Distinction of the distribution areas of genus *Rhanterium* and comparison of the habitat preferences of species by maximum entropy modeling

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Abstract. The objective of this study is to distinguish the distribution areas of *Rhanterium adpressum* and *Rhanterium suaveolens* and show the hybrid zone of *Rhanterium intermedium*. Two models of distribution with high predictive accuracy were obtained for *R. adpressum* (AUC=0.98±0.006) and *R. intermedium/suaveolens* (AUC=0.98±0.01). Precipitation of the driest month and temperature seasonality contributed most to the model of *R. adpressum,* with 27.8 % and 21.8 %, respectively. On the other hand, precipitation and mean temperature of the driest quarter contributed most to the model of *R. intermedium/suaveolens,* with 26.4 % and 20.8 %, respectively. Response curves of the species to bioclimatic factors and elevation show that *R. adpressum* prefers high-altitude habitats (888.74m), less hot (18.65 °C) and rainy (140.72 mm). *R. intermedium/suaveolens* species are distributed in warmer areas (21.61 °C), at lesser height (255.18 m) and with less rain 86.62 mm.

Key words: *Rhanterium adpressum*, *R. intermedium*, *R. suaveolens*, species distribution modeling

Introduction

Genus *Rhanterium* Desf. (1799) belongs to *Inuleae* tribe of *Asteraceae*. The species of that genus are strongly branched shrubs, stems and leaves coated with whitish hairs, with small leaves, always sessile, slightly dentate and deciduous, with spherical involucres, and capitula formed of several rows of bracts (Ozenda 2004). The genus includes four species, namely: *R. epapposum* Oliv. (1881) endemic to the Arabian Peninsula, *R. adpressum* Coss. & Dur. (1855) distributed in South Morocco, Mauritania and West Algeria, and the third species *R. suaveolens* Desf. (1799) spreading from East Algeria to South Tunisia and Libya. A hybrid species named *R. intermedium* Pomel (1874) is distributed in the meeting areas of the two latter species in Central Algeria and has characteristically intermediate morphology between *R. adpressum* and *R. suaveolens,* occasionally close to one or another of the two (Wiklund 1986).

R. adpressum is generally recognized by its large multiflower capitula and subglobular involucres, with bracts densely appressed. This is a plant much appreciated by camels and used by local people in the production of cheese and as firewood (Gauthier-Pilters 1961). *R. suaveolens* stands out with its narrow, pointed and, when mature, revolute involucral bracts. The general characteristics of *R. intermedium* are the medium or small capitula, with a degree of outward bending of involucral bracts to 45° and average length of the lamina (Wiklund 1986).

R. adpressum and *R. intermedium/suaveolens* species grow in sandy or clayey plains, sandy or silty riverbeds,

and on sand dunes in arid to hyper-arid climatic zones extending from the west to the east of Algeria. These zones border on the Saharan Atlas and highlands in the north and the beginning of Sahara in the south (4 to 8°E, 29 to 35°N). Elevations in these areas decrease eastwards, starting from 1000–1200 m in the west and reaching 50–200 m in the east. The vegetative cycle begins in the autumn, with a flowering period generally between April and June, but occasionally blooming is observed earlier in November and December, when the plants take advantage of autumn rains.

Literature does not show any works dealing with studies on *R. intermedium,* apart from a comparative study by Wiklund (1986). Most studies published in recent years involve the biochemical aspects of *R. adpressum* or *R. suaveolens* by studying the biological properties of phenolic or lipid extracts and essential oils (Hamia & al. 2013; Boussoussa & al. 2016; Chemsa & al. 2016; Elhouiti & al. 2017), or by studying the nutritional values considering the importance of these plants as a fodder resource (Chehma &Youcef 2009). The present study focuses on the ecological properties and compares the distinct differences between the habitats of the species.

The objective of this study is to model habitats suitability of *R. adpressum* and *R. suaveolens* species, to distinguish their distribution areas and show the zone, in which the hybrid species *R. intermedium* is distributed, with an analysis of habitat preferences for each species. The results will contribute to the Maghreb studies interested in these three species by highlighting their biochemical potential or their genetic variations. Furthermore, the populations of *R. adpressum* and *R. suaveolens* have an allopatric model of speciation, which enhances the knowledge of distribution areas for in-depth studies of ecology and genetics.

Material and methods

Study area and species occurrence

The study area extended from western to eastern parts of Algeria (-4.7°E-7.5°E, 29°N-35°N) and in the south from the Saharan Atlas to the north of Sahara. The investigated species in that area were *Rhanterium suaveolens* Desf. (1799), *Rhanterium adpressum* Coss. & Dur. (1855) and *Rhanterium intermedium* Pomel (1874), with a synonym: *Rhanterium suaveolens* Desf. ssp. *intermedium* (Pomel) (Quezel & Santa 1963).

The points of presence were picked out from the digitized herbarium of the National Museum of Natural History of France (https://science.mnhn.fr/institution/mnhn/collection/p/item/search), in addition to our own observations. One hundred and ten points were obtained for *R. adpressum,* generally in Bechar (–3.7–0.4°E, 29.6–32.2°N), Naama (–1.1–0.1°E, 32.3–33°N) and Laghouat (2–3°E, 33.2–33.9°N). For the prediction of suitable habitats of *R. suaveolens* and *R. intermedium*, 100 points were used. Verification of the scientific names followed the International Plant Names Index (https://www.ipni.org), while geo-referencing of the occurrence points used the Geoplaner website (https://www.geoplaner.com).

Climatic predictors and predictive modeling

This study was based on the presence-only technique favored by the presence-absence data collection technique (Thompson & al. 2009). Nineteen bioclimatic variables, plus the altitude factor, were used to accomplish the distribution model and habitat suitability analysis. The variables were derived from temperature and precipitation, generally indicative of the trends for these two parameters, which were considered ecologically more sensitive for demarcating the physio-ecological tolerances of the habitat than the simple variables of temperature and precipitation (Graham & Hijmans 2006; Pramanik & al. 2018). These 20 variables were downloaded from the WorldClim website (https://www.worldclim.org), version 2, with a resolution of 30 arc seconds (~1 Km). The data were interpolation results from the historical records (1970–2000) of monthly temperature and precipitation.

Modeling of distribution of the *Rhanterium* species was carried out with MaxEnt 3.4.1, which provided good results even for small samples (Phillips & al. 2006; Elith & al. 2011). The evaluation of obtained models was based on the Area Under Curve (AUC), which varied between 0 to 1, where a model with AUC≥0.9 signified a very high performance (Thuiller & al. 2005). General parameters of the model execution were 10 replications of cross-validation, max iteration at 500, regularization multiplier in default value (1), and in logistic ASC output format. Response curves of the studied species to bioclimatic variables were generated as mean values, with standard deviation of 10 replications for cross-validation. Some of these curves were redrawn with SigmaPlot 12.5 to present them in the results.

Results

Two models of good quality were obtained for *R. adpressum* and *R. intermedium/suaveolens* with Area Under Curve (AUC), of 0.98±0.006 and 0.98±0.01, respectively. Bioclimatic predictors with majority contribution to the MaxEnt models have been given in Table 1. Precipitation in the driest month and quarter was the predictor which contributed most to the obtained models (27.8 % to the model of *R. adpressum* and 26.4 % to the model of *R. intermedium/suaveolens*). Furthermore, temperature seasonality also contributed greatly to these two models (21.8 % and 18.7 %, respectively), knowing that that predictor measured the temperature changes during the year. Between the two models, temperature-derived factors contributed more than 60 % to the *R. intermedium/suaveolens* model, contrary to the *R. adpressum* model, where precipitation factors contributed up to 55 %.

The distribution map of *Rhanterium* species in Algeria generated by the two models of MaxEnt is shown in Fig. 1. These species are distributed to the south of the Saharan Atlas and to the north of Sahara, from Bechar in the west to ElOuadi in the east, on a stretch up to 1100 km long and about 500 km wide. *R. adpressum* is distributed in South Morocco and Mauritania, and in Algeria from the west to the center (4°E, 32–33°N), while distribution of *R. suaveolens* begins just after 5°E, 31–35°N to Tunisia and Libya. Between these two areas (red lines in Fig. 1), the hybrid species *R. intermedium* is distributed between 3–4°E and 29–34°N.

Table 1. High contribution percentage to the development of two habitat-suitability prediction models for *R. adpressum* and *R. intermedium/suaveolens*.

R. adpressum	
Precipitation of driest month	27.8 %
Temperature seasonality (coefficient of variation)	21.8 %
Precipitation of driest quarter	10.5 %
Precipitation of wettest quarter	9.9 %
Annual temperature range	7.9 %
Mean temperature of warmest quarter	5.8 %
R. intermedium/suaveolens	
Precipitation of driest quarter	26.4 %
Mean temperature of driest quarter	20.8 %
Temperature seasonality (coefficient of variation)	18.7 %
Precipitation of coldest quarter	5.7 %
Precipitation of wettest month	5.1 %
Annual mean diurnal range	4.6 %

Four responses of the *Rhanterium* species to environmental factors after 10 replications for cross-validation are shown in Fig. 2. These responses show the preferences of these species for each factor. The values with their standard deviation are given in Table 2. For both factors, the mean annual temperature and mean temperature of the driest quarter, the response interval of *R. adpressum* is lower than of the other two species *R. intermedium/suaveolens,* with a ≤0.65 probability of

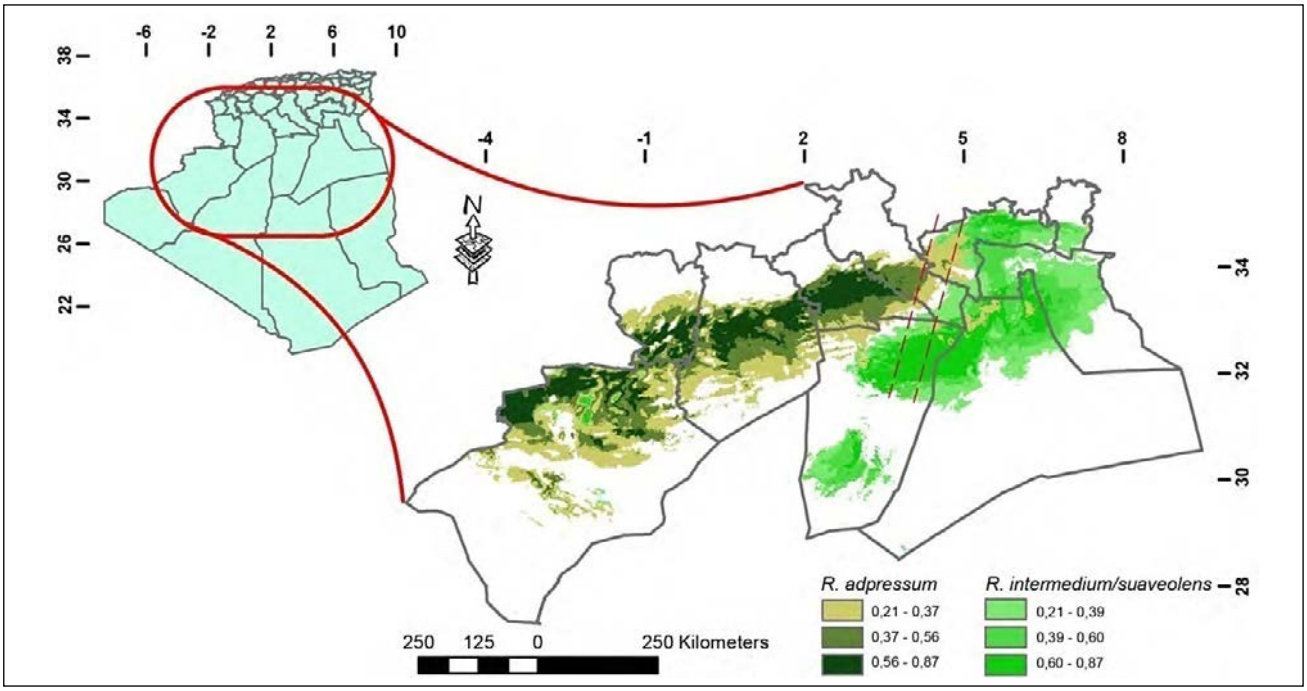

Fig. 1. Distribution models of *R. adpressum* and *R. intermedium/suaveolens*. Red lines show the areas of the hybrid species.

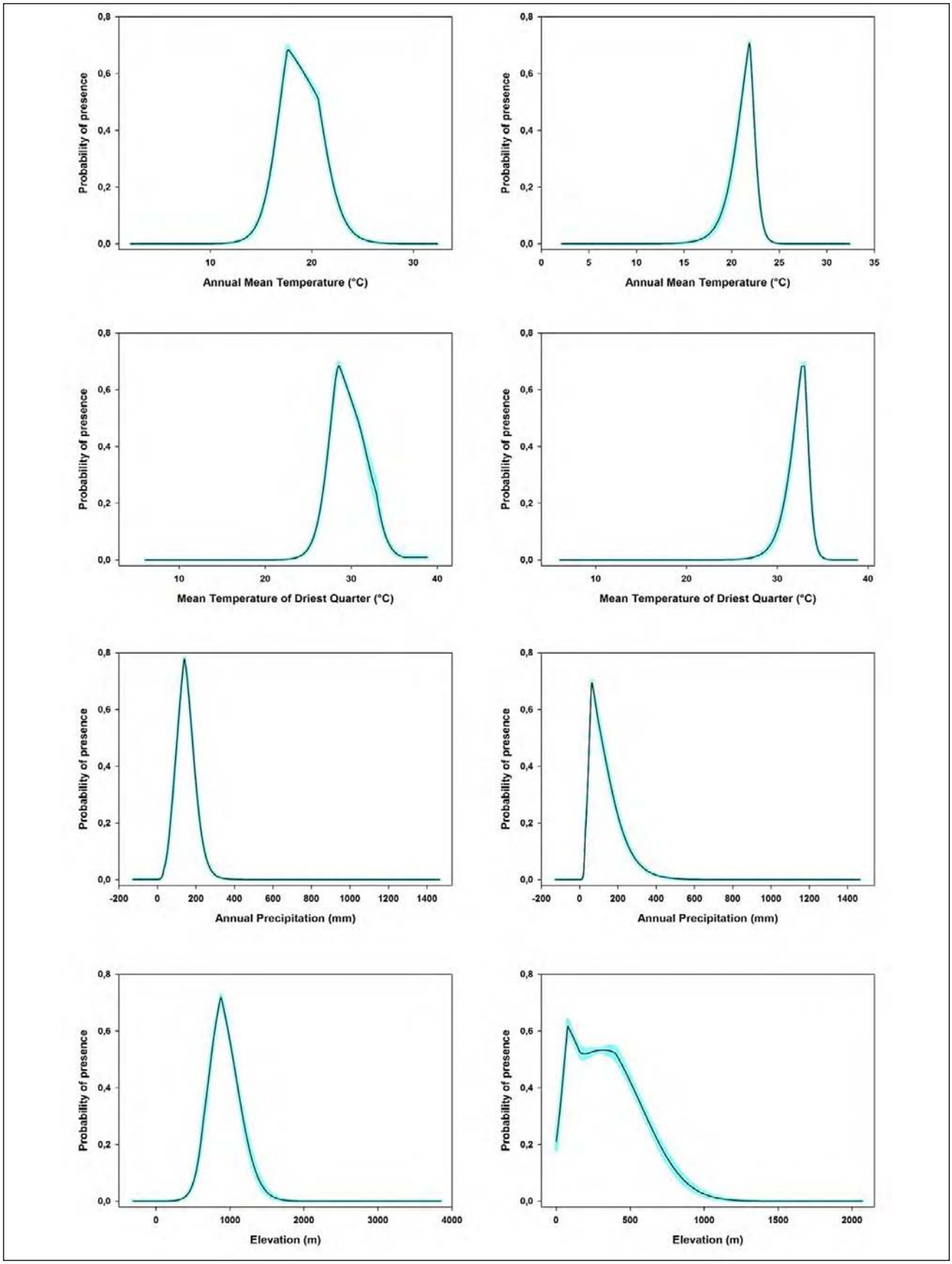

Fig. 2. Response curves of *R. adpressum* (left) and *R. intermedium/suaveolens* (right) to four environmental predictors.

Table 2. Mean values of bioclimatic variables characterizing habitat preference of *R. adpressum* and *R. intermedium/suaveolens* species, with their standard deviations.

	R. adpressum	*R. intermedium/ suaveolens*
Annual mean temperature (°C)	18.65±1.19	21.61±0.44
Annual mean diurnal range (°C)	13.34±0.26	13.03±0.48
Isothermality (%)	35.80±0.92	34.53±1.34
Temperature seasonality (coefficient of variation) (%)	841.05±16.31	860.40±12.28
Max temperature of warmest month (°C)	36.36±1.18	39.91±1.06
Min temperature of coldest month (°C)	–0.08±1.02	2.91±0.38
Annual temperature range (°C)	36.76±0.54	36.73±0.73
Mean temperature of wettest quarter (°C)	16.89±1.46	12.44±0.49
Mean temperature of driest quarter(°C)	29.08±0.88	32.65±0.37
Mean temperature of warmest quarter (°C)	28.95±0.99	32.50±0.48
Mean temperature of coldest quarter (°C)	8.35±0.88	11.34±0.32
Annual precipitation (mm)	140.72±25.26	86.62±19.75
Precipitation of wettest month (mm)	18.27±3.01	11.42±2.15
Precipitation of driest month (mm)	2.89±1.08	1.63±0.75
Precipitation seasonality (coefficient of variation) (%)	34.70±6.38	43.83±2.28
Precipitation of wettest quarter (mm)	49.02±7.70	26.38±4.89
Precipitation of driest quarter (mm)	16.58±6.27	6.70±1.94
Precipitation of warmest quarter (mm)	16.97±6.74	5.05±1.36
Precipitation of coldest quarter (mm)	38.78±7.74	21.69±4.45
Elevation (m)	888.74±94.89	255.18±114.52

presence. Contrary to the annual precipitation, where the areas of *R. adpressum* are rainier than those of the other two species. Despite the difference in climatic factors in both zones, the elevation factor shows distinctive variance between these species: *R. adpressum* in the West prefers high altitudes, contrary to *R. intermedium/ suaveolens,* which prefer low altitudes.

Generally, the habitats of *R. adpressum* occupy characteristically an average altitude of 888.74 m (SD=94.89 m), with a mean annual temperature of 18.65 °C (SD=1.19 °C) and annual precipitation of 140.72 mm (SD=25.26 mm). The habitats of *R. intermedium/suaveolens* species occupy characteristically an average altitude of 255.18 m (SD=114.52 m), with a mean annual temperature of 21.61 °C (SD=0.44 °C) and annual precipitation of 86.62 mm (SD=19.75 mm).

Discussion

The results show two distinct distribution areas, the first for *R. adpressum* in the Northwest and the second in the Northeast Algeria for *R. suaveolens,* with a meeting zone between the two for the hybrid species *R. intermedium,* with its high morphological variability, as compared to the two typical species *R. adpressum* and *R. suaveolens*. On the basis of specimens stored in the National Museum of Natural History of France, Wilklund (1986) detailed the comparative descriptions of these three species and suggested a distribution map similar to the models obtained by MaxEnt (Fig. 1). According to his measurements, he saw specimens within the hybrid species, which were intermediate or close to one of the other two species. He also pointed to the fact that similar variation might appear without hybridization in zones subject to great ecological changes, which were thus similar to zones of intergradation. These zones resulted from an environmental gradient (longitudinal and altitudinal in this study). They were formed *in situ* by primary intergradation or by secondary contact between populations that diverged allopatrically. However, the origin of such formation could not be determined easily (Abbott 2017).

The two species *R. adpressum* and *R. suaveolens* are distributed in regions classified as sub-Mediterranean semidesert grasslands and shrublands, and seldom in desert areas. According to the the aridity index (AI), these areas can be arid for *R. adpressum* (AI=0.10±0.05) and hyperarid for *R. suaveolens* (AI=0.05±0.03). It appears from the results that the two zones have different climatic characteristics in addition to the altitude factor, which differs significantly. According to Wiklund (1986), the overlapping of these two zones (red lines in Fig. 1) shows in progression a complete separation of the two zones, placing *R. adpressum* and *R. suaveolens* species in an allopatric model of speciation.

There are two mechanisms, by which the climate can lead to speciation: niche divergence and niche conservatism. In the first case, several populations occupy different habitats and differences in climatic conditions would impose divergence over time. In the second case, for allopatric populations, climate differences in space could serve as a dispersal barrier and the incipient species would adapt and tolerate the new conditions (Wiens 2004). Niche conservatism could be an important aspect of speciation, especially under long-term climate changes (Hua & Wiens 2013).

The relationship between elevation or altitudinal gradient and speciation has been widely discussed (Steinbauer & al. 2016, 2017). Furthermore, large areas additionally increase the probabilities of speciation and allopatric divergence (Losos & Schluter 2000).

In this study, the intrinsic ecological factors are limiting variables for the distribution areas of *R. adpressum* and *R. suaveolens* species. However it is important to report the impact of other abiotic or biotic factors, such as soil properties, competition and tolerance of cold, and the consideration that perennial plants may develop resistance to suboptimal environmental conditions (Wiens 2004; Aguilée & al. 2018; AitMouheb & al. 2018).

In this study, habitat suitability modeling differentiated the distribution areas of *R. adpressum* and *R. suaveolens* species and showed the meeting areas, where the hybrid species *R. intermedium* was found. With the response curves of the species to bioclimatic factors, habitat preferences of these species have been analyzed. Distinction of the hybrid zone is an important step for future genetic or ecological studies that would contribute to understanding the isolation and speciation mechanisms, considering these zones as "natural laboratories for evolutionary studies" and "windows on evolutionary process".

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