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Modelling the potential distribution and habitat suitability of the alien fungus *Clathrus archeri* in Romania

Ciprian Bîrsan[1]*, Constantin Mardari[1], Ovidiu Copoţ[1] and Cătălin Tănase[2]

1 Anastasie Fătu Botanical Garden, Alexandru Ioan Cuza University, 7-9 Dumbrava Roșie, 700487 Iași, Romania
2 Department of Biology, Faculty of Biology, Alexandru Ioan Cuza University, Carol I 20A, 700505 Iași, Romania
* Correspondence: ciprian.birsan@uaic.ro

ABSTRACT:
Clathrus archeri is a saprophytic fungus native to the southern hemisphere which was introduced in Europe in the early twentieth century. Although it is naturalized in most regions of Central Europe, in Romania it is considered rather a rare species because it has been identified in only a few localities. Because of the rapid expansion of its range throughout Europe some authors assign this species an invasive potential. The objective of the paper was to identify both the potential distribution area and the potential suitable habitats for expansion in Romania and to highlight the environmental variables driving the probability of its occurrence. The maximum entropy model approach implemented in Maxent was used to model the species' potential distribution. The results highlighted altitude, snow cover length, the mean temperature of the driest quarter, and precipitation in the coldest quarter as the most important predictors of species' potential distribution in Romania. The map of the predicted distribution showed that the highest probability of occurrence for this species is in the mountainous and adjacent areas, while the map of habitat suitability confirmed that the best environmental conditions are in the Carpathians, while the most unfavourable are in the south-eastern regions of the country.

Keywords:
abiotic factors, alien species, *Clathrus archeri*, winter climate, precipitation, suitable habitat

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INTRODUCTION

Clathrus archeri (Berk.) Dring is one of the two species of the genus *Clathrus* in Romania (the other species is *Clathrus ruber*). The *Clathrus* species have brightly coloured and oddly shaped sporiferous bodies. The dissemination of spores is realized by insects (Boomsluiter 2017) over short distances (Vellinga & Kuyper 2012).

Clathrus archeri avoids calcareous soils and regions with an extreme continental climate, hot dry summers and frosty winters (Parent *et al.* 2000). According to the observations of Johnson & Jürgens (2010), the sporiferous bodies of *C. archeri* with long, coloured arms, covered with a brown gleba in the early stages, which then turns black, are regularly visited by insects due to the smell they emit.

Clathrus archeri is a saprophytic fungus native to the southern hemisphere, specifically Australia and New Zealand (Parent & Thoen 1986; Pietras *et al.* 2016). It was introduced in Europe in the early twentieth century (first record in 1914, France, Vosges Mountains) and then gradually spread to several European countries (Stebel 2015). The hypothesis accepted by several authors is that the species arrived with sheep wool or military equipment from Australia during the First World War (Parent *et al.* 2000; Salcedo *et al.* 2006). According to the same authors, this species is naturalized in most regions of Central Europe. It was also reported in other European countries with a warmer climate, from the southern and western parts of the continent. In the Netherlands, after the first report in 1973, *C. archeri* slowly spread to the southern and eastern regions of the country. Since 2008, the number of occurrences has increased significantly, especially in the north and northeast parts of the Netherlands and also in the vicinity of those already reported. The species occurred in shady places, on nutrient-rich and humid soils and on wood and leaves. The fungus was also identified on the Iberian Peninsula (Sarrionandia *et al.* 2010). The appearance of the sporiferous bodies was from the end of summer to autumn in the Basque Country, with a spike in October due to the mild and favourable climate near the Atlantic Ocean. From an altitudinal point of view, most localities were located around 700 m a.s.l. (Urquijo 2013).

Although the species prefers humid regions, with tropical influences, it also grows well in other areas with a harsher climate. In Poland, after the first report in 1973, it became frequent in certain areas, spreading from southern Poland, initially towards the centre, and afterwards to the west, while sporadic occurrences were reported in the north of the country (Pietras *et al.* 2016). There was an increase in reports of new localities (post-2004) in habitats with strong anthropogenic influences and in their vicinity (Wojewoda & Karasiński 2010). After the first report from Lower Silesia (in 1973), during the 1980s, *C. archeri* populated natural and anthropogenic habitats with various plant communities on the Polish side of the Carpathian Mountains, on the south-eastern slopes (Stengl-Rejthar & Wojewoda 1985; Wojewoda 2003). In 2015, sporiferous bodies were identified in an abandoned meadow with *Solidago gigantea* and at the edge of a young birch forest (Stebel 2015), marking an extension of its distribution in this part of Poland. With over 90 reports, *C. archeri* is the most widespread species among the exotic, non-native species in Poland. About 65% of occurrences were reported from forest habitats (Szczepkowski & Obidziński 2012).

In Lithuania, the first report of this species dates back to September 2011, when the species was identified on the ground, on a semi-open slope, covered with shrubs and herbaceous vegetation, surrounded by a plantation of *Picea abies* and *Pinus sylvestris*. The fungus was found in the west of the country, characterized by a milder climate, influenced by the Baltic Sea. This was the first record for the eastern region of the Baltic Sea (Motiejūnaitė *et al.* 2016). The species was also reported from other countries located in Central Europe (i.e. Germany, Switzerland, Austria, the Czech Republic, Slovakia) or Western Europe (i.e. Denmark, Netherlands, the United Kingdom) (Kreisel 2006; Desprez-Loustau *et al.* 2010). Data on the geographical distribution of the species is far from complete, as information about new locations is continuously accumulating (Kreisel 2006; Desprez-Loustau *et al.* 2010).

Clathrus archeri is considered a rare macromycete in Romania (Tănase & Pop 2005) and was consequently included on the Red List of macromycetes. The species was also included on the red lists of other countries (Gyosheva *et al.* 2006; Didukh 2009), although in Ukraine, due to active dissemination both at district and country level, it was concluded as inappropriate to maintain this species on the national Red Book of threatened species (Heluta & Zykova 2018).

Currently, in Romania, it is considered a rare species because it has been identified in only a few localities. After the first report in 1996 (Béres 1996), an expansion was observed in the historical province of Maramureș (Northern Romania). Thus, in Béres (2012), the authors reported seven new locations where the species was identified between from July and October in habitats with various physical-geographical characteristics and different floristic compositions. The altitudes ranged between 300 m in Mociar (in a forest dominated by oak and hornbeam) up to 900 m in Bârsana-Secătura in a hygro-mesophilic pasture. In Maramureș it is called the "devil›s mushroom" (due to its repulsive smell and red colour), and because of some common superstitions, in some areas sheep grazing on meadows with *Clathrus* is avoided. Later, in 2013, in the Eastern Carpathians two new locations were discovered in the Bârgău and Gurghiu Mountains. The highest known location in Romania (Bîrsan *et al.* 2014) is situated in the southernmost area of Poiana Repaș, at approximately 1200 m a.s.l. (Gurghiu Mountains). According to first-hand information from József Szabó, *C. archeri* was also identified in July 2015 in the Homorod Valley, in the Harghita Mountains at an altitude of about 760 m a.s.l. Another location in Romania was reported in August 2018 in Piatra Nierges, in the Ciuc Mountains at approximately 1000 m a.s.l. (Matus *et al.* 2018) in a mesic mountain meadow.

An invasive species is defined as an alien species which becomes established in natural or semi-natural ecosystems or habitats, acting as an agent of change, which threatens the native biological diversity (IUCN 1999). There are several stages when a non-native species arrives in a new territory: introduction, naturalization and invasion. An alien species is considered invasive when it has a major impact on colonized habitats causing changes in their composition by producing abundant breeding individuals over a large area and away from the parent plants (Pyšek *et al.* 2004; Desprez-Loustau 2009). It is difficult to assess invasion status for fungi, for many reasons, such as phylogeny, reproduction biology and introduction pathways (Desprez-Loustau *et al.* 2010). According to the literature, the studied species is considered to have expansion behaviour, especially in Poland, where it was largely investigated (Kopij 2012; Pietras *et al.* 2016). The species was also largely recorded in the British Isles, the Iberian and Italian Peninsulas and Central Europe (MyCoPortal 2018).

The importance of species distribution modelling (SDM) has rapidly increased especially in the context of climate change and human disturbance which influence species distributions. A widely used SDM tool is Maxent (Maximum Entropy) which uses species occurrences and environmental data to predict the potential geographical distribution of a species. This tool is highly regarded as it can predict species distribution with high accuracy using only a small sample size (Phillips *et al.* 2006), which is often the case with invasive species (Pietras *et al.* 2018; Pietras & Kolanowska 2019).

The aims of the study were: (i) to identify the potential distribution area of *C. archeri* in Romania using species distribution models, (ii) to determine the environmental factors driving the probability of occurrence; (iii) to explore the specific suitable habitats for the expansion of its area in Romania.

MATERIALS AND METHODS

Study area. The study area is represented by Romanian territory, which comprises 238397 km^2. With five biogeographic regions Romania is considered the second richest country in terms of biogeographic diversity (pontic, steppic, pannonian, continental, and alpine), thus showing study suitability for a high variety of environmental gradients. Forests cover the largest part of the Romanian

Table 1. Species occurrences used in spatial modelling

Latitude	Longitude	Location	Date	Data source
N 47°16’57.1”	E 24°56’37.1”	Munții Bârgăului	7/18/2013	Bîrsan *et al.* 2014
N 46°38’29.9”	E 25°10’42”	Munții Gurghiului	7/14/2013	Bîrsan *et al.* 2014
N 45°54’58.8”	E 22°18’25”	Pădurea Groși	9/9/2017	personal observations
N 46°21’41.2”	E 25°27’56.5”	Homorodul Mare	7/9/2015	József Szabó
N 46°11’10.3”	E 25°58’14.5”	Piatra Niergeș	8/23/2018	Matus *et al.* 2018
N 47°49’51.6”	E 23°42’09.3”	Tăul lui Dumitru	6/6/2020	personal observations
N 47°55’19.9”	E 23°49’39”	Iapa	8/23/1993	Béres 2012
N 47°54’42.2”	E 23°43’08.5”	Săpânța-Jilerescu	7/28/1993	Béres 1996, 2012
N 47°57’36.9”	E 24°00’28.1”	Bocicoi	10/1/2006	Béres 2012
N 47°54’12.3”	E 23°52’19.9”	Dealul Solovan	10/1/1996	Béres 1996, 2012
N 47°56’35”	E 23°57’48.3”	Mociar	7/29/2008	Béres 2012
N 47°53’14.5”	E 23°54’13.1”	Vadul Izei-Valea Șugău	9/30/2001	Béres 2012
N 47°53’11.5”	E 24°01’50.9”	Bârsana-Secătura	10/8/1996	Béres 2012
N 45°46’31”	E 25°05’58.6”	Poiana Narciselor	7/17/2018	Johnsson 2018
N 46°50’43.5”	E 22°24’21.4”	Cheile Cuților	6/6/2020	GBIF
N 46°41’32.1”	E 23°34’34.3”	Micești	8/26/2014	iNaturalist
N 47°20’45.4”	E 25°58’16.2”	Văleni Stânișoara	6/6/2020	personal observations
N 45°28’37.1”	E 23°05’12.1”	Barbat	6/6/2020	personal observations
N 44°41’30.8”	E 22°20’21.2”	Eșelnița	7/8/2019	iNaturalist
N 45°19’34.2”	E 22°24’56.8”	Turnu Ruieni	6/27/2020	iNaturalist
N 46°40’04.6”	E 23°06’35.5”	Mărișel	7/8/2020	iNaturalist
N 46°40’31.2”	E 22°59’26.7”	Beliș	11/4/2018	iNaturalist
N 46°47’35.1”	E 22°56’11.5”	Margău	9/1/2018	iNaturalist
N 46°56’06.6”	E 22°50’43.2”	Poieni	7/19/2018	iNaturalist
N 45°39’51.5”	E 24°06’35.6”	Cisnădioara	8/3/2018	MyCoPortal

Table 2. Reclassification of Corine Land Cover classes

Class code	Level	Class	New class code	New class
111, 112, 121, 121, 122, 123, 124, 131, 132, 133, 141, 142, 511, 512, 522, 523, 331, 332, 333, 334, 335, 411, 421, 422, 423	1	artificial surfaces, water bodies, wetlands and open spaces with little or no vegetation	1	little or no vegetation
211, 212, 213	2	arable land	2	arable land
221, 222, 231, 321, 322, 241, 242, 243, 244	3	pastures, natural grasslands, moors and heathland, heterogeneous agricultural areas, agro-forestry areas, permanent crops	3	areas with grassland either in patches or full, seasonally grazed by sheep
311	3	broad-leaved forest	4	broad-leaved forest
313	3	mixed forest	5	mixed forest
312	3	coniferous forest	6	coniferous forest
323, 324	3	sclerophyllous vegetation, transitional woodland-shrub	7	sclerophyllous and transitional woodland-shrub

Carpathian Mountains, while the hills and plains are dominated by agricultural land cover (both by arable land and pastures). The study area is situated between N 48°15'06" and N 43°37'07" latitude, and E 20°45'44" and E 29°41'24" longitude. The elevational gradient shows an approximate cover equality among the three types of geomorphological features (plains, hills and mountains), from the Black Sea coast (0 m) to the Făgăraș Mountains (2544 m).

Occurrence records and environmental data. The 26 occurrence locations of *C. archeri* were obtained from specific databases (MyCoPortal 2018; GBIF 2020; iNaturalist 2020), field observations and literature (Table 1). In order to reduce the spatial sampling bias, all occurrences were filtered using a 10 km grid-based method. In order to discover which environmental variables have the most significant influence on the geographic distribution of *C. archeri* in Romania, we used 19 bioclimatic variables and elevation, (Fick & Hijmans 2017) with a resolution of 30 arc sec (ca. 1 km). We calculated the De Martonne Aridity Index (DMAI) for the annual period according to Quan *et al.* (2013), while pH at 5 cm depth was downloaded from the SoilGrids database (Hengl *et al.* 2017).

To estimate how the ecosystem type influences the distribution of fungal species (Hottola & Siitonen 2008; Zhou & Dai 2012; Copoț & Tănase 2017), we used Corine Land Cover with a spatial resolution of 250 m (https://land.copernicus.eu/pan-european/corine-land-cover/clc-2012). Furthermore, the 43 Corine Land Cover classes were reclassified into 9 classes (Table 2), in order to increase the significance of the most common types of habitats where the species was identified (e.g. grassland, forests).

Modelling procedure. We used the maximum entropy model (Phillips *et al.* 2006), implemented in R software (R Development Core Team 2012) because it has been shown to perform better than other modelling methods (Elith *et al.* 2006). Based on the maximum entropy algorithm, Maxent uses occurrence records and environmental data layers to predict the geographic distribution of a species (Phillips *et al.* 2006). One of the main reasons for using Maxent is the capacity to produce valuable results with small sample sizes when compared to other species distribution modelling methods (Hernandez *et al.* 2006).

We used VIF (Variance Inflation Factor) to check for the collinearity of the variables (Dormann *et al.* 2013). The Maxent model was computed using the 10-fold cross-validation method for each set of variables tested. At first, it was deemed to be a model using the uncorrelated variables. We removed one predictor at a time step-wise using the jackknife technique for test occurrences and percent contributions (van Gils *et al.* 2012). We continued with this procedure until each of the remaining variables had at least a 5% contribution. In the Maxent models we used 1.0 as the regularization parameter (beta-multiplier), linear and quadratic models, 1000 as the maximum number of iterations, and 0.00001 as the convergence threshold. The other Maxent modelling parameters were kept as the default. For pseudo-absences we used 10000 background points.

In order to test the model performance, we used the AUC (Area Under The Curve). It takes values from 0 to 1, where 0.5 indicates a random distribution and 1 a perfect model performance. AUC can be further classified, indicating low accuracy (<0.7), good accuracy (0.7-0.9), or high accuracy (>0.9) (Swets 1988). In order to obtain *C. archeri* habitat suitability distribution in Romania, we used the classification proposed by Yang *et al.* (2013): least potential (<0.2), moderate potential (0.2-0.4), good potential (0.4-0.6), and high potential (>0.6).

RESULTS

Important factors in the prediction of *Clathrus archeri* distribution. According to the jackknife test and the selection of variables depending on their significance, the most important predictors of *C. archeri* distribution in Romania are altitude (ALT), snow cover length (SL), the mean temperature of the driest quarter (bio9), and precipitation in the coldest quarter (bio19). In Romania, both the driest quarter and the coldest quarter are between December and February, indicating winter time.

The training gain in the jackknife test shows the relative contribution of each of the environmental variables used in the final Maxent model (Fig. 1). The highest individual gain was shown for the snow cover length, thus providing the most useful information in isolation (Fig. 1). Precipitation in the coldest quarter has the most information as it decreases the gain the most when omitted. The temperature of the coldest quarter has the least information by itself, as it shows the lowest gain in isolation and decreases the gain the least when omitted (Fig. 1).

Snow cover length was the most effective single variable for predicting the potential distribution of *C. archeri* when the predictive performance was measured using AUC. Altitude and winter precipitation were also important variables when analysed individually.

Following the response curves for the four environmental variables, the species' optimal ecological niche (defined using 0.6 as the threshold) can be defined as: average winter temperatures between -5˚C and 0˚C, winter precipitations above 130 mm/season, season snow cover length above 11 weeks, and altitude ranging from 500 to 1700 m a.s.l. (Fig. 2a-d).

These results emphasize the importance of winter precipitation for *C. archeri* in Romania. When also taking the snow cover length into consideration, it becomes obvious that winter characteristics have a limiting impact on the occurrence of *C. archeri* in Romania, as highlighted in the response curves (Fig. 2a-d).

Table 3. Predicted area for *Clathrus archeri* in Romania

County	No suitability		Low suitability		Medium suitability		High suitability	
	Predicted area (km²)	Area ratio (%)	Predicted area (km²)	Area ratio (%)	Predicted area (km²)	Area ratio (%)	Predicted area (km²)	Area ratio (%)
Alba	3647	58.38	965	15.45	706	11.3	929	14.87
Arad	6415	82.56	1170	15.06	177	2.28	8	0.1
Argeş	4874	71.32	1864	27.28	89	1.3	7	0.1
Bacău	4342	65.63	1994	30.14	277	4.19	3	0.05
Bihor	2923	38.65	2600	34.38	965	12.76	1074	14.2
Bistriţa-Năsăud	139	2.59	1629	30.4	1912	35.68	1678	31.32
Botoşani	4577	92.54	369	7.46	0	0	0	0
Braşov	1310	24.4	1500	27.94	1138	21.2	1421	26.47
Brăila	4766	100	0	0	0	0	0	0
Bucureşti	234	94.35	14	5.65	0	0	0	0
Buzău	5867	96.35	194	3.19	28	0.46	0	0
Călăraşi	5003	98.54	74	1.46	0	0	0	0
Caraş-Severin	2200	25.75	1625	19.02	1421	16.63	3297	38.59
Cluj	2456	36.81	1697	25.43	811	12.15	1709	25.61
Constanţa	7016	100	0	0	0	0	0	0
Covasna	888	23.94	1792	48.31	833	22.46	196	5.28
Dâmboviţa	3127	77.4	887	21.96	26	0.64	0	0
Dolj	6895	93.01	518	6.99	0	0	0	0
Galaţi	4427	99.91	4	0.09	0	0	0	0
Giurgiu	1999	56.56	1535	43.44	0	0	0	0
Gorj	4252	76.01	1010	18.06	247	4.42	85	1.52
Harghita	1976	29.73	3822	57.51	688	10.35	160	2.41
Hunedoara	2595	36.69	1779	25.15	841	11.89	1858	26.27
Iaşi	4879	90.05	539	9.95	0	0	0	0
Ialomiţa	4448	100	0	0	0	0	0	0
Ilfov	1516	93.99	97	6.01	0	0	0	0
Maramureş	66	1.05	200	3.19	615	9.81	5391	85.95
Mehedinţi	3148	63.6	1409	28.46	284	5.74	109	2.2
Mureş	4147	61.74	1890	28.14	481	7.16	199	2.96
Neamţ	3183	54.11	2406	40.9	279	4.74	14	0.24
Olt	5109	92.99	385	7.01	0	0	0	0
Prahova	3548	75.3	1036	21.99	111	2.36	17	0.36
Sălaj	126	3.26	1397	36.1	1559	40.28	788	20.36
Satu Mare	556	12.62	2244	50.92	605	13.73	1002	22.74
Sibiu	3157	58.09	736	13.54	568	10.45	974	17.92
Suceava	1967	23.01	2958	34.61	2366	27.68	1256	14.7
Teleorman	4537	78.41	1249	21.59	0	0	0	0
Timiş	7984	91.56	418	4.79	219	2.51	99	1.14
Tulcea	8399	100	0	0	0	0	0	0
Vâlcea	4746	82.27	659	11.42	225	3.9	139	2.41
Vaslui	4754	90.11	522	9.89	0	0	0	0
Vrancea	3739	76.95	567	11.67	441	9.08	112	2.31

Potential distribution of *Clathrus archeri* in Romania. The 19 bioclimatic variables derived from the WorldClim - Global Climate Data are well known for their usefulness when predicting the geographical distribution of invasive species. Adding other variables also increases the chances of correctly developing a prediction model. Using four variables (altitude, snow cover length, precipitation in the coldest quarter, and the mean temperature of the driest quarter), the mean AUC reached 0.831, which demonstrates the accuracy of the model.

The predicted distribution map of *C. archeri* in Romania (Fig. 3) showed that the highest probability of occurrence for this species is in the mountainous areas. Also, the habitat suitability map (Fig. 4) confirms that the best environmental conditions (class 3) for *C. archeri* are in the Carpathians, while the most unfavourable are in the south-eastern parts of Romania.

According to the predicted distribution (Table 3), the most suitable areas for *C. archeri* in Romania are found in the counties from central and northern Roma-

Fig. 1. Jackknife training gain for evaluating the relative importance of environmental variables for the potential distribution of *Clathrus archeri* (average over 10 replicate runs): taken as individual (blue bars); taken without variables (cyan bars), relative to all variables (red bar).

nia (over 1000 km^2): Maramureş, Caraş-Severin, Bihor, Bistriţa-Năsăud, Braşov, Cluj, Hunedoara, Satu Mare, and Suceava. On the other hand, the south- and south-eastern counties (e.g. Brăila, Călăraşi, Galaţi, Ialomiţa, and Constanţa) are the least suitable for the presence of this species. Each county counts for different area-ratio suitability, with the highest probability (over 30%) being found in the counties of Maramureş, Bistriţa-Năsăud and Caraş-Severin. Altogether, approximately 63.8% of Romanian territory (roughly 152000 km^2) is unsuitable for the species' presence, while approximately 19.2% has low presence probability (45000 km^2). The remaining 17% represents moderate and highly suitable areas (41000 km^2), with 9.46% of Romania's area (approximately 22500 km^2) being highly suitable for *C. archeri* presence.

Nonetheless, the species could potentially occur (but with a significantly lower probability) in habitats from the hilly areas surrounding the Southern and Eastern Carpathians (discontinuous areas from the Iaşi, Dâmboviţa, or Bacău counties).

DISCUSSION

In Romania, the alpine biogeographical region is represented by the Carpathian Mountains area of 800 km in length covering 23% of the territory. This biogeographical region includes mountain peaks, intramontane depressions as well as hills alongside the mountain range. Due to the cold and humid climate with long winters and short summers, it offers specific conditions to which plants and animals have adapted, sheltering endemic species and priority habitats. The Carpathian Mountains belong to the temperate continental climate zone with different nuances, influenced by altitude, latitude and longitude. As the altitude increases, the average annual temperatures decrease (values between 8°C at the base and -2°C in the ridge of the highest mountains), and the average amount of precipitation increases from 750 mm to 2000 mm. There are different climatic influences along the mountain chain (Baltic in the northern part, Oceanic in the western part, continental in the eastern part, and Mediterranean in the southern part), which all impact on the species composition in the alpine biogeographical region.

Along the Carpathian Mountains, *C. archeri* occurs in various forest habitats, preferring soils with high humidity. It has also been reported in meadows, orchards, and gardens. The seasonal dynamics are such that the sporiferous bodies of the species occur from June to October, exceptionally and occasionally in November (Fig. 3). It appears to have formed viable populations in favourable habitats and the latest reports are a consequence of the current expansion of the species range throughout Europe. There is still no information about the interactions between this species and native fungi.

Different hypotheses regarding the dispersal pathways of the *C. archeri* species, especially along the Carpathians, may be formulated. In time, there was an extension of this species' area from the historical Maramureş to the south and southwest of the country. It also found favourable environmental conditions in the Apuseni Mountains. Considering the historical Maramureş province as its origin (first record), and the subsequent records towards the Eastern Carpathians and Western (Romanian) Mountains, we could hypothesize that the direction of the spread was from the north to the south-east and south-west, following the high hills and low mountains arches. The new records of the species in the extreme southwest of Romania suggests another entry point in the country, from South-Eastern Europe, and pathways for colonizing new areas from the Serbian Carpathians.

Among the variables which influence the potential distribution of *C. archeri* in Romania, winter bioclimatic predictors have been highlighted (Fig. 1). According to the response curves, high precipitation and reduced temperatures during winter might favourise fungus development (Fig. 2c, d). In the Romanian climatic context, the optimal temperature values are found at high and medium elevations in the Carpathian region, where the water deficit is also moderate. Microhabitats from hilly areas with a milder climate and high humidity are also preferred by *C. archeri*. Conversely, in the plain areas, characterized by dry and hot summers and low precipitation in winter, the probability of occurrence is very low (Fig. 2b).

According to the results of this study, the winter period is an important factor which limits *C. archeri* distribution in Romania. There may be numerous explanations for this phenomenon. One could refer to the climatic characteris-

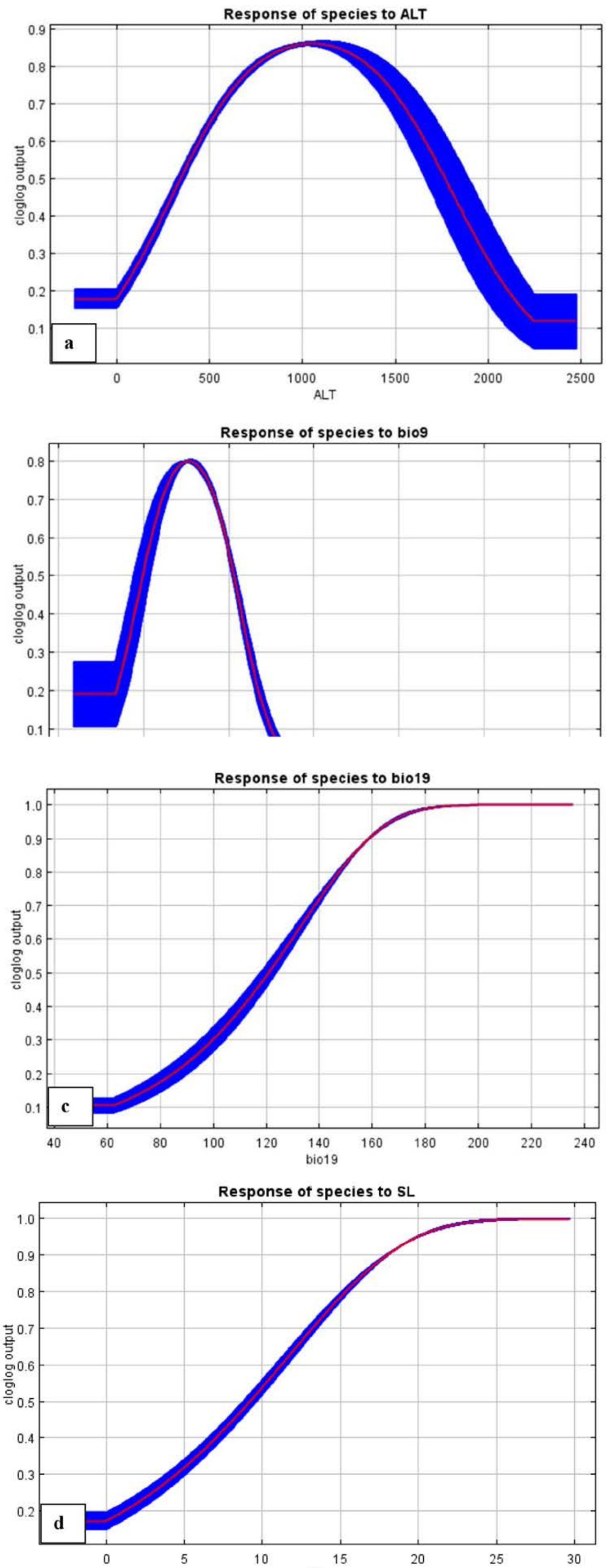

Fig. 2. Probability relationships between the dominant climate factors and geographic distribution of *Clathrus archeri*: **(a)** altitude (m); **(b)** mean temperature of the driest quarter (°C); **(c)** precipitation in the coldest quarter (mm); **(d)** snow cover length (weeks).

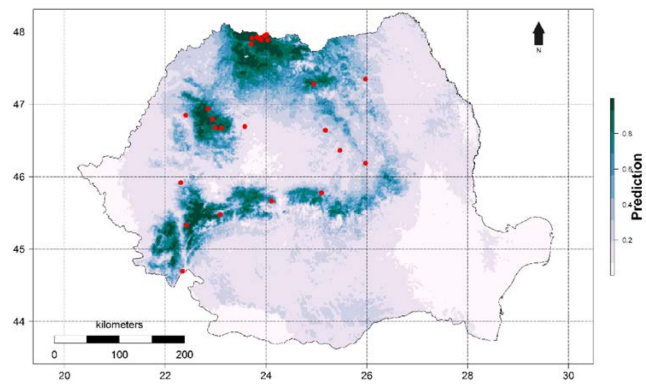

Fig. 3. Map of the predicted potential distribution of *Clathrus archeri* in Romania (the red dots represent *Clathrus archeri* occurrences).

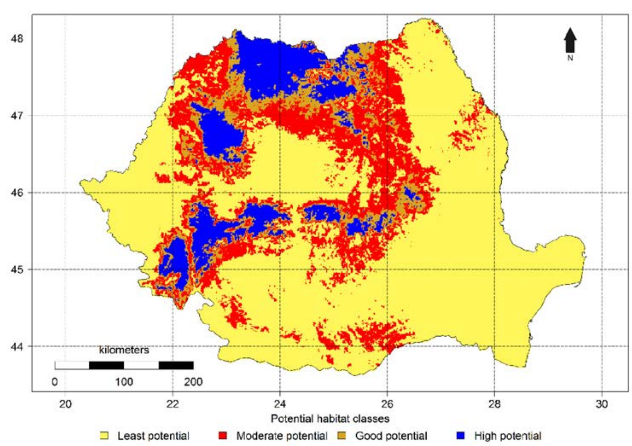

Fig. 4. Map of the predicted potential distribution depending on the habitat suitability for *Clathrus archeri* in Romania.

tics and the altitude of the areas where *C. archeri* is most likely to occur, including habitats at moderately high altitudes (Fig. 2a). More specifically, distribution was predicted to occur at elevations mainly between 500 and 1700 m altitude, which accounts for the hills and mountains of low-to-medium altitude in Romania. Still, this species seems to avoid the Moldavian Plateau and the Getic Plateau, as well as the eastern part of the Eastern Carpathians. In these regions, oceanic precipitation is usually less frequent than in the western part, due to oceanic atmospheric circulation and orographic convection. This highlights the fact that the species is confined not only to an altitudinal gradient, but also to a continentality one. This might explain why the most suitable habitats for this species are not found in the eastern and south-eastern parts of Romania, but in the western half.

The second is related to the three main winter characteristics with an important influence on the probability of the occurrence of *C. archeri*. Thus, the species' response to snow cover length suggests (Fig. 2d) that the most suitable habitats are places with a long period of snow cover. It is a well-known fact that snow is a great insulator, protecting the ground from freezing and heat loss in winter (Zhang 2005). Even in extreme environments, such as in Alaska, snow-covered land surfaces show a higher ground temperature (Zhang *et al.* 1997) compared to snow-free soil. Thus, in lower temperatures, snow-covered soil will have higher temperatures during winter time. This also applies to the studied species, as its most suitable habitats are places with moderately low winter temperatures, between -5˚C and 0˚C (Fig. 2b).

According to a study carried out in Canada's temperate to arctic zones, an increase in minimum soil temperatures was related to higher precipitation, especially in drier areas, while the frequency of soil freeze-thaw cycles decreased (Henry 2008). This means that in Romania's low-precipitation regions (the eastern and southern hilly and plain regions), soil freezing occurs more often. In mild winters, if the snow cover stratum is not well developed, soil freezing might occur (Hardy *et al.* 2001), as deep snow areas have higher soil temperatures (Mundra *et al.* 2016). *Clathrus archeri* is found in areas with winter precipitation above 130 mm (Fig. 2d), which ensures the water necessary for a thick snow cover. Our results suggest that only a well-developed snow stratum provides full protection against soil freezing, thus ensuring the survival of the mycelium. Similar results, highlighting that climatic conditions (precipitation and mean temperature) are important predictors driving the occurrence of *C. archeri* fruitbodies, have been published for Poland (Pietras *et al.* 2016). The results of this study are in agreement with those published in Pietras *et al.* (2021), who presented a global assessment of both the potential suitable habitats and the limiting factors for *C. archeri*. Their comprehensive analysis underlined the importance of climatic conditions, as well as the presence of highly suitable regions in Central Europe and the Carpathian Mountains, for the expansion of the species.

Study limitations. There are certain drawbacks to using SDM, from the sampling bias to the geographic scale and overlooked variables. In the case of many fungal species, the recordings based on the ephemeral fruitbodies is a well-known pitfall for sampling bias, which can be accentuated in the case of invasive species or in the classical close-to-localities sampling. Using some of the multiple methodological approaches developed over the past years, we managed to overcome the problems we encountered. Including other variables in the macrofungi SDM may serve to improve the modelling, as possible important variables might be overlooked in climatic-only-based SDM. Nevertheless, the importance of scale and resolution should be taken into account, because certain variables reflect the reality differently (as in the case of slopes, where the topographic reality is better represented in finer resolutions). Thus, the results of this modelling must be considered only for the area and the time accounted for, and only with the considered variables. As Pietras *et al.* (2016) mentioned, a phylogeographical study could explain the present dispersal pathways, and, together with climate change scenarios the spatial modelling could offer valuable insights into the future distribution of this species and other macrofungi.

CONCLUSIONS

Considering the present distribution in Romania, *C. archeri* is rather a rare species, but with a recent expansion of its area, particularly in mountainous areas. The main areas for potential distribution are the Carpathians range and the extra-Carpathian hills, especially in the western part of the country. The environmental variables with a significant influence on the potential distribution of this species are snow cover length as well as precipitation in the coldest quarter. The species is more likely to occur in areas with a thick layer of snow, which does not melt in winter, at higher altitudes, where the water deficit is low.

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REZIME

Botanica SERBICA

Modelovanje potencijalne distribucije i pogodnost staništa alohtone gljive *Clathrus archeri* u Rumuniji

Ciprian Bîrsan, Constantin Mardari, Ovidiu Copoţ i Cătălin Tănase

Clathrus archeri je saprofitna gljiva poreklom sa južne hemisfere koja je u Evropu unesena početkom dvadesetog veka. Iako je naturalizovana u većini regiona Centralne Evrope, u Rumuniji se smatra prilično retkom vrstom, jer je pronađena na samo nekoliko lokaliteta. Zbog brzog širenja njenog areala po Evropi, neki autori ovoj vrsti dodeljuju invazivni potencijal. Cilj rada bio je da se identifikuje potencijalna distribucija i potencijalno pogodna staništa za širenje u Rumuniji, kao i da se istaknu ekološke promenljive koje određuju verovatnoću pojavljivanja. Da bi se modelirala potencijalna distribucija vrste, korišćen je pristup maksimalnog entropijskog modela implementiran u Maxentu. Rezultati su istakli nadmorsku visinu, visinu snežnog pokrivača, srednju temperaturu najsušnijeg kvartala i količinu padavina najhladnijeg kvartala kao najvažnije prediktore potencijalne distribucije vrste u Rumuniji. Mapa potencijalne distribucije pokazala je da je najveća verovatnoća pojave ove vrste u planinskim i njima susednim oblastima, dok je karta pogodnosti staništa potvrdila da su najbolji ekološki uslovi u Karpatima, a najnepovoljniji u jugoistočnim delovima zemlje.

Ključne reči: abiotički faktori, strane vrste, *Clathrus archeri*, zimska klima, količina padavina, pogodno stanište