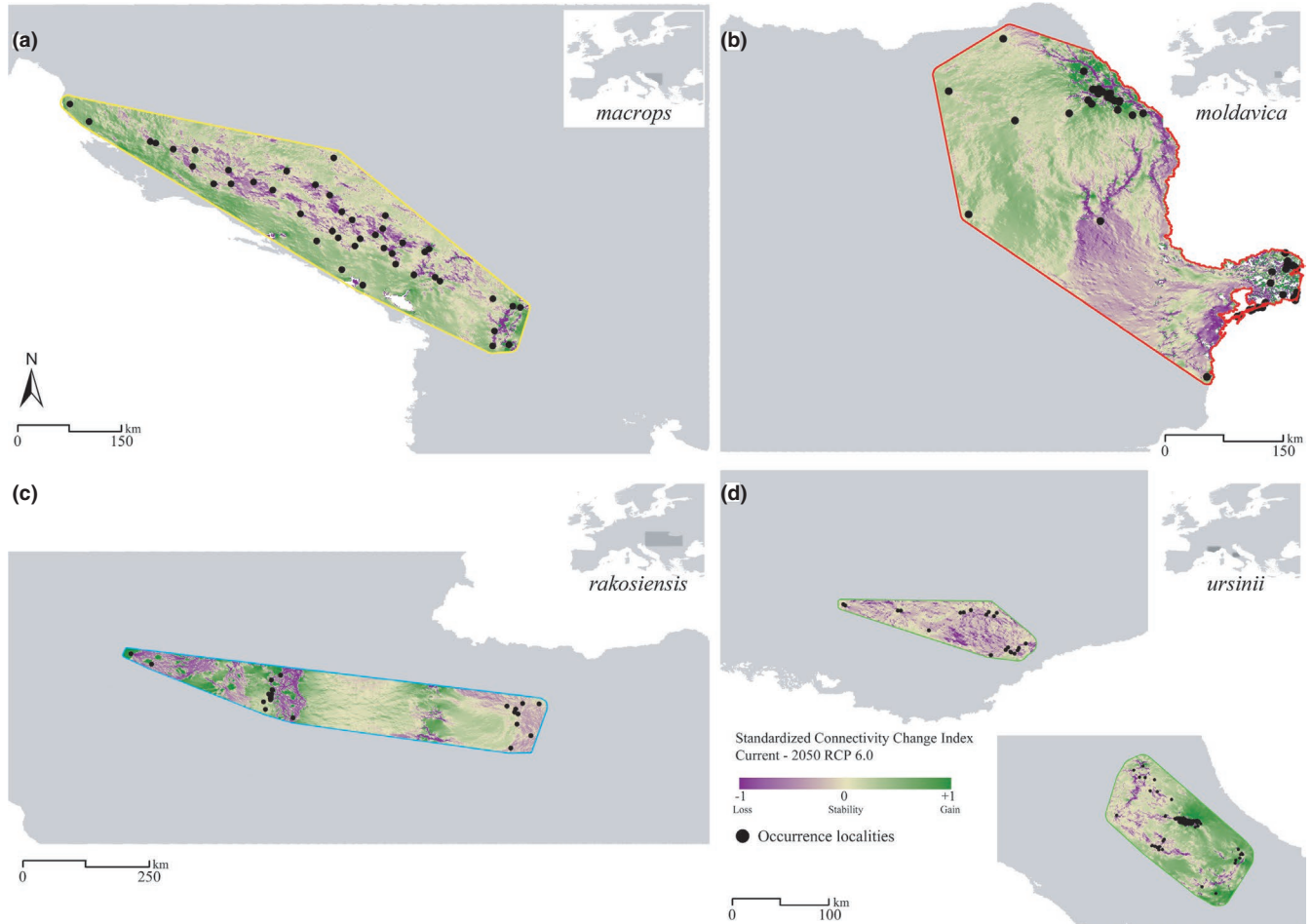


FIGURE 4 Variation of connectivity for *Vipera ursinii* under the 2050_RCP6.0 scenario. Standardized connectivity variations, reported in terms of the standardized connectivity change index (SCCI, introduced in this study) among occurrence localities of (a) *macrops*, (b) *moldavica*, (c) *rakosiensis* and (d) *ursinii* (upper: French, lower: Italian range) subspecies. Areas are cropped to a 15-km buffered minimum convex polygon, calculated over the “post-1992” occurrences

3.5 | Corridors to future suitable areas

Binarized future predictions for *macrops* (thresholds: 10th percentile = 4, $TSS_{max} = 3$, with the former chosen as more conservative) result in a “salt and pepper” pattern of suitable areas around the main Dinaric core in Montenegro. The connections from current *macrops* occurrence localities to patches predicted as suitable in the future are more robust and widespread in the Dinaric core than in the peripheral sub-networks (Figure 5a, Appendix S5a). Under the 2050_6.0 scenario, the two sub-networks (Moldova and Danube delta regions) emerging for *moldavica* would be well connected to the surrounding binarized (thresholds: 10th percentile = $TSS_{max} = 5$) future suitable patches, while the vast central future suitable patch would be more connected to the Moldova populations than to the ones populating the Danube delta (Figure 5b). Differently, under 2050_8.5, the suitable central patch does not appear, and the Moldova and Danube sub-networks remain confined to their respective current territories (Appendix S5b). The proximity of future suitable patches (binarization thresholds: 10th percentile = $TSS_{max} = 5$) to the currently occupied areas, under both 2050_6.0 and 2050_8.5,

causes a “radial” arrangement of corridors for the Hungarian *rakosiensis* populations; the two populations occurring at the Austria/Hungary border result as connected to future suitable patches as well. Differently, for the Romanian populations low connectivity is predicted only towards the nearest (westernmost) future suitable areas (Figure 5c, Appendix S5c). A similar “radial” connectivity towards the fragmented and scattered patches predicted to be suitable (binarization thresholds: 10th percentile = $TSS_{max} = 4$) under both the future scenarios is also observed for the French and the Italian *ursinii* populations (Figure 5d, Appendix S5d).

3.6 | Corridors from current populations to extinct ones

Regarding the possibility of recolonization of occurrence areas where *V. ursinii* has not been recorded since 1992, higher future connectivity towards these latter is predicted for *macrops* in 2050_6.0 than in 2050_8.5 (Figure 6a, Appendix S6a). A similar trend is observed for *moldavica*; in particular, its westernmost “pre-1992” population

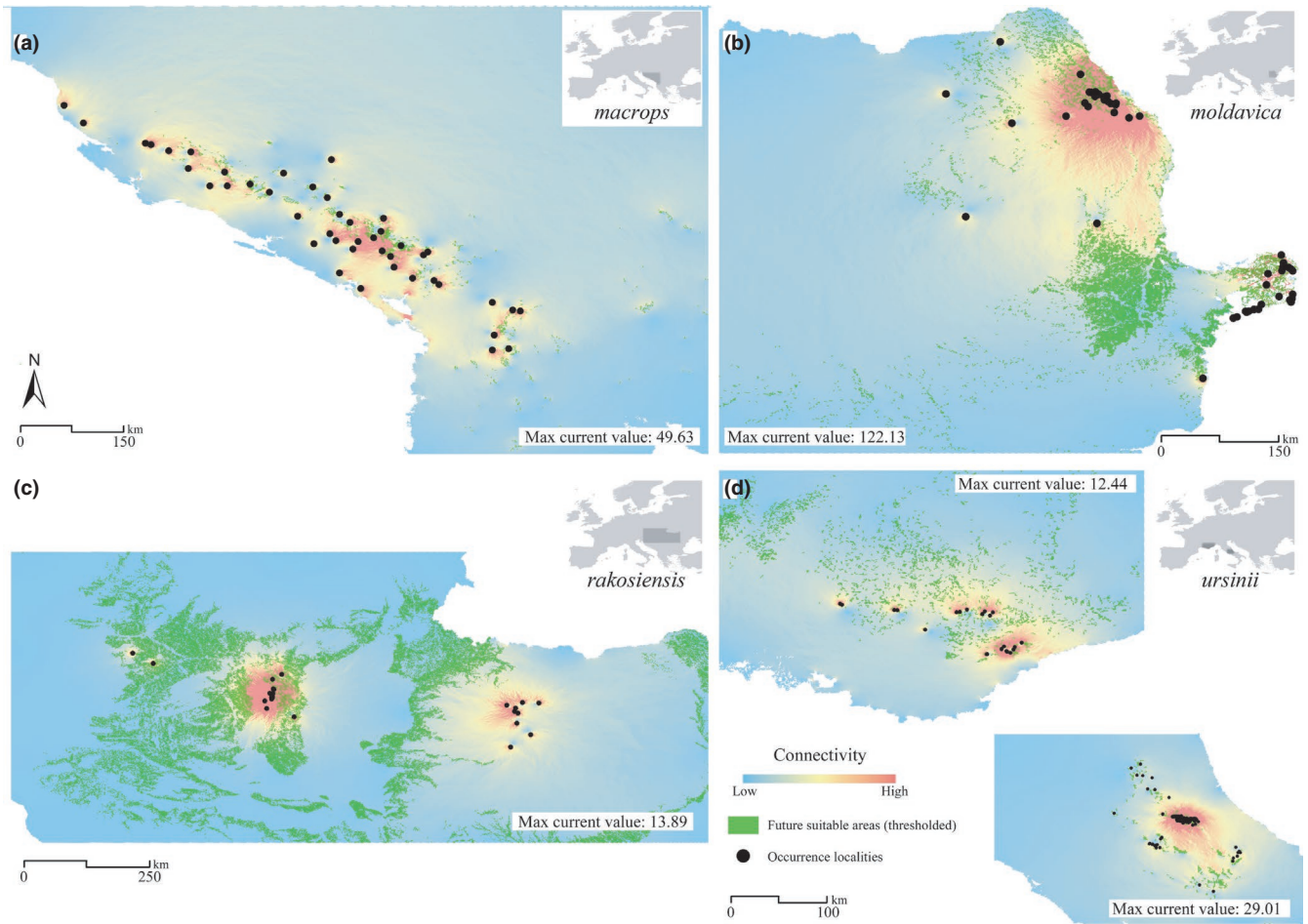


FIGURE 5 Connectivity of *Vipera ursinii* populations to future suitable areas. Connectivity *sensu* McRae et al. (2008) among the present (“post-1992”) occurrence localities and the future (2050_RCP6.0 scenario) inferred suitable areas, binarized based on the 10th percentile of training presences threshold, for (a) *macrops*, (b) *moldavica*, (c) *rakosiensis* and (d) *ursinii* (upper: French, lower: Italian range) subspecies

is poorly connected to a near, isolated existing one, while higher connectivity appears between the other current and “pre-1992” populations under both scenarios (Figure 6b, Appendix S6b). High connectivity is reported between the extinct Austrian populations of *rakosiensis* and the two present populations near the Austria/Hungary border; the other “pre-1992” populations are potentially highly connected to the present ones as well (although connectivity decreases under 2050_8.5), except for the isolated, easternmost Romanian population (Figure 6c, Appendix S6c). The French “pre-1992” *ursinii* populations are predicted to be scarcely or not connected to current ones in both future scenarios, while higher potentiality of recolonization is predicted within the Italian range, except for the southernmost populations (Figure 6d, Appendix S6d).

3.7 | The role of PAs in the corridors' future preservation

In the future 2050_6.0 and 2050_8.5 scenarios, both Natura 2000 sites and NDAs are predicted to cover territories in which connectivity

will remain stable or slightly increase ($SCCI \geq 0$) (Appendix S7a), assuring protection to areas of potential inter-populations exchange. Exceptions to this general trend emerge for *moldavica*, for which PAs are predicted to cover some areas either losing or gaining connectivity, and *rakosiensis*, for which PAs would mainly protect territories predicted to noticeably gain connectivity (Appendix S7a). The connections to patches predicted as suitable in the binarized future projections of the weighted SDMs are instead poorly protected for all the subspecies, as only low-connectivity areas are likely to be protected by both Natura 2000 and NDA sites (Appendix S7b). A similar trend is also found for the territories predicted as suitable in the future and potentially connecting present populations with extinct ones (Appendix S7c).

4 | DISCUSSION

Understanding the drivers shaping the observed distribution of species and predicting potential future host areas is a crucial matter for conservation biology. Human-induced pressures, such as climate and land use changes, will force species to move, often

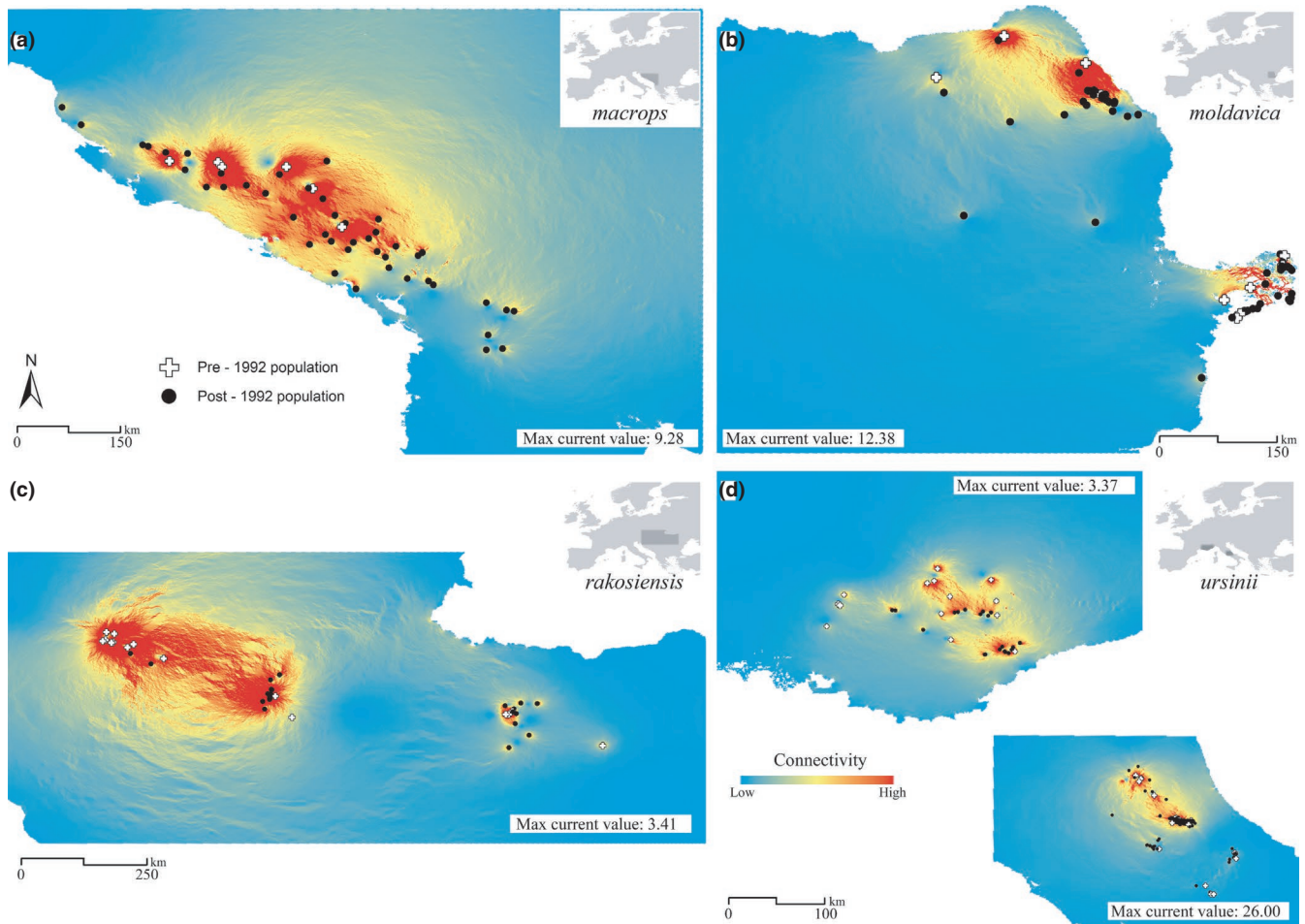


FIGURE 6 Future connectivity of current *Vipera ursinii* populations to extinct ones. Connectivity *sensu* McRae et al. (2008) under the 2050_RCP 6.0 future scenario among the present (“post-1992”) occurrence localities and the ones no more reported after 1992 (“pre-1992”), for (a) *macrops*, (b) *moldavica*, (c) *rakosiensis* and (d) *ursinii* (upper: French, lower: Italian range) subspecies

leading to a general biodiversity drop due to the impossibility for many taxa to adapt (Guo et al., 2018; Littlefield et al., 2019; Newbold, 2018). Both fast climate changes and pervasive anthropic land use require a tremendous effort from the scientific community to give adequate responses, which must be translated into “real-world” management strategies and territorial policies (Elsen et al., 2020).

The workflow here proposed aims at maximizing the yield of available geographical data, with the only requirement of collecting such data at the highest possible precision (e.g. GPS). The coupled implementation of ecological niche modelling, describing a particular part of a species' realized niche (e.g. climate preferences), and advanced GIS spatial analyses may greatly help in comprehensively investigating distribution patterns (Peterson & Soberón, 2012) and (re)colonization potentiality from accessible data. The multistep approach we propose is also consistent with the hierarchical approach proposed by Pearson and Dawson (2003): climate envelopes describe a general pattern which must be refined through fine-scale inferences, based for instance upon topographic and land use information.

Integrating ENMs' output with standardized occurrence frequencies representing preferences of the target taxon in terms of habitat types and altitudinal range (or other “ground-level” variables) to produce weighted SDMs permits to narrow down the potential distribution of the taxon to the peculiarity of the studied territories. The relevant information that factors acting at local scales may add to outputs from climate-based ENMs is introduced in the post-modelling “couple-and-weigh” process, as also implemented by Mendes et al. (2020) through a “boolean” approach.

In our case study, resorting to four *V. ursinii* subspecies, the predictive performance of the weighted SDMs increased, in terms of Boyce index values, compared with that of their component climate-based ENMs as well as compared with ENMs including topography and habitat types as predictors. Moreover, our “couple-and-weigh” approach avoids *a priori* discarding areas supposed to be non-suitable based on ENMs' output (i.e. a binary approach). Indeed, as revealed by our GIS sampling of habitat type and elevation value upon GPS-precision occurrences, some meadow vipers can also be found in semi-natural areas (such as traditionally cultivated market gardens or rural areas) or at altitudes considered slightly outside of their optimal range. This

information describes a part of the species' ecological plasticity and should be integrated into the modelling framework to obtain a more realistic delimitation of its distribution. This, in turn, permits to produce friction maps containing as much information as possible about the potentiality of certain areas to favour the persistence of existing populations and/or to connect these latter with others, improving the corridors modelling step. On the other hand, the additive nature of this "couple-and-weigh" approach may lead to inconsistencies in the resulting weighted SDMs: for instance, if the SDM derives from poorly calibrated ENMs predicting suitable areas where the species is totally absent, the contribution of the ENMs' output in the "couple-and-weigh" phase could increase weighted suitability in these areas. Nonetheless, the standardized occurrence frequencies for the habitat/altitude (or any other additional predictor) class(es) covering such territories would likely be low, thus lowering the final weighted suitability. Future enhancement is anyway advisable in this regard.

Within the weighted suitability maps obtained for the target *V. ursinii* subspecies in the current scenario, some linear and scattered unsuitable areas emerge in the middle of suitable territories, disrupting their continuity. When analysing these patches in detail, linear lowly suitable areas appear to be associated with rivers and their riparian strips, roads and other infrastructures, while small and diffuse polygonal unsuitable patches mainly represent cities and towns. Based on the connectivity networks obtained for the current scenario, massifs and high-altitude plateaus offer shelter and possibility of inter-population exchange to the "mountain" *V. ursinii* subspecies (*ursinii* and *macrops*); outside of these territories, the connections are very scarce. Corridors emerging for the "lowland" subspecies (*moldavica* and *rakosiensis*) refer to different topographic elements: the lowland plains, which can correspond to linear (e.g. river valleys) or planar (e.g. the Danube delta) features, delineate connections for the *moldavica* populations; similarly, river valleys and cultivated lands define narrow or medium-sized corridors for *rakosiensis*.

A shared future emerges from projections of the weighted SDMs obtained for *macrops* and *ursinii*, suggesting that the combination of climate change and limited extent of favourable habitats would constrain these subspecies within shrinking suitable environments. Contrarily, the vast lowlands of Eastern Europe offer wider suitable territories to *moldavica* and *rakosiensis*, though the fragmentation inferred from corridors modelling would result in only specific areas likely hosting connections among populations.

Apart from the influence of topography on inter-population connectivity, human-related activities noticeably threaten the persistence and possibility of range expansion for many *V. ursinii* populations. Indeed, the presence of roads (used by meadow vipers for basking or displacements) and intentional killings were shown to depress *ursinii* Italian population (Filippi & Luiselli, 2004); severe impact from intentional killing was also reported for *moldavica* (Zamfirescu et al., 2011). Alteration of specific habitats triggered by biotic factors represents an additional common menace for both "mountain" and "lowland" subspecies. For instance, the expansion of the dwarf

mountain pine (*Pinus mugo*) in a part of the Italian *ursinii* range reduces basking areas (Filippi & Luiselli, 2004), while the presence of wild boars (*Sus scrofa*) was shown to negatively affect some Italian *ursinii* populations (Filippi & Luiselli, 2004) as well as *moldavica* ones (Halpern et al., 2007; Zamfirescu et al., 2011).

About the future predictions, weighted suitable areas show different trends depending on the subspecies considered: some are predicted to shrink or to remain stable, while others are predicted to experience suitability drops in some territories and gains in others (see Appendix S2). This is mirrored in the modelled connectivity, as many connections among "post-1992" populations are predicted to decrease dramatically. In this context, the early warning given by Ferchaud et al. (2011) about possible local extinctions in French *ursinii* populations driven by genetic isolation is reinforced by our results. Similarly, the negative SCCI values found in Hungary represent an additional warning for the conservation of *rakosiensis*, whose low genetic variability already led to neonatal malformities and chromosomal abnormalities (Újvári et al., 2002).

Moreover, medium connectivity towards the future binarized suitable areas mainly involves territories in the immediate proximity of occurrence localities of "post-1992" populations. In contrast, no potential for connection towards distant future suitable areas emerges. Likewise, the potential future recolonization of former occurrence localities is predicted only for "pre-1992" populations located near the "post-1992" ones. These results are in line with the peculiar habitat preferences each subspecies has, but it should be considered that most of the habitats covering occurrence localities are classified, following Janssen et al. (2016), as Endangered and Vulnerable (Console et al., 2020). In this context, traditional agricultural practices (manual mowing and low-density grazing) are deemed to favour the preservation of habitats to which *macrops* (Jelić & Baškiera, 2014), French *ursinii* (Lisse et al., 2012) and *moldavica* populations are associated. On the other hand, they might also lead to increased intentional killings, as observed for *moldavica* by Zamfirescu et al. (2009). Grazing is considered to have detrimental effects upon *V. ursinii* only when its pressure is high, as reported for the Italian *ursinii* (Luiselli, 2004). Conversely, a lack of grazing was shown to pose at risk some French *ursinii* populations due to habitat changes (Lisse et al., 2012).

Taking into account all these changes in connectivity and the current pressures upon *V. ursinii*, the need for conservation measures appears urgent. Therefore, we analysed the role of existing nationally designed areas (NDAs) and Natura 2000 sites in protecting inferred corridors and future suitable territories for *V. ursinii*. The PAs' networks are predicted to protect territories in which stable or slightly increasing connectivity is observed, although with varying coverage, depending on the specific subspecies and future scenario considered. On the other hand, connections to future suitable patches, as well as to "pre-1992" localities, occur mainly outside NDAs and Natura 2000 sites: this means that potential colonization of future suitable territories would be subject, for all the subspecies, to high risk of failure, particularly if the corridors connecting such areas to

currently occupied ones will undergo intense human pressure. In the light of our results, the future suitable areas emerging from the binarized projections of the obtained weighted SDMs can be defined as ex situ refugia, *sensu* Ashcroft (2010). We invite PAs' managers, conservationists and all the involved stakeholders to enhance the debate about conservation measures possibly assuring the preservation of these refugia from climate change and human pressures, as well as a better connection with extant occurrence localities. As suggested by Shoo et al. (2013), these measures should be tailored to the specific territorial contexts, considering the dispersal capability of the target *V. ursinii* subspecies (the longest reported inter-annual dispersal distance is 361 m for *rakosiensis* (Újvári & Korsos, 1987)).

Ecological connectivity is crucial for many species currently facing population decline: the possibility to mix genes or properly translocate individuals towards new suitable territories may slow down biodiversity loss. The future potential of interconnection among current populations, which would permit revitalizing low-density populations (or recolonization of former occurrence areas), must be carefully evaluated in the light of further small-scale studies. For instance, the studies on *rakosiensis* (Péchy et al., 2015) focusing upon the ongoing ex situ conservation and habitat reconstruction are leading to higher chances of avoiding target populations to become extinct (European LIFE NAT/HU/000799).

The approach we presented here requires further advances, to refine the post-modelling process: the ongoing progress in remote sensing (Maxwell et al., 2018; Randin et al., 2020) and the current effort in producing fine-scale spatial predictions of land use changes (European Environmental Agency, 2015; Holman et al., 2017) provide higher accuracy to the scenarios we reported, at least in terms of future habitat availability. Future land use (or habitat) projections having spatial extent and resolution consistent with climate data would be necessary to further take advantage of the approach we propose.

Also, the temporal resolution may be sharpened if needed (e.g. analysing connectivity variations along 5–10 years intervals), provided that appropriate environmental data are available. Moreover, citizen-science data (Fraisl et al., 2020; Robinson et al., 2020) could enrich the bulk of occurrences for most species, further improving the knowledge about their habitat preferences, although some species would likely be underrepresented as they are unknown to most people or difficult to observe.

Finally, it is essential to underline that to get the best out of the multistep approach we devised here, integrating post-modelling GIS analyses on ENMs and ecological corridor modelling should be preferably handled by experts in the target species needing conservation actions.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13410>.

DATA AVAILABILITY STATEMENT

All data used for the analyses are freely downloadable online; occurrence localities of each subspecies are available on the Dryad repository at <https://doi.org/10.5061/dryad.sbccc2fr6w>.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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