Acta Bot. Croat. 84 (2), 193–201, 2025
DOI 10.37427/botcro-2025-017

CODEN: ABCRA 25
ISSN 0365-0588
eISSN 1847-8476

Past, present and future of an alien fungus *Clathrus archeri* in Croatia

Sven D. Jelaska*, Damjana Levačić

University of Zagreb, Faculty of Science, Department of Biology, Marulićev trg 20, HR-10000 Zagreb, Croatia

Abstract – *Clathrus archeri* (Berk.) Dring, an alien saprotrophic fungus originating from Australia and New Zealand has been present in Europe for over 100 years. From its first observation in 1920 in France, it has spread all over Europe, and is among the better surveyed alien saprotrophic fungi with respect to its spread and distribution. Despite this, data about *C. archeri* in Croatia in the scientific literature are very scarce. To fill the current gap on the presence and distribution of *C. archeri* in Croatia, we collected reliable available data on its presence, analysed several environmental factors (climate, soil acidity, topography) on those localities, and developed habitat suitability models using Maxent software. We found out that the fungus has been present in Croatia for over 20 years, so we synthesized information on 25 observations, which were all but one placed in the Continental NATURA 2000 biogeographical region of the country. Localities were situated between 104 and 532 m a.s.l., with mean annual temperatures ranging from 8.1 to 10.9 °C, and annual precipitation ranging between 815 and 1620 mm. On all localities acid soil reactions were present with pH values below 6.8. Although the current number of observations is moderate, in terms of its spatial distribution we can consider *C. archeri* a widespread alien fungus in Croatia. Based on the habitat suitability models developed here, and data about its ecology from the literature, we can expect more and spatially broader observations of *C. archeri* in the future.

Keywords: GBIF, iNaturalist, octopus stinkhorn, Phallaceae, stinkhorns, velika polipovka

Introduction

For a long time, fungi have been overlooked in the invasion science literature, apart from the fungal pathogens that have strong negative impacts on biodiversity and the economy (e.g. in the agriculture). Symbiotic fungi have been to some extent surveyed, but saprotrophic fungi rarely (Desprez-Loustau et al. 2007, 2010). According to Desprez-Loustau et al. (2007), lack of the quantification of the impacts of non-pathogenic alien fungi may be a major reason for the scarcity of surveys and the data on them. In last 15 years, a number of European countries have compiled lists of alien fungi (see Voglmayr et al. 2023, for countries and references), but as shown from the example of Austria in which they expanded their first checklist (Voglmayr and Krisai-Greilhuber 2002) with an almost five-fold increase in the second edition (Voglmayr et al. 2023), it is an ongoing process. As highlighted by Voglmayr et al. (2023) plant pathogens are the dominant ecofunctional group in the list of Austrian alien fungi, which is the case in other countries as well. Saprobionts are still generally underrepresented in alien fungi lists. It should be noted that biogeography of fungi is much less known and clear than that of plants and animals (Desprez-Loustau et al. 2007).

Among the alien saprotrophic fungi in Europe, *Clathrus archeri* (Berk.) Dring is one of the better known, with lots of papers reporting on its distribution across Europe (see the review by Parent and Thoen 1986, and Parent et al. 2000). One reason for this may be the peculiar appearance of its sporocarps (Fig. 1), making it easier for identification, and attracting more attention, even from non-fungi experts and the general public.

According to Parent and Thoen (1986) the first record in Europe of this fungus, originating from Australia and New Zealand, is from 1920 in Vosges, France (Lemasson 1923 in Parent and Thoen 1986), where it is believed to have most probably arrived with wool products. From there it gradually spread all over Europe. It has been recorded in great variety of habitats including different types of forests (deciduous, coniferous – natural and plantations, mixed coniferous-deciduous), grasslands, orchards, disturbed habitats, gardens (Parent and Thoen 1986, Bîrsan et al. 2014, Pietras et al. 2016, Brännhage and Gross 2020). However, although it can be found in a diversity of habitats it does prefer humid and acidic soil (Parent and Thoen 1986, Pietras et al. 2016).

Published data on *C. archeri* in Croatia are extremely scarce and to our knowledge, with respect to the scientific lit-

* Corresponding author e-mail: sven.jelaska@biol.pmf.unizg.hr

Fig. 1. *Clathrus archeri* observed by authors in November 2023 in Donji Stupnik (left image – eggs; middle image – sporocarp) and Donje Ladanje (right image – sporocarp). Pen in the left image is 14 cm long. Photo: Sven D. Jelaska.

erature, these are: Tkalčec et al. (2005) in which the species is mentioned for Croatia for the first time in the scientific literature; Kranjčev (2008) who reports on its presence in two locations in northwest Croatia; Pietras et al. (2021) who included in their analysis one locality (out of four) on the fungus's presence in Croatia deposited on GBIF.org on October 26th, 2018. Apart from the scientific literature, *C. archeri* was included in all three editions of the "Ordinance on Protection of Fungi" (Official Gazette 1998–2002), but was omitted from the subsequent "Ordinance on Designation of Wild Taxa as Protected or Strictly Protected" (Official Gazette 2006) and "Red Book of Croatian Fungi" (Tkalčec et al. 2008). Preliminary inclusion of *C. archeri* on the list of protected fungi was probably a result of a lack of data and information on the fungus' origin, which happened in other countries as well, in the Eastern part of Europe where *C. archeri* arrived and was observed later (e.g. Romania – Tănase and Pop 2005, Bulgaria – Gyosheva et al. 2006, Ukraine – Didukh 2009). Increased knowledge and data collected resulted in its removal from the Red Book of Ukraine (Heluta et al. 2022).

To fill the current gap in the knowledge of the presence and distribution of *C. archeri* in Croatia, we collected reliable available data on its presence, based on which we analysed the ecological preferences of the species. Furthermore, we developed habitat suitability models to get some indication on its potential overall distribution in Croatia, which can be also used for planning future research on the species.

Material and methods

To gather information on the presence of *C. archeri* in Croatia we have searched for fungus's records in GBIF.org (https://www.gbif.org/); iNaturalist.org (https://www.inaturalist.org/), Mushroomobserver.org (https://mushroomobserver.org/) and Wood (2008). Furthermore, we have used several query terms in different combinations ("*Clathrus*", "*archeri*", "*Anthurus*", "Devil's fingers", "Octopus stinkhorn", "velika polipovka", "Croatia", "Hrvatska") in the following sources:

– Portal of Croatian scientific and professional journals (https://hrcak.srce.hr/en)

– Croatian Research Information System (https://www.croris.hr/)

– Scopus (https://www.scopus.com)

– Internet web pages

Queryings scientific literature sources revealed just two publications in which *C. archeri* was mentioned: Tkalčec et al. (2005) and Kranjčev (2008). Only the latter gave locations (two) for the fungus in Croatia. GBIF.org did not contain all the localities present in iNaturalist, because of licensing restrictions assigned to some observation records. We have contacted owners of these observations and obtained permission to use their observations in this analysis. They are presented in Tab. 1 with corresponding links, while data present in GBIF on April, 24th 2024 can be found in the GBIF.org (2024) downloaded data set.

From the Internet web pages search, we have included three results (No. 1, 5, and 19 in Tab. 1) that mentioned month and year of observation, in addition to a locality that could be georeferenced. For such location in the Karlovac City area (No. 1 in Tab. 1) there was an observation in GBIF.org (2024) with exact coordinates, hence we used that location but kept the web source presented in Tab. 1 for being among the first data of the presence of the fungus in Croatia. Descriptions of two locations of *C. archeri* in Kranjčev (2008) were sufficiently precise in just one case, the presence of which we confirmed in November 2023 (No. 3 in Tab. 1) and assigned coordinates using the Global Navigation Satellite System (GNSS). Overall, we have synthesized data on 25 locations of *C. archeri* in Croatia (Fig. 2) with the oldest data originating in 2004.

To develop habitat suitability models, we used Maxent software (Phillips et al. 2024), 22 data with exact coordinates on the occurrences of *C. archeri* in Croatia (Tab. 1) and two sets of environmental variables. In the first iteration, we used eight climatic variables (mean temperature and amount of precipitation per meteorological season) based on a 30-year period (1960–1990, Croatian Meteorological and Hydrological Service). In the second iteration, in addition to climatic variables, pH value (in H_2O) of the topsoil (0–5 cm depth) was used. For latter we used a dataset available for Europe (Poggio et al. 2021). All environmental variables were prepared as 300 m resolution grids.

Tab. 1. Localities of *Clathrus archeri* in Croatia with WGS84 coordinates, month and year of observation, and source of data (all web sources accessed on April 24, 2024.). * localities observed by the Authors, ** – coordinates approximated, localities not used for the Maxent models

No.	X-coordinate	Y-coordinate	Month	Year	Source
1	15.59496	45.52655	December	2019	GBIF.org (2024)
			October	2004	https://www.svijet-gljiva.com/katalog-gljiva/item/91-clathrus-archeri
2**	16.91227	46.14785	October	2007	Kranjčev (2008)
3*	16.14177	46.28702	November	2023	GBIF.org (2024)
			October	2007	Kranjčev (2008)
4	16.13286	46.26402	September	2010	https://mushroomobserver.org/52525
5**	16.12500	45.63459	June	2012	https://www.24sata.hr/ reporteri/u-sumi-kod-busevca-pronasao-je-rijetku-vrstu-smrdljive-gljive-271077
6	15.59853	45.52442	October	2012	GBIF.org (2024)
7	16.03694	45.66291	October	2017	GBIF.org (2024)
8	17.60421	45.35970	September	2018	https://www.inaturalist.org/observations/193238448
9	17.60344	45.35771	September	2018	https://www.inaturalist.org/observations/193238557
10	15.20384	45.27234	October	2018	GBIF.org (2024)
11	15.74351	45.63000	September	2019	GBIF.org (2024)
12	17.49942	45.55693	November	2019	https://www.inaturalist.org/observations/36022378
13	17.63949	45.57991	August	2020	GBIF.org (2024)
14	17.31514	45.41640	September	2022	https://www.inaturalist.org/observations/134201619
15	16.31555	46.43399	October	2022	https://www.inaturalist.org/observations/197127579
16	15.78877	45.76543	October	2022	https://www.inaturalist.org/observations/139409586
17	15.91247	45.31635	October	2022	GBIF.org (2024)
18	15.91247	45.31624	October	2022	GBIF.org (2024)
19**	16.01816	45.56576	October	2022	https://institutzeleni.wordpress.com/2022/10/09/prica-iz-vukomerickih-gorica/
20	17.69796	45.55104	November	2022	https://www.inaturalist.org/observations/141909715
21	17.67791	45.62665	November	2022	https://www.inaturalist.org/observations/142387360
22	14.31846	45.08774	April	2023	GBIF.org (2024)
23	16.15927	46.29094	August	2023	GBIF.org (2024)
24*	15.82043	45.72737	November	2023	GBIF.org (2024)
25	15.99926	45.66489	November	2023	https://www.inaturalist.org/observations/206601927

Given the number of occurrence data, we have used all as a training set. Consequently, only Area Under Curve (AUC) for the training set was available. Three localities to which exact coordinates could not be assigned (No. 2, 5, and 19 in Tab. 1), were used as an independent test data set to evaluate the habitat suitability models developed.

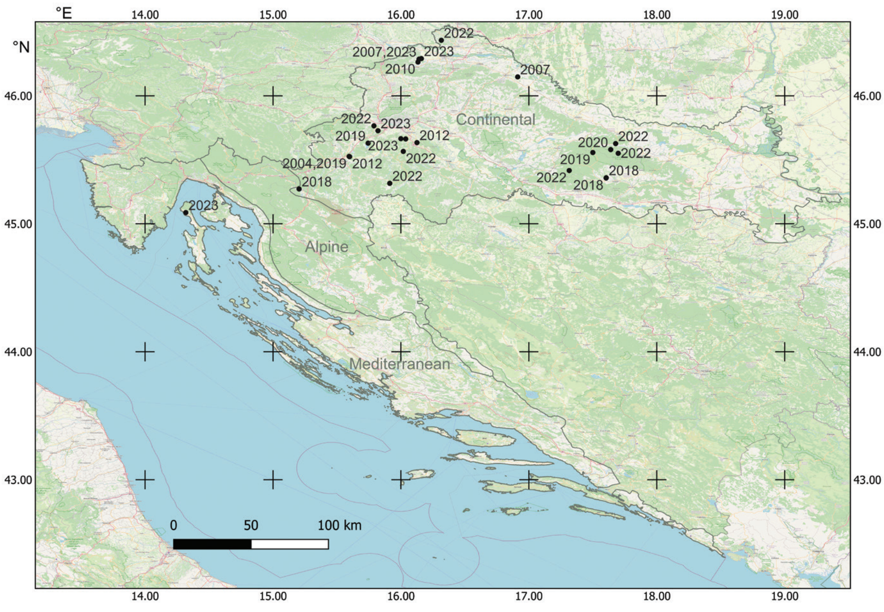

Fig. 2. Distribution of *Clathrus archeri* in Croatia (details of localities in Tab. 1), with NATURA2000 biogeographical regions indicated. Background map is OpenStreetMap (Base map and data from OpenStreetMap and OpenStreetMap Foundation (CC-BY-SA). https://www.openstreetmap.org and contributors)

In addition to climatic and pH variables mentioned above, we assigned values of elevation and slope (based on a 300 meter resolution digital elevation model of Croatia) to all 25 localities, and calculated several descriptive statistical measures (minimum, maximum, mean, 10th and 90th percentile) to get some insight into the ecological preferences of *C. archeri* in Croatia. Elevation and slope were not included in habitat suitability modelling since elevation is correlated to climate (positively with precipitation, and negatively with temperature) and value of slope can vary significantly on short distances, and hence could increase uncertainty of the habitat suitability model.

At two locations (No. 3 and 24 in Tab. 1, Donje Ladanje and Donji Stupnik respectively) where we observed *C. archeri* in November 2023 we collected soil samples. After removing the leaf litter, upper 5 cm of the soil was sampled with a cylindrical corer (8 cm in diameter) in triplicates around the observed sporocarp (with a distance of 1 m between the subsamples) and stored as a composite sample representative for the location. Samples were transported to the laboratory where they were air dried at room temperature. To measure pH values, a combined electrode pH meter (HANNA HI 99121, Direct soil pH meter) was used on suspensions composed of 10 g of soil and 25 mL of distilled water. Prior to measuring, the suspensions were covered for 30 min with occasional stirring. Organic matter content was determined by annealing in a muffle furnace (INKO LP-08). According to the NRM Laboratories methodology (Davies 1974) ground soil samples were first dried in an oven at 110 °C for 24 h, then weighed for 5 g samples, transferred to porcelain bowls, and heated in the muffle furnace at 430 °C for 2 h. After annealing, the samples were transferred into a desiccator for cooling and weighed again the next day. The organic matter content was determined using mass differences. Both pH and organic matter content measurements were made of three random subsamples from the composite soil sample of each locality, and expressed as mean values.

Results

Except for one in the Mediterranean region, all localities of *C. archeri* were situated in the Continental NATURA 2000 biogeographical region, with no localities recorded in the Alpine region (Fig. 2). Localities were situated between 104 and 532 m a.s.l., with 10th and 90th inter-percentile ranging from 109 to 381 m a.s.l. (Tab. 2).

The 10–90 inter-percentile range for mean annual temperature was 9.6 to 10.8 °C, and for annual precipitation 831

Tab. 2. Environmental variables values for *Clathrus archeri* localities (Tab. 1) in Croatia. pH – pH value of topsoil in 0 – 5 cm depth, elevation (m a.s.l.), slope (°), –prec – precipitation (mm) and –temp – temperature (°C) for four seasons (sp – spring, su – summer, a – autumn, w – winter) and annual (y–). min – minimum, max – maximum, mean – average, perc10 and perc90 – 10% and 90% percentiles for each environmental variable.

No.	Approximate locality	pH	elevation	slope	spprec	suprec	aprec	wprec	yprec	sptemp	sutemp	atemp	wtemp	ytemp
1	Karlovac	5.4	108	0.0	242	282	312	230	1066	10.7	19.8	11.2	1.7	10.8
2	Podravski bregi	5.5	125	0.0	199	273	221	157	850	10.7	19.4	10.4	0.4	10.2
3	Donje Ladanje	5.4	217	3.8	216	298	247	174	935	10.1	18.9	10.1	0.3	9.9
4	Veliki Novaki	6.2	215	1.0	218	300	249	176	943	10.1	18.8	10.1	0.3	9.8
5	Buševec, Velika Gorica	5.5	104	0.0	207	262	259	182	909	10.9	20.0	11.1	1.3	10.8
6	Karlovac	5.3	108	0.0	241	282	311	230	1063	10.7	19.8	11.2	1.7	10.8
7	Gudci	5.4	121	0.0	208	264	262	184	917	10.7	19.8	11.0	1.2	10.7
8	Jaguplije	6.0	214	5.1	192	257	216	150	815	10.4	19.5	10.4	0.3	10.2
9	Jaguplije	5.9	213	5.1	192	257	216	150	815	10.5	19.5	10.4	0.3	10.2
10	Sveti Petar (Ogulin)	6.2	365	7.4	368	380	484	387	1620	9.0	18.2	10.1	0.8	9.5
11	Donja Zdenčina	5.7	111	0.4	218	267	280	200	966	10.8	19.9	11.2	1.6	10.9
12	Brestovac	5.8	509	5.5	248	338	253	181	1021	8.5	17.6	8.7	–1.1	8.4
13	Sekulinci	6.0	229	4.4	199	270	217	153	840	10.3	19.3	10.2	0.1	10.0
14	Gornja Šumetlica	5.5	532	10.1	253	338	265	190	1046	8.1	17.2	8.4	–1.4	8.1
15	Gornji Mihaljevec	6.3	231	0.8	207	292	230	162	891	10.2	18.8	10.0	0.1	9.8
16	Mala Gorica	6.3	151	0.7	224	284	282	201	991	10.4	19.4	10.7	1.0	10.4
17	Blatuša	5.8	149	2.8	248	286	317	237	1088	10.3	19.5	10.8	1.2	10.5
18	Blatuša	5.8	149	2.8	248	286	317	237	1088	10.3	19.5	10.8	1.2	10.5
19	Gornji Hruševec	5.4	153	2.4	214	269	272	192	947	10.4	19.5	10.7	1.0	10.4
20	Čačinci	6.1	235	5.9	198	270	216	152	835	10.3	19.3	10.1	0.1	9.9
21	Bokane	6.1	165	4.1	196	264	215	153	828	10.7	19.7	10.5	0.4	10.4
22	Dragozetići, Cres	6.8	392	5.3	339	281	493	410	1524	9.8	19.1	11.6	2.8	10.8
23	Maruševec	6.0	202	3.7	213	294	244	172	923	10.3	19.0	10.2	0.4	10.0
24	Donji Stupnik	5.1	128	0.0	218	275	276	196	964	10.6	19.7	10.9	1.2	10.6
25	Donja Lomnica	5.3	120	1.0	208	264	262	184	919	10.6	19.7	10.9	1.1	10.6
	min	5.1	104	0.0	192	257	215	150	815	8.1	17.2	8.4	–1.4	8.1
	max	6.8	532	10.1	368	380	493	410	1620	10.9	20.0	11.6	2.8	10.9
	mean	5.8	209.9	2.9	228.6	285.3	276.6	201.6	992.1	10.2	19.2	10.5	0.7	10.2
	perc10	5.3	109	0.0	197	262	216	152	831	9.3	18.4	10.1	0.1	9.6
	perc90	6.3	381	5.7	251	323	317	237	1088	10.7	19.8	11.2	1.6	10.8

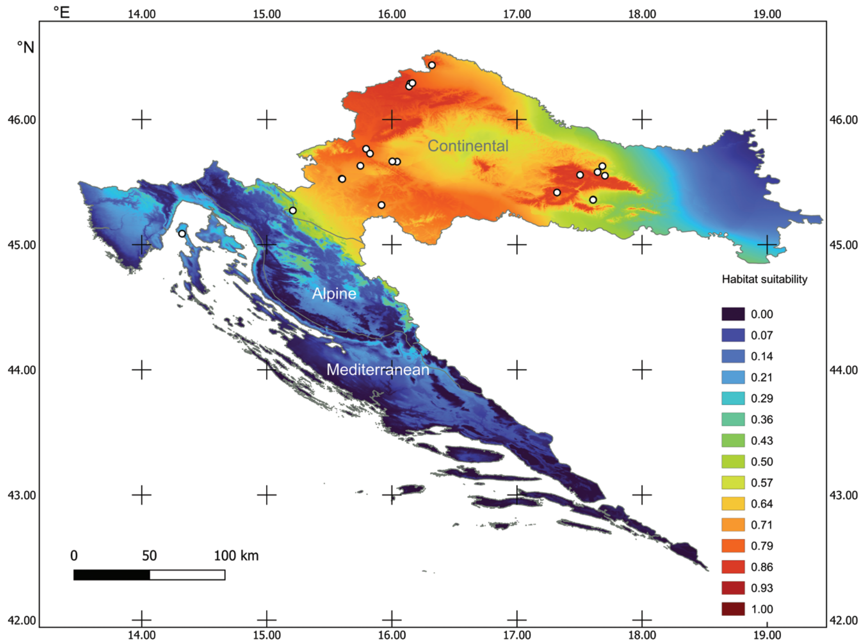

Fig. 3. Maxent habitat suitability model for *Clathrus archeri* in Croatia based on eight climatic variables (mean temperature and amount of precipitation per meteorological season). Colours on the map, with corresponding number indicates habitat suitability for *C. archeri* in range from 1 (red – presumed 100% suitable habitat) to 0 (blue – 0% suitable habitat). White circles indicate *C. archeri* occurrences in Croatia used to build the model, NATURA 2000 biogeographical regions indicated.

to 1088 mm. With respect to the seasonal precipitation amounts, there were no seasons with less than 150 mm at any locality (Tab. 2). Soil reaction ranged from 5.1 to 6.8, with 10–90 inter-percentile range being 5.3 to 6.3 (Tab. 2), both corresponding to the acidic part of the pH scale. Our measurements of soil reaction sampled at two localities in a stand of planted Eastern White Pine *Pinus strobus* L. (No. 3 in Tab. 1) and in the *Epimedio-Carpinetum betuli* (Horvat 1938) Borhidi 1963 forest (No. 24 in Tab. 1) have shown an even lower pH, of 4.3 and 4.1, respectively. Regarding organic matter content, the mean value for Donje Ladanje (No. 3 in Tab. 1) was 19.14% and for Donji Stupnik (No. 24 in Tab. 1) 16.75%, indicating that soils at both localities were rich in organic matter.

Climate-only habitat suitability model (Fig. 3) and Climate-pH habitat suitability model (Fig. 4) yielded a very

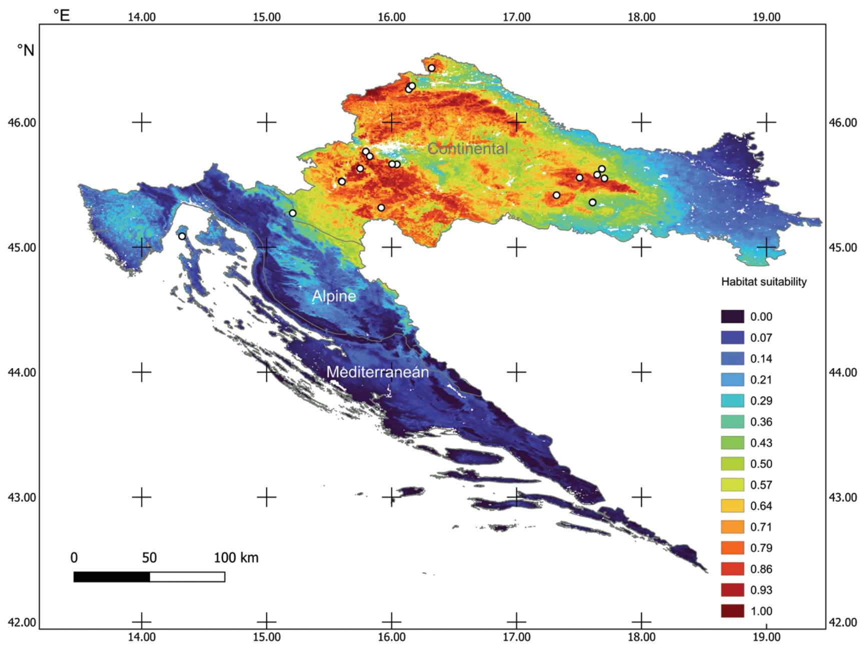

Fig. 4. Maxent habitat suitability model for *Clathrus archeri* in Croatia based on eight climatic variables (mean temperature and amount of precipitation per meteorological season) and pH value of soil in 0–5 cm depth. Colours on the map, with corresponding number indicates habitat suitability for *C. archeri* in range from 1 (red – presumed 100% suitable habitat) to 0 (blue – 0% suitable habitat). White circles indicate *C. archeri* occurrences in Croatia used to build the model, NATURA 2000 biogeographical regions indicated.

Tab. 3. Variable contributions to Maxent habitat suitability models for *Clathrus archeri* in Croatia. Abbreviations: w – winter, a – autumn, su – summer, sp – spring, temp – mean temperature, prec – total amount of precipitation, pH – pH value of topsoil in 0 – 5 cm depth.

Model with climate data			**Model with climate data and pH value of topsoil**		
Variable	Percent contribution	Permutation importance	Variable	Percent contribution	Permutation importance
			pH	53.1	12.5
suprec	48.9	9.2	wprec	19.4	58.8
wprec	22.5	47.5	spprec	8.5	11.5
aprec	19.3	12.6	aprec	8.4	0
sptemp	5.4	0	suprec	7.2	1.4
spprec	2.2	14.5	wtemp	3.2	13.5
wtemp	1.7	16.2	sptemp	0.3	2.4
atemp	0	0	atemp	0	0
sutemp	0	0	sutemp	0	0

similar general spatial pattern at country level, with Climate-pH based model seemingly being spatially more specific in terms of areas with high suitability.

The latter model also contains some no-data areas, as a consequence of the lack of pH data for water body areas and human settlements. The majority of predicted suitable habitats are in the Continental biogeographical region where most of the recorded localities are situated. There are some moderately suitable areas in the Alpine region, in which, however, there are currently no records of *C. archeri*. Those areas are mostly in parts adjacent to the Continental region around the Kupa, Dobra and Una rivers, and in lower elevation parts corresponding to the presence of flat depressions within the karst known as "polje" (e.g. Cerničko polje, Gacko polje, Krbavsko polje). Within the Mediterranean region, very low habitat suitability was predicted by both Maxent models, with slightly higher values in the Northern Adriatic where one locality exists (No. 22 in Tab. 1). For both habitat suitability models, area under curve (AUC) of the receiver operating curve (ROC) had similar values, AUC = 0.817 for Climate-only and AUC = 0.827 for Climate-pH model (Tab. 3).

Precipitation variables contributed more to the models than the temperature variables. Summer precipitation had the highest percentage of contribution to the Climate-only model, while the pH of topsoil had the highest percentage to the Climate-pH model. Winter precipitation was second best in terms of the percentage of the contribution to the models, but had by far the highest permutation importance indicating that models were heavily dependent on it (Tab. 3). On three localities that were not used for habitat suitability modelling (No. 2, 5 and 20 in Tab. 1), both models predicted high values of suitability: 0.68, 0.67 and 0.75, respectively, for Climate-only model; 0.75, 0.79 and 0.89 for Climate-pH model.

Discussion

The history and introduction of *C. archeri* in Croatia remain unclear. Its first mention in Božac (1984) in his popular guide to fungi cannot be considered the first evidence of its presence in Croatia because the exact geographical extent covered by the guide is not defined. At that time Croatia was a part of former Socialist Federative Republic of Yugoslavia. Furthermore, in the book's preface the author explains that the most frequently used criterion for inclusion of fungi species in the book was their high frequency in "our regions" (which could be referred to other constituent republics of the former country beside Croatia) and in Central Europe. The latter could mean that *C. archeri* found its place in the book without actually being present in Croatia. However, at that time *C. archeri* had already been recorded (1966) in Slovenia (also part of the former country) for quite a long time (Vrščaj et al. 2004, Stanič 2024). In 1998, *C. archeri* was included in the first list of protected fungi in Croatia (Official Gazette 1998), and remained there in the second (published also in 1998) and third edition (published in 2002). We could not trace back the background for this inclusion, since the first mention of *C. archeri* in the literature is that of Tkalčec et al. (2005) in their paper on gasteral Basidiomycota of Croatia in which they note that their reference for *C. archeri* was the first for Croatia. Tkalčec (personal communication) found it in 1999 in two locations in the western part of Croatia. Without new evidence, this could be regarded as the year of the fungus's first observation in Croatia. Nevertheless, given the pace of spread eastward from its initial introduction to France in 1920 (Lemasson 1923 in Parent and Thoen 1986), and subsequent first observations in Switzerland in 1942 (Vischer 1943), Austria in 1948 (Lohwag 1948) and Slovenia in 1966 (Vrščaj et al. 2004, Stanič 2024), it is possible that the fungus was present in Croatia from the 1980s or early 1990s, but remained unnoticed. Although we cannot be sure of the exact time of its arrival, with a fair amount of certainty we can consider that it arrived from the Slovenia.

The data given here show that *C. archeri* is much more widespread in Croatia than was considered previously, according to the scientific literature. Both habitat suitability models imply that it could occupy even larger areas than presently, at least across the majority of the NATURA 2000 Continental biogeographical region in Croatia. High values of predicted habitat suitability models at locations that were not used in building the models, as well as reasonably high AUC values work in favour of the predicted models' reliabilities. In both models, precipitation turned out to be more important than temperature in defining the suitability for *C. archeri*. In habitat suitability models for Romania (Bîrsan et al. 2021) and on a global level (Pietras et al. 2021) there were the same findings, with the coldest quarter of the year's precipitation contributing the most to their models. Here, winter precipitation (which corresponds to the precipitation of the coldest quarter) was the most important among the climate variables in the Climate-pH model, while it was second most important, after summer precipitation, in the Climate-only model (Tab. 3). The Mediterranean part of Croatia has a distinct dry season during the summer, hence this could play an important role in defining potential niche of the species in Croatia. Pietras et al. (2016) found that in Poland *C. archeri* is mostly present in areas with annual precipitation greater than 600 mm. They confirmed its presence in part of Poland with low mean annual precipitation (550 mm), but during the year with an exceptionally wet season. The only location so far known in the Mediterranean part of Croatia is in the Northern Adriatic, which does not have such dry summer periods as those in Central and Southern parts of the Adriatic, where summer precipitation is mostly below 150 mm, which in combination with highly permeable limestone bedrock leads to dry soil conditions.

Another important aspect that could limit *C. archeri* in the Mediterranean part of Croatia is the soil reaction. In their review of the fungus's presence in Europe, Parent and Thoen (1986) found it to favour acidic soils, reporting a pH range in France from 4.5 to 6, which matches our own measurements from two localities having pH value of 4.1 and 4.3, and pH values (Tab. 2) obtained from the dataset available for Europe (Poggio et al. 2021). The Croatian coast is characterised by limestone bedrock and the consequent alkaline soil reaction. In Giovanetti et al. (2014), soil reactions measured across the Croatian part of Adriatic coast, except for one sample with a pH value of 6.2, ranged from 7.7 to 8.1. The importance of the soil reaction for *C. archeri* is supported by the fact that it was the most important variable in the Climate-pH model. Nevertheless, given the fact that the fungus is present in the Mediterranean region, and that there is one observation (iNaturalist. org 2018) from May 2018 in the Slovenian part of the Istria peninsula very close (1.2 km) to the Croatian border, it is reasonable to expect the fungus' presence in Istria, although neither of the models (Fig. 3 and Fig. 4) predicted high suitability there. Consequently, both models seem to underestimate the suitability in the Mediterranean region, although we believe that only the Northern part of the Adriatic, which is not characterised by as low summer precipitation and alkaline soil reaction as the more Southern areas, is concerned.

The presence of highly suitable areas in the Alpine region in which there are no known localities, does not necessarily mean that the models overestimate the suitability for *C. archeri* in these parts of Croatia. Indeed, there are no ecological constraints for the fungus there, since that area has a lot of precipitation as well as parts with acid soils. Although the maximum elevation of localities of *C. archeri* presented here is just 532 m a.s.l., with 90% of locations appearing below 400 m a.s.l. (Tab. 2), the species can be found at much higher elevations e.g. 1200 m a.s.l. in Romania (Bîrsan et al. 2014), or as reported by Parent and Thoen (1986) even up to 2000 m a.s.l. The fact that currently known localities in Croatia are mostly below 400 m a.s.l., could be merely a consequence of prevalence of incident observations during field visits that were not targeted specifically to survey the presence of *C. archeri*. Some of those observations could be from edible fungi collectors who prefer this elevation belt that corresponds to distribution of pedunculate (*Quercus robur* L.) and sessile (*Q. petraea* (Matt.) Liebl.) oak forests, known for their fungi richness. An additional explanation could be the very short duration of the fungus' visible presence which lasts approximately just one week per individual sporocarp. This includes the egg phase, which can be observed up to 5 days. However, without dissection it is impossible to record an observation, since other stinkhorn fungi also develop eggs. We expect that sampling effort (in this case actually simply the number of field days, given the non-targeted nature of it) is much higher in lower elevations, hence the higher probability of observing *C. archeri* there.

In the future, we could expect an increase in the presence of *C. archeri* in Croatia in terms of its abundance and occupancy area. Even at present, on various social networks photographs of the fungus from Croatia can be found, but without details on its geographical origin, hence they could not be used here. It is not easy to predict how much this increase might be, and how long it would last. In their analysis of the impact of climate change on *C. archeri*, Pietras et al. (2021) used three scenarios for the year 2080 expecting the fungus' range contraction in Central Europe, including the Continental region of Croatia from which currently the majority of observations derive. Depending on the climate change scenario employed, there could be some range expansion in the areas that overlap with the Mediterranean region in Croatia. However, Pietras et al. (2021) developed their models exclusively with bioclimatic variables, without data on soil acidity, which could play a significant role in shaping the future of *C. archeri* distribution.

Almost 20 years after its first mention for Croatia in the scientific literature (Tkalčec et al. 2005) and just one short note in the meantime reporting on two localities (Kranjčev 2008) we reveal that *C. archeri* is nowadays, in terms of its spatial distribution, a widespread alien fungus in Croatia. Open access data provided by international networks like GBIF and iNaturalist were indispensable for this analysis. Consequently, these data should be an integral part in further efforts in increasing our knowledge on alien fungi, and other taxa, presence and distribution in Croatia, that are otherwise poorly covered in the scientific literature. In addition, efforts to raise the awareness of such species among colleagues and the general public, as well as of the importance of observations being deposited on platforms like GBIF and/or iNaturalist could significantly contribute to the amount of available observational records. Habitat suitability models can help in planning field surveys, which is especially useful for taxa with low cost-efficiency field work, as *C. archeri* is, due to its short sporocarp longevity.

Acknowledgements

This paper was published on the occasion of the 100th anniversary of Acta Botanica Croatica.

We would like to thank iNaturalist observers Nevio Biškupić, Marko Doboš, Eva Janeković, Sara Srša and Edi Thür for granting permission to use their data in this paper. The editor and two reviewers have provided constructive and valuable comments that helped us improve the manuscript, for which we are grateful. This research was funded by the University of Zagreb, Croatia, grant number 20286538–Distribution and ecological profiles of invasive plants.

References

Bîrsan, C., Cojocariu, A., Cenuşă, E., 2014: Distribution and ecology of *Clathrus archeri* in Romania. Notulae Scientia Biologicae 6(3), 288–291. https://doi.org/10.15835/nsb639389

Bîrsan, C., Mardari, C., Copoţ, O., Tănase, C., 2021: Modelling the potential distribution and habitat suitability of the alien fungus *Clathrus archeri* in Romania. Botanica Serbica 45(2), 241–250. https://doi.org/10.2298/BOTSERB2102241B

Božac, R., 1984: Šest stotina gljiva naših krajeva (Six hundred mushrooms of our regions). Mladost, Zagreb.

Brännhage, J., Gross, A., 2020: Factsheet Neomyceten. Tintenfischpilz und Roter Gitterling. Eidg. Forschungsanstalt WSL, Birmensdorf, 3 S.

Davies, B. E., 1974: Loss-on-ignition as an estimate of soil matter. Soil Science of America. Proceedings, 38, 150–151.

Desprez-Loustau, M. L., Robin, C., Buée, M., Courtecuisse, R., Garbaye, J., Suffert, F., Sache, I., Rizzo, D. M., 2007: The fungal dimension of biological invasions. Trends in Ecology and Evolution 22(9), 472–480. https://doi.org/10.1016/j.tree.2007.04.005

Desprez-Loustau, M. L., Courtecuisse, R., Robin, C., Husson, C., Moreau, P., Blancard, D., Selosse, M., Lung-Escarmant, B., Piou, D., Sache, I., 2010: Species diversity and drivers of spread of alien fungi (*sensu lato*) in Europe with a particular focus on France. Biological Invasions 12, 157–172. https://doi.org/10.1007/s10530-009-9439-y

Didukh, Y. P., 2009: The Red Data Book of Ukraine Flora. Global consulting, Kyiv.

GBIF.org, 2024: GBIF Occurrence Download. Retrieved April 24, 2024 from https://doi.org/10.15468/dl.6mreqj

Giovanetti, M., Vuković, N., Jelaska, S. D., 2014: Australian acacias across eastern Adriatic – abundant but not aggressive. Periodicum Biologorum 116(3), 275–283.

Gyosheva, M. M., Denchev, C. M., Dimitrova, E. G., Assyov, B., Petrova, D. R., Stoichev, G. T., 2006: Red List of fungi in Bulgaria. Mycologia Balcanica 3, 81–87.

Heluta, V. P., Zykova, M. O., Hayova, V. P., Prydiuk, M. P., Shevchenko, M. V., 2022: An update to the species list of fungi in the Red Data Book of Ukraine. Ukrainian Botanical Journal 79(3), 154–168. https://doi.org/10.15407/ukrbotj79.03.154

iNaturalist.org, 2018: Devil's-Fingers (*Clathrus archeri*). Retrieved April 24, 2024 from https://www.inaturalist.org/observations/12907117

Kranjčev, R., 2008: Velika polipovka, Čekinjava pločašica, Vijugavo-mesnata mirisnica (Devil's fingers, Eyelash cup, White false truffle). Šumarski list 9–10, 492.

Lohwag, K., 1948: *Anthurus muellerianus* Kalchbr., var. *aseroëformis* Ed. Fischer, ein neuer Pilz für Österreich. Österreichische Mykologische Gesellschaft. 20.

Official Gazette, 1998–2002: Pravilnik o zaštiti gljiva (Ordinance on protection of fungi). NN 79/1998, NN 115/1998, NN 34/2002.

Official Gazette, 2006: Pravilnik o proglašavanju divljih svojti zaštićenim i strogo zaštićenim (Ordinance on designation of wild taxa as protected or strictly protected). NN 7/2006.

Parent, G. H., Thoen, D., 1986: État actuel de l'extension de *Clathrus archeri* (Berkeley) Dring (syn.: *Anthurus archeri* (Berk.) Ed. Fischer) en Europe et particulièrement en France et au BÉnÉlux. Bulletin trimestriel de la Société mycologique de France 102(3), 237–272.

Parent, G. H., Thoen, D., Calonge, F. D., 2000: Nouvelles données sur la répartition de *Clathrus archeri* en particulier dans l'Ouest et le Sud-Ouest de l'Europe. Bulletin trimestriel de la Société mycologique de France 116(3), 241–266.

Phillips, S. J., Dudík, M., Schapire, R. E., 2024: Maxent software for modelling species niches and distributions (ver. 3.4.1). Retrieved April 24, 2024 from http://biodiversityinformatics.amnh.org/open_source/maxent/

Pietras, M., Rudawska, M., Iszkuło, G., Kujawa, A., Leski, T., 2016: Distribution and molecular characterization of an alien fungus *Clathrus archeri* in Poland. Polish Journal of Environmental Studies 25(3), 1197–1204. https://doi.org/10.15244/pjoes/61230

Pietras, M., Kolanowska, M., Selosse, M., 2021: Quo vadis? Historical distribution and impact of climate change on the worldwide distribution of the Australasian fungus *Clathrus archeri* (Phallales, Basidiomycota). Mycological Progress 20, 299–311. https://doi.org/10.1007/s11557-021-01669-w

Poggio, L., de Sousa, L. M., Batjes, N. H., Heuvelink, G. B. M., Kempen, B., Ribeiro, E., Rossiter, D., 2021: SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. SOIL 7(1), 217–240. https://doi.org/10.5194/soil-7-217-2021

Stanič, I., 2024: Karta razširjenosti za *Clathrus archeri*. Podatkovna zbirka gliv Slovenije Boletus informaticus (Distribution map of *Clathrus archeri*. Data collection of Slovenian fungi Boletus informaticus). In: Ogris, N. (ed.), Web portal Boletus informaticus. Retrieved April 24, 2024 from https://boletusinformaticus.si/sre_karta.aspx?idorg=b59ac192-6ef6-4504-b0e6-234c1643c481

Tănase, C., Pop, A., 2005: Red List of Romanian Macrofungi Species. In: Mihăilescu, S. (ed.), Bioplatform – Romanian National Platform for Biodiversity, 101–107. Academiei Române, Bucureşti.

Tkalčec, Z., Mešić, A., Antonić, O., 2005: Survey of the Gasteral Basidiomycota (Fungi) of Croatia. Natura Croatica 14(2), 99–120.

Tkalčec, Z., Mešić, A., Matočec, N., Kušan, I., 2008: Crvena knjiga gljiva Hrvatske (Red Book of Croatian fungi). Ministry of Culture, State Institute for Nature Protection, Zagreb.

Vischer, W., 1943: Ein für die Schweiz neuer Pilz *Anthurus aseroeformis* Ed. Fischer. Schweizerische Zeitschrift für Pilzkunde 21, 17–20.

Voglmayr, H., Krisai-Greilhuber, I., 2002: Pilze. In: Essl, F., Rabitsch, W. (eds.), Neobiota in Österreich, 181–195. Umweltbundesamt, Vienna.

Voglmayr, H., Schertler, A., Essl, F., Krisai-Greilhuber, I., 2023: Alien and cryptogenic fungi and oomycetes in Austria: an annotated checklist (2nd edition). Biological Invasions 25, 27–38. https://doi.org/10.1007/s10530-022-02896-2

Vrščaj, D., Erjavec, Š., Boh, A., Stanič, I., Piltaver, A., Seljak, G., Tratnik, B., Malovrh, B., Tortić, M., Čebulec, M., Šerod, S., Vrhovnik, F., Arko, J., Dolenc, F., Oblak, V., Vrhovec, B., Kavčič, Z., Seršen, J., Kavrečič, B., Bertosi, M., Hočevar, S., Haas, H., Ivanovič, A., Kaiser, S., Ujčič, M., Moser, M., Kosec, J., Koprek, F., Munda, A., Šmauc, A., Dolenc, A., Hudoklin, V., Mohorčič, V., Arzenšek, B., Kovač, A., Velikonja, P., Markovič, D., Kelhar, M., Podgornik, G., Lekše, J., Jurc, M., Goršak, B., Hudohmet, M., Jurc, D., Poličnik, M., Grebenc, T., Bertoncelj, F., Bračko, B., Bohte, T., Gerhold, A., Voss, W., Oblak, F., Kovše, J., Miller, O., Tkalčeč, Z., Došler, B., Fink, A., Pirnat, F., Kalchbrenner, K., Krajnc, J., Škulj, M., Hrovatič, M., Klemenčič, J., Jenko, V., Knoll, L., Tratnik, V., Dolšak, F., Kraigher, H., Kranjc, M., Breitenbach, J., Kotlaba,F., Petkovšek, M., Wettstein, R., Agerer, R., Loose A., Pec, M., Potokar, A., Beenken, L., Cortese, D., Černigoj, F., Klun, J., Oblak, N., Rozman, J., Schild, E., Šajn, V., Šarič, Zaletel, A., Arko, V., Babšek, J., Batič, F., Bech, W., Berden, J., Bračun, F., Celič, I., Cesar, M., Cetto, B., Doganoc, N., Godec, B., Goleš, L., von Höhnel, F. X. R., Hvastja, C., Jurc, B., Kocjančič, K., Korošec, V., Kovačič, F., Lindtner, V., Ljubič, F., Novak, J., Palfner, G., Pavlič, J., Perušek, R., Petkovšek, V., Pilat, A., Pouzar, Z., Rižnar, I., Rupel, M., Schinner, F., Sonc, M., Svrček, M., Toplak, I., 2004: Priloga Glive v Sloveniji (Contribution to Fungi in Slovenia). In: Jurc, D. (ed.), Seznam vrst in razširjenost makromicet v Sloveniji z analizo stopnje ogroženosti, 52–52. Gozdarski inštitut Slovenije, Ljubljana.