Distribution changes of the toxic mushroom *Amanita phalloides* under climate change scenarios and its potential risk over indigenous communities in Mexico

Abril VILLAGRÁN-VÁZQUEZ¹, Roberto GARIBAY-ORIJEL² and Carolina URETA^{1,3}*

¹ Departamento de Ciencias Atmosféricas, Instituto de Ciencias de la Atmósfera, Universidad Nacional Autónoma de México, Circuito de la Investigación Científica s/n, Ciudad Universitaria, 04510 Ciudad de México, México.

² Laboratorio de Sistemática y Ecología de Micorrizas, Instituto de Biología, Universidad Nacional Autónoma de México, Circuito Exterior s/n, 04510 Ciudad de México, México.

³ Investigadora por México Conahcyt, Departamento de Ciencias Atmosféricas, Instituto de Ciencias de la Atmósfera, Universidad Nacional Autónoma de México, Circuito de la Investigación Científica s/n, Ciudad Universitaria, 04510 Ciudad de México, México.

*Corresponding author: carolinaus@atmosfera.unam.mx

Received: November 14, 2022; accepted: April 20, 2023

RESUMEN

Amanita phalloides es un hongo ectomicorrízico mortal nativo de Europa que ha sido introducido en Norteamérica y cuya distribución se ha expandido en las últimas décadas. Esta especie es morfológicamente muy similar a especies silvestres comestibles y si su distribución se expande a México puede representar un riesgo para comunidades locales. El propósito de este estudio fue evaluar si existe idoneidad climática para A. phalloides en Norteamérica y si se empalma con comunidades micofilicas de México en un escenario climático base y en escenarios de cambio climático. Para identificar la aptitud climática se modeló a la especie con el algoritmo que obtuvo el mejor desempeño (MaxEnt) después de una prueba piloto con presencia de especies y ocho variables climáticas seleccionadas con criterios biológicos y estadísticos. Se trabajó con CanESM5 porque las evaluaciones de este modelo indican que simula bien el clima de Norteamérica, y con el SSP5-8.5 para ser consistentes con el principio precautorio. Los resultados sugieren que, aunque la especie no ha sido registrada en México, al utilizar registros europeos para modelar se encuentra aptitud climática en 33.61% del país en el escenario base, la cual se empalma con 70% de las comunidades indígenas, que son las mayores consumidoras de hongos silvestres. En escenarios de cambio climático, se espera un incremento en la aptitud climática de México y disminuciones en Estados Unidos y Canadá. Cuando se usan únicamente los registros norteamericanos para modelar, prácticamente no se encuentra aptitud climática en México. En cualquier caso, la implementación de campañas de alerta en México es necesaria.

ABSTRACT

Amanita phalloides is a native European deathly ectomycorrhizal mushroom that was introduced to North America and has been expanding its distribution during the last decades. This species is morphologically similar to wild edible mushrooms and if its distribution expands to Mexico, it could represent a risk in terms of food security for local communities. The aim of this study was to evaluate the potential climatic suitability that exists for *A. phalloides* in North America and overlay it with the distribution of mycophilic communities in Mexico under a baseline climatic scenario and climate change scenarios. To find climatic suitability we modeled its potential distribution with the algorithm that had the best predictive power after pilot test (MaxEnt) using species presences and eight climatic variables chosen with biological and statistical criteria. We worked with CanESM5 because it is one of the best models to simulate climate in North America and

SSP5-8.5 scenario in order to be consistent with the precautionary principle. Our results suggest that even when the species has not yet been registered in Mexico, when using European records to model, this country presents 33.61% of climatic suitability for this species under the baseline scenario, potentially affecting about 70% of indigenous communities which are the main consumers of edible mushrooms. Under climate change scenarios, an increase in climatic suitability is expected in Mexico, while decreases are expected in United States and Canada. When using North American records to model, almost no climatic suitability is found in Mexico; however, the implementation of warning campaigns in Mexico is still needed.

Keywords: climate change, populations with different climatic niche, ecological niche modeling, toxic fungi, climatic suitability.

1. Introduction

Amanita phalloides is a native European deathly ectomycorrhizal mushroom that was introduced to North America at the beginning of the 20th century, expanding its distribution since then (Pringle et al., 2009). Since its introduction in the continent, it has been responsible for several intoxications including deaths (Beug et al., 2006). In North America, A. phalloides is distributed in the Pacific northwest from San Francisco to British Columbia and in the northeast from Maryland to Maine (Wolfe et al., 2010). The possible consequences of this species reaching Mexican territory are of great risk since wild edible mushrooms (WEM) are highly consumed by several Mexican rural communities from different ethnic origins, becoming an essential part of their culture, a main food source and an alternative income (Boa, 2004; Garibay-Orijel et al., 2010; Garibay-Orijel and Ruan Soto, 2014).

A. phalloides is morphologically similar to other edible species of Amanita as A. rubescens complex, A. vaginata complex, etc., increasing the probability of a confusion that can become a deadly intoxication (Chang and Buswell, 1996). In general, Mexican-indigenous communities have a wide knowledge of their fungal resources and can identify toxic from non-toxic mushrooms (Garibay-Orijel et al., 2006; Ruan-Soto, 2018). However, the knowledge varies between people living in different ecosystems or geographic areas, as well as their traditions and mycological practices (Ruan-Soto et al., 2007). Therefore, some intoxications happen as a consequence of a bad identification associated to loss of knowledge or transculturation (Hernández-Rico, 2011). These confusions may become more frequent if toxic species colonize new geographic areas as a result of changes in the environment such as anthropogenic climate change.

Anthropogenic climate change is one of the main threats to biodiversity through direct and indirect impacts (IPCC, 2022). Fungi are not the exception, but there is very little scientific literature that shows how climate change has impacted their biology and ecology (e.g., Kauserud et al., 2012; Lankau et al., 2015; Guo et al., 2017; Bidartondo et al., 2018). A. phalloides is a toxic mushroom that has expended its distribution in the last decades (Pringle et al., 2009; Wolfe et al., 2010). Wolfe et al. (2010) used European records to calibrate an ecological niche model to project climatic suitability in North America under a baseline scenario (current climatic conditions) to identify climatic suitability. Their main results show that even when presences have only been registered in the United States, there is also climatic suitability in Canada and Mexico. Therefore, the objectives of this study were to understand the changes on A. phalloides observed distribution in Europe over the last decades, to model the species distribution under climate change scenarios, and to analyze the role that its historic distribution and distribution trends under climate change might play in terms of food security for Mexican indigenous communities.

2. Materials and methods

2.1 Model calibration

The basic information to carry out the ecological niche modeling are geographic records and climatic variables. We obtained the geographic records of *A. phalloides* between 1950-2019 from the Global Biodiversity Information Facility (GBIF) (Wolfe et al., 2010; Mushroom Observer, 2019). With these data, firstly we visualized the change in the distribution of this toxic mushroom across time and geographic space: 1950-1975, 1975-2000, and 2000-2019.

Afterwards, we used records from 1970-2019 to carry out the modeling and identify climatic suitability in North America under a baseline scenario and two different time-series: 2050 (2041-2060), and 2070 (2061-2080). We used records from 1970-2019 to calibrate the model given that in this time there was more certainty about the taxonomic identification of *A. phalloides* (Pringle and Vellinga, 2006). We obtained a final number of records of 435 in Europe and 339 in North America. To avoid sampling bias and to achieve a better modeling result, we tested different minimum records distances and used 30 km in Europe to avoid aggregation. In North America the minimum distance between records was 10 km.

Climatic variables were obtained from WorldClim (https://www.worldclim.org/), where 19 bioclimatic variables have been created. These variables have more biological sense than only using annual tendencies; they also represent limiting values and variability (Fick and Hijmans, 2017). From these 19 climatic variables we chose eight using biological and statistical criteria (Table I). The number of variables were reduced through a correlation matrix (eliminating those highly correlated variables; R > 0.8) and choosing the most important variables in *A. phalloides* biology. The variables had a 5-min resolution (~10 km), which has proven to give sound results for biological systems at continental scales (Ureta et al., 2022).

We used the CanESM2 general circulation model, whose last generation (CMPI5) has a good performance for Mexico and the Northern Hemisphere in general (Altamirano et al., 2021). Given that there is no independence between generations of general

Table I. Bioclimatic variables used for the ecological niche modeling.

ID	Variable
BIO4	Temperature seasonality
	(standard deviation ×100)
BIO5	Max temperature of warmest month
BIO6	Min temperature of coldest month
BIO12	Annual precipitation
BIO14	Precipitation of driest month
BIO17	Precipitation of driest quarter
BIO18	Precipitation of warmest quarter
BIO19	Precipitation of coldest quarter

circulation models, we can assume that CanESM5 (CMIP6) still has a good performance for Mexico and the Northern hemisphere. General circulation models are mathematical models of the atmospheric and oceanic circulation that allow the projection of climatic conditions at specific times. These models have different alternatives of scenarios or socioeconomic hypothesis that range from optimistic to pessimistic (O'Neill et al., 2020). In this study we used the pessimistic scenario SSP5-8.5 in the time-series 2050 (2041-2060) and 2070 (2061-2080) to have an insight of the consequences through a precautionary principle approach (UN, 1992).

2.2 Climatic potential distribution of Amanita phalloides

To choose the final modeling algorithm, we firstly carried out a pilot analysis using seven different algorithms (MaxEnt, MARS, CTA, SVM, RF, GBM, and ANN) (Thuiller et al 2009) Table II and using different predictive power metrics (ROC tests, Kappa, and TSS) to evaluate their performance (Allouche et al., 2006; Peterson et al., 2008). These three metrics are based on omission and commission errors. For the algorithm evaluation we used the multimodel platform BIOMOD in R (Thuiller et al., 2009). The algorithm with best performance was MaxEnt (Phillips et al., 2006) (Table II).

To improve the MaxEnt performance, different parameter combinations were evaluated through the ENMeval package proposed by Muscarella et al. (2014). The ENMeval tool helps identifying the best feature combinations to optimize the modeling. We used the 10 best combinations. The criteria to select the combinations were based on the ROC test, omission rate, and AICc (Akaike, 1974). We compared the validation metrics between the default tuning and the suggested by default and the models obtained through tuning the algorithm with best performance. To obtain the variables that contributed more to the model we used a Jacknife test. We used 70% of the European records to calibrate the model and 30% to validate it. We carried out 10 replicates and used the cloglog suitability output, since it has been suggested as the most adequate to estimate presence probability (Phillips et al., 2017).

Once we got the best algorithm tuning we carried out three different experiments under the baseline

Algorithm	AUC	Omission rate	Sensibility	Specificity	Kappa	TSS
MaxEnt	0.8415	0.1585	0.8414	0.8415	0.2465	0.6830
MARS	0.8339	0.1662	0.8337	0.8342	0.5851	0.6679
СТА	0.8219	0.1735	0.8264	0.8175	0.6435	0.6439
SVM	0.8371	0.1634	0.8365	0.8377	0.6741	0.6743
RF	0.5267	0.8004	0.1995	0.805	0.0490	-0.1504
GBM	0.8344	0.1662	0.8337	0.8351	0.6686	0.6688
	0.8179	0.1821	0.8178	0.8179	0.6355	0.6358

Table II. Validation metrics used to select the best algorithm.

AUC: area under the curve; omission rate: number of records out of the suitability area predicted; sensibility: assuming absences when there are presences; specificity: assuming presences when there are absences; kappa: name of a statistic test (validation metric for prediction power); TSS: true skill statistic. MaxEnt: Maximum entropy, MARS: Multivariate adaptive regression splines, CTA: Classification tree analysis, SVM: Support vector machine, RF: Random forest, GBM: Gradient boosting machines, ANN: Artifical neural networks.

scenario (1970-2000): (1) using 100% of the European records to calibrate the model and the North American records for validation; (2) using 70% of the South European records to calibrate the model, 30% of the South European records for validation and projecting suitability in North America, and (3) using the North American records to calibrate (70%) and validate the model (30%), projected also to North America. For the experiment (1), we used 100% of the European records to calibrate the model, given that we had an independent database for its validation in North America. To convert all of our suitability maps into binary maps (presence/absence), we used the minimum suitability value in which there was at least one North American presence. With these three experiments we evaluated the potential risk for the species finding climatic suitability in Mexico.

We carried out two different experiments under climate change scenarios: (1) using all European records, and (2) using only North American records. These two experiments allowed us to have a better understanding of the potential risk of *A. phalloides* reaching Mexico under climate change scenarios with the populations that already exist in our continent vs. the potential risk if all European populations reach the continent.

To identify the areas under greater risk of intoxication in Mexico, we overlaid two different suitability maps with a map of the indigenous languages of Mexico (INEGI, 2010): (1) climatic suitability (representing lower risk), and (2) climatic suitability + biological suitability map (representing the highest risk). A. phalloides establishes ectomycorrhizal relationships; consequently, its distribution not only depends on the climatic niche, but it strongly depends on the distribution of plant hosts. Even when biotic variables were not directly incorporated into the modeling, the climatic suitability map was overlaid with the potential distribution map of ecosystems in which this mushroom develops: boreal forest, coniferous forest, temperate mountain forest, temperate forest, wet subtropical forest, and subtropical mountain forest. In this way and under the assumption that these plant communities will be static across time, it is possible to identify geographic areas where climatic and biotic suitability occur under a baseline scenario and climate change scenarios. The map of indigenous languages is a way to infer where the mycophylic communities are. The consumption and commercialization of WEM is not exclusive to indigenous communities, but in Mexico all indigenous communities are mycophylic and use this resource (Garibay-Orijel and Ruan-Soto, 2014). Also, indigenous populations are at greater risk in terms of food security (González-Martell et al., 2022); consequently, the overlay of indigenous populations with the suitability of A. phalloides under a baseline and a climate change scenario helps identifying areas of greater intoxication risk. Even though there are high emigration rates of indigenous people in Mexico, their ancestral territories are fixed and indigenous population always remains there.

3. Results

3.1 Historic, current, and future distribution of Amanita phalloides

The first time-period visualized was from 1950 to 1975, given that before this time records have greater taxonomic uncertainty. In this period, the great majority of GBIF records were localized in the north of the European continent and some observations occurred in United States and Canada (Fig. 1). In the next time-period (1976-2000), GBIF records start to appear in the north of Italy, France and even Spain. Finally, in the last time-period (2000-2018) European and North American records became more abundant in warm areas such as the south of Italy, Spain and Portugal (Fig. 1). In the United States this mushroom distribution reaches the Mexican border in the east coast.

The first climatic suitability experiment (baseline scenario, 1970-2000, using all European records), shows that *A. phalloides* can expand its distribution down to Mexico (Fig. 2). In this scenario Mexico has climatic suitability in 34% of its area, while this percentage in the United States and Canada accounts to 56 and 15%, respectively (Fig. 3). When we overlaid the map of indigenous communities with the climatic suitability map we obtained that about 70% of the indigenous communities' areas have climatic conditions suitable for the development of this toxic

mushroom. This area comprises the original territories of at least 17 Mexican indigenous groups that consume traditionally wild mushrooms: Tarahumaras in Chihuahua; Tepehuanos, Coras, and Huicholes in Nayarit and Jalisco; Huastecos, Tepehuas, Nahuas, and Totonacos in Veracruz; Chinantecos, Mazahuas, Mazatecos, Mixes, and Zapotecos in northern Oaxaca; and Choles, Tzeltales, Tzotziles, and Tojolabales in Chiapas (Fig. 3). The percentage of indigenous communities' areas that overlay with climatic and biological suitability (potential distribution of known hosts) under the baseline scenario was of 5% (Table III). The main affected communities were Tarahumaras, Tepehuanes and Nahuas, who can be considered at highest risk.

Climatic suitability was also found in very warm areas of Mexico such as the Yucatan peninsula, where the natural hosts of *A. phalloides* do not occur. This result is the main reason why we decided to carry out the second experiment using the South European records to project into North America. The second experiment helped us to confirm that the projected climatic suitability in warm areas of Mexico and the United States originates from populations distributed in the south of Europe (Fig. 2).

To have a better insight of a more realistic risk of *A. phalloides* expanding its distribution to Mexico we carried out a third experiment that used only North

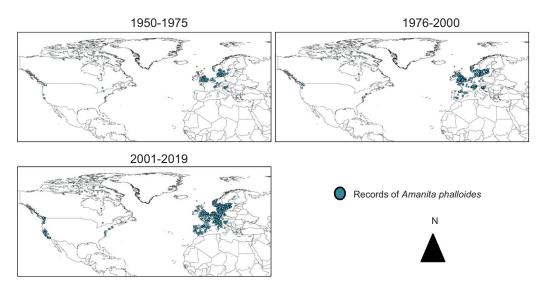


Fig. 1. Observed distribution of Amanita phalloides across time.

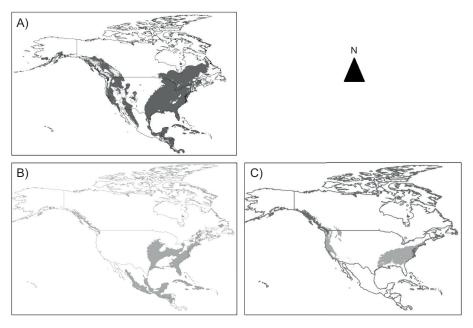


Fig. 2. Climatic suitability of *Amanita phalloides* under the baseline scenario. (a) Using European records to calibrate the model, (b) using south-European records to calibrate the model, and (c) using North American records to calibrate the model.

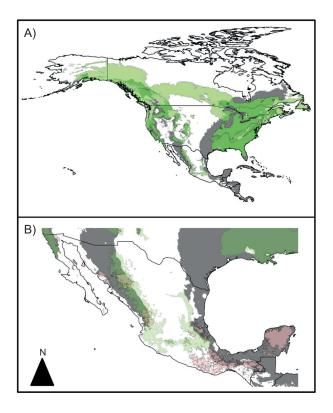


Fig. 3. Potential distribution map of *Amanita phalloides* using European records. (a) Overlap between *A. phalloides* potential distribution and the distribution of its vegetation hosts in North America. (b) Overlap between *A. phalloides* potential distribution, host distribution and indigenous territories in Mexico. Grey: potential distribution of *A. phalloides*; green: potential distribution of its hosts; pink: indigenous territories.

American records to model climatic suitability (Fig. 2). In this experiment, the coincidence of climatic suitability with pine and oak forests is very clear, but there are areas with this vegetation type in which the species has not yet been registered. Very scarce climatic suitability could be found in Mexico with this experiment, significantly reducing the risk to local communities except for Cochimies and Kumiais, which inhabit a small area in the north of Baja California and hardly consume WEM.

3.2 Amanita phalloides under climate change scenarios

When using all European records to carry out the modeling, for the 2050 scenario (SSP5-8.5) the suitability decreases only -4% (52% of climatic suitability) in the United States, while in Canada the suitability is reduced -11.3% (3.7% of climatic suitability) (Fig. 4). In contrast, climatic suitability in Mexico increases up to +46% (80% of climatic suitability). In other words, the climatic suitability of *A. phalloides* is expected to reach further south (warmer areas). Under scenario 2070, *A. phalloides* will further increase its climatic suitability in the Unites States and Mexico by +2(54%) of climatic suitability) and +4% (84% of climatic suitability), respectively. In Canada the climatic suitability remains the same in comparison to 2050. When overlaying the distribution of indigenous communities in Mexico with the future climatic suitability of A. phalloides, we found that in comparison to the baseline scenario there is a reduction in co-occurrence in scenario 2050 and an increase of co-occurrence in 2070 (64 and 70%, respectively). These climatic suitability increases under climate change scenarios (2050 and 2070) is not reflected in the percentages of area with low (climatic suitability) and high risk (climatic and biological suitability) (Table III). The percentage of low-risk area is lower in 2050 than under the baseline scenario and higher under the 2070 scenario. A lower percentage of high-risk area is expected to co-occur with indigenous communities (~3 and 2% for 2050 and 2070, respectively) than under the baseline scenario. Still, a high number of communities are expected to be affected: Tarahumaras, Tepehuanes, Otomíes, Nahuas, and Pames.

When using North American records to carry out the modeling, we found that under climate change

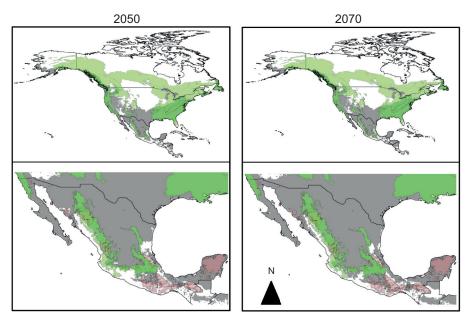


Fig. 4. Climatic suitability of *Amanita phalloides* under the baseline scenario and climate change scenarios (2050 and 2070) using European records. Overlap between *A. phalloides* potential distribution and the distribution of its vegetation hosts in North America and indigenous territories in Mexico. Grey: potential distribution of *A. phalloides*; green: Potential distribution of its hosts; pink: indigenous territories.

Table III. Percentage of indigenous area that coincides with climatic and biological suitability (high risk) and climatic suitability only (low risk).

Scenario	Low risk			High risk		
	Baseline	2050	2070	Baseline	2050	2070
Percentage	68.414	63.660	69.960	5.183	3.351	2.234

scenarios there is almost no climatic suitability in Mexico (Fig. 5), while under the baseline scenario climatic suitability remains only in a small portion of the Baja Californian Peninsula, where indigenous communities are scarce but still exist (Cochimies and Kumiais).

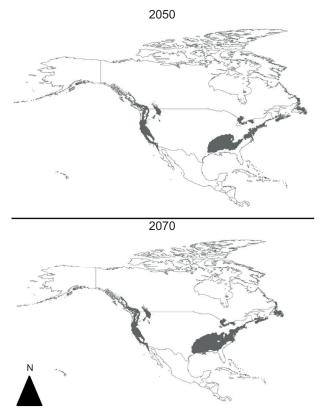


Fig. 5. *Amanita phalloides* climatic suitability maps under climate change scenarios using just North American records. The suitability in these maps shows that current *Amanita phalloides*' populations in the United States are expected to have low climatic suitability in Mexico under the climate change scenarios used.

4. Discussion

4.1 Historic and observed distribution of Amanita phalloides

Amanita phalloides records, which were revised and visualized from 1950 to 2019, show that with time this mushroom has been recorded in a wider area through Europe and North America. In Europe, A. phalloides is strongly associated with oaks and species from the Fagaceae family. Between 1950 and 1975, records were concentrated in the northern region of the European continent, where mushrooms have been intensively studied (Wollan et al., 2008). In more recent years (1976-2000), A. phalloides was registered in GBIF for the first time on the east and south regions of Europe. This lack of A. phalloides registers in GBIF prior to 1980 from southern Europe might be a database bias since the species has been distributed in Spain, Portugal, and Italy for decades (F. Martínez, A. Rinaldi, S. Goncalvez com. pers.). Experts also agree that the species has become more abundant in southern Europe, suggesting that thermophilic genotypes adapted to the Mediterranean climate.

In the United States, during the period from 2001 to 2019, there was a great increment of A. phalloides distribution across the western coast, and associations with new endemic hosts were registered (Wolfe and Pringle, 2012). The fact that this mushroom can establish ectomycorrhizal associations with new hosts unveils that its distribution is not necessarily restricted to its known hosts. The association with new hosts in introduction areas has already been reported in other species from the same genus such as Amanita muscaria (Vellinga et al., 2009). In areas where oaks are frequent, they remain as the main host of the species (Wolfe and Pringle, 2012). In the east coast, A. phalloides is restricted to parks and pine-forest plantations. In this geographic area, the species is more associated to pines than to oaks. Even when changes of hosts have

been registered in the United States, there is no genetic isolation from European populations, confirming that genetic divergence is recent (Pringle et al., 2009).

4.2 Potential distribution of Amanita phalloides

The modeling suggests important differences between the observed distribution of *A. phalloides* in the North American range and the potential distribution under baseline and climate change scenarios. Our results reveal that, when all European records are considered, the species finds climatic suitability in Canada, the United States, and Mexico. Our results also show that there are geographic areas with climatic suitability that do not co-occur with vegetation types with which the species has been historically associated.

After obtaining the results of the second experiment (modeling with European southern records) it is evident that these southern populations mainly determine climatic suitability in Mexico. In contrast, the third experiment (using North American records) suggests that, until now, populations present in the United States do not find climatic suitability in most of Mexico under current and climate change scenarios. One explanation is that populations in North America are locally adapted and, consequently, they have their own climatic niche that cannot be found in Mexico. The ecological niche, and consequently the climatic niche, is a species' ecological characteristic, but there are studies that suggest different ecological niches for different taxonomic levels beneath the species (Nakazawa et al. 2010; Ureta et al. 2012).

The other explanation would be that the territorial expansion of the species in North America is due to a slow dispersal over short distances. Therefore, populations in the USA have not yet faced the climates of Mexico, although they are already very close to the border. However, it is a fact that the species niche is quite broad if all geographic records are considered and, until now, there is no genetic isolation between North American and European populations (Pringle et al., 2009). So, even when the short-term risk might be low, there is still a risk of A. phalloides intoxication for Mexican indigenous communities because of North American approaching populations. If the precautionary principle is considered, we should warn local authorities and communities in sites where climatic suitability (using European records), vegetation

hosts, and indigenous communities overlay. A priority area for this warning campaign should be Chihuahua in northern Mexico. In this region, the original Tarahumara group subsists in precarious conditions and during the rainy season they supplement their diet with WEM (Moreno-Fuentes et al., 2004).

As an ectomycorrhizal species, it could be thought that *A. phalloides* distribution should be restricted to the distribution of its historical hosts, but it has already been demonstrated that this species is capable of adapting to new hosts in a few years (Vellinga et al., 2009). Our results show that the species has an enormous climatic potential if we consider its entire distribution (ecological niche), but also that there are populations with different climatic thresholds (i.e., European southern populations or populations in the United States). If populations from southern Europe reach the American continent, about 70% of the indigenous communities could be at risk of intoxication.

4.3 Potential distribution of Amanita phalloides under climate change scenarios

Amanita phalloides suitability under climate change scenarios is expected to decrease in the east and west coasts of the United States and Canada, at the same time that the climatic suitability increases in the northwest, southeast and center of Mexico. This increase in Mexico's climatic suitability represents a higher risk in terms of food security for local communities given that A. phalloides is morphological similar to other WEM. Up to 23 species of Amanita are consumed traditionally in Mexico (Garibay-Orijel and Ruan-Soto, 2014); of these, the most similar to A. phalloides are the Amanita caesarea complex (A. arkansana, A. bassi, A. caesarea s.l., A. calyptratoides, A. calvptroderma, A. hayalyuy, A. hemibapha, A. jacksonii, A. laurae, A. tecomate, and A. yema), consumed by the 17 indigenous groups; and the Amanita rubescens complex (A. novinupta, A. amerirubescens, and A. rubescens s.l.), consumed by Nahuas, Totonacos, Tarahumaras, Tzeltales, Tzotziles, and Tojolabales. Amanita phalloides can also be confused with other edible mushrooms as Armillaria mellea s.l., consumed by Huicholes, Mazatecos, Tzeltales, and Nahuas (Martínez Alfaro et al., 1983; Villarreal and Pérez-Moreno, 1989; Moreno-Fuentes et al., 2004; Garibay-Orijel et al., 2006; Robles-Porras et al., 2006; Lampman, 2007; Sheppard et al., 2008; Haro-Luna et al., 2019; López-García et al., 2020; Ramírez-Terrazo et al., 2021).

Even when mushroom intoxications are not one of the main causes of deaths in rural communities in Mexico, they represent a health problem that affects ancestral cultural practices and local economies (Ruan-Soto et al., 2007). Mushroom intoxications can happen by a lack of experience in recognizing edible from toxic mushrooms (Guzmán, 1987). Although people that traditionally eat them have a strong mycological knowledge, it is true that species are changing their distribution due to climate change and it is possible that new toxic species appear in areas where people is not used to them.

The expected shift in A. phalloides' distribution is towards southern areas in contrast to the general tendency of temperate species moving north to cooler areas. In most studies, the pattern is that temperate species will shift their distribution to temperate areas in northern latitudes and higher altitudes (Araújo and Rahbeck, 2006; Urban, 2018; Mamet et al., 2019; Osland et al., 2021). Our results are based on observed records in which the species has recently been recorded abundantly in southern Europe. However, if only the North American populations are used in the modeling, the risk for local communities is lower. This result makes us highlight that when exotic populations are successful, they adapt locally and change their ecological requirements (Fitzpatrick and Keller, 2015). This gives a strong argument to carry out ecological niche modeling with taxonomic entities below the species level (Ureta et al., 2012). It was very helpful to identify in this study populations that represent a higher risk in Mexico under current and climate change scenarios.

Finally, it is important to recognize that model transferring to other climatic scenarios and geographic areas comes with uncertainty (see Table SI and Figs. S1-S4 in the supplementary material). The variables in the baseline scenario exhibit a range of values that can be exceeded in other scenarios or periods. This situation diminishes the model performance. Also, new variables' combinations can be present, also diminishing the predictive power of the model. Consequently, it is important to identify geographic areas where uncertainty is greater and be cautious about the results (Mesgaran et al., 2014).

Acknowledgments

We thank Anne Pringle for her insightful comments and Amaranta Ramírez Terrazo for the picture used in the graphical abstract. We also thank Fernando Martínez, Andrea Pieroni and Susana Goncalvez for their commentaries on *A. phalloides* distribution in southern Europe. RGO was funded by the project UNAM-PAPIIT IN212521.

References

- Akaike H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19: 716-723. https://doi.org/10.1109/TAC.1974.1100705
- Allouche O, Tsoar A, Kadmon R. 2006. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43: 1223-1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x
- Altamirano del Carmen MA, Estrada F, Gay-García C. 2021. A new method for assessing the performance of general circulation models based on their ability to simulate the response to observed forcing. Journal of Climate 34: 5385-5402. https://doi.org/10.1175/ JCLI-D-20-0510.1
- Araújo MB, Rahbek C. 2006. How does climate change affect biodiversity? Science 313: 1396-1397. https:// doi.org/10.1126/science.1131758
- Beug MW, Shaw M, Cochran KW. 2006. Thirty-plus years of mushroom poisoning: Summary of the approximately 2,000 reports in the NAMA case registry. McIlvainea 16: 47a68
- Bidartondo MI, Ellis C, Kauserud H, Kennedy PG, Lilleskov E, Suz LM, Andrew C. 2018. Climate change: Fungal responses and effects. In: State of the world's fungi, chpt. 9 (Willis KJ, Ed.). Royal Botanical Gardens Kew, Richmond, England, 62-69.
- Boa ER. 2004. Wild edible fungi: A global overview of their use and importance to people. Non-Wood Forest Products 17. Food and Agriculture Organization of the United Nations, Rome, Italy, 147 pp.
- Chang ST, Buswell JA. 1996. Mushroom nutriceuticals. World Journal of Microbiology and Biotechnology 12: 473-476. https://doi.org/10.1007/BF00419460
- Fick SE, Hijmans RJ. 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37: 4302-4315. https://doi.org/10.1002/joc.5086

- Fitzpatrick MC, Keller SR. 2015. Ecological genomics meets community-level modelling of biodiversity: Mapping the genomic landscape of current and future environmental adaptation. Ecology Letters 18: 1-16 https://doi.org/10.1111/ele.12376
- Garibay-Orijel R, Cifuentes J, Estrada-Torres A, Caballero J. 2006. People using macro-fungal diversity in Oaxaca, Mexico. Fungal Diversity 21: 41-67.
- Garibay-Orijel R, Ruan-Soto F, Estrada-Martínez E. 2010. El conocimiento micológico tradicional, motor para el desarrollo del aprovechamiento de los hongos comestibles y medicinales. In: Hacia un desarrollo sostenible del sistema de producción-consumo de los hongos comestibles y medicinales en Latinoamérica: avances y perspectivas en el siglo XXI, cap. 16 (Martínez-Carrera D, Curvetto N, Sobal M, Morales P y Mora VM, Eds.). Red Latinoamericana de Hongos Comestibles y Medicinales-COLPOS-UNSCONACYT-AMC-UAEM-UP-AEP-IMINAP, Puebla, Mexico, 243-270.
- Garibay-Orijel R, Ruan-Soto F. 2014. Listado de los hongos silvestres consumidos como alimento tradicional en México. In: La etnomicología en México. Estado del arte (Moreno-Fuentes A, Garibay-Orijel R, Eds.). Red de Etnoecología y Patrimonio Biocultural (CONACYT)-Universidad Autónoma del Estado de Hidalgo-Instituto de Biología UNAM-Sociedad Mexicana de Micología-Asociación Etnobiológica Mexicana-Grupo Interdisciplinario para el Desarrollo de la Etnomicología en México-Sociedad Latinoamericana de Etnobiología, Hidalgo-Tlaxcala, 91-112.
- GBIF. 2019. Global Biodiversity Information Facility. Available at: https://doi.org/10.15468/dl.3f65k8 (accessed 2019 September 19).
- González-Martell AD, Sánchez-Quintanilla EE, García-Aguilar N, Contreras-Hernández T, Cilia-López VG. 2022. Vulnerability for food insecurity: Experiences of indigenous families in the Huasteca Potosina region, Mexico. Estudios Sociales. Revista de Alimentación Contemporánea y Desarrollo Regional 32: 2-14. https://doi.org/10.24836/es.v32i59.1162
- Guo Y, Li X, Zhao Z, Wei H, Gao B, Gu W. 2017. Prediction of the potential geographic distribution of the ectomycorrhizal mushroom *Tricholoma matsutake* under multiple climate change scenarios. Scientific Reports 7: 46221. https://doi.org/10.1038/srep46221
- Guzmán G. 1987. Un caso especial de envenenamiento mortal producido por hongos en el Estado de Veracruz. Revista Mexicana de Micología 3: 203-209.

- Haro-Luna MX, Ruan-Soto F, Guzmán-Dávalos L. 2019. Traditional knowledge, uses, and perceptions of mushrooms among the Wixaritari and mestizos of Villa Guerrero, Jalisco, Mexico. IMA Fungus 10: 16. https://doi.org/10.1186/s43008-019-0014-6
- Hernández-Rico GN. 2011. Taxonomía y etnomicología del género Amanita Pers., en el municipio de Acaxochitlán, Hidalgo. M.Sc. thesis. Universidad Autónoma del Estado de Hidalgo, Mexico.
- INEGI. 2010. Catálogo de localidades indígenas en México. Instituto Nacional de Estadística y Geografía. Available at: https://idegeo.centrogeo.org.mx/layers/ geonode:catlocindigenas_2010/layer_info_metadata (accessed 2022 January 17).
- IPCC. 2022. Summary for policymakers. In: Climate change 2022: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (Pörtner H-O, Roberts DC, Poloczanska ES, Mintenbeck K, Tignor M, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V, Okem A, Eds.). Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge and New York, 3-33. https://doi:10.1017/9781009325844.001
- Kauserud H, Heegaard E, Büntgen U, Halvorsen R, Egli S, Senn-Irlet B, Krisai-Greilhuber I, Dämon W, Sparks T, Nordén J, Høiland K, Kirk P, Semenov M, Boddy L, Stenseth NC. 2012. Warming-induced shift in European mushroom fruiting phenology. Proceedings of the National Academy of Sciences 109: 14488-14493. https://doi.org/10.1073/pnas.1200789109
- Lampman AM. 2007. Ethnomycology: Medicinal and edible mushrooms of the Tzeltal Maya of Chiapas, México. International Journal of Medicinal Mushrooms 9: 1-5. https://doi.org/10.1615/IntJMedMushr.v9.i1.10
- Lankau RA, Zhu K, Ordónez A. 2015. Mycorrhizal strategies of tree species correlate with trailing range edge responses to current and past climate change. Ecology 96: 1451-1458. https://doi.org/10.1890/14-2419.1
- López-García A, Pérez-Moreno J, Jiménez-Ruiz M, Ojeda-Trejo E, Delgadillo-Martínez J, Hernández-Santiago F. 2020. Traditional knowledge of mushrooms of biocultural importance in seven communities in the Chinantec region of the state of Oaxaca, Mexico. Scientia Fungorum 50: e1280. https://doi.org/10.33885/ sf.2020.50.1280
- Mamet SD, Brown CD, Trant AJ, Laroque CP. 2019. Shifting global *Larix* distributions: Northern expansion

and southern retraction as species respond to changing climate. Journal of Biogeography 46: 30-44. https://doi.org/10.1111/jbi.13465

- Mesgaran MB, Cousens RD, Webber BL. 2014. Here be dragons: A tool for quantifying novelty due to covariate range and correlation change when projecting species distribution models. Diversity and Distributions 20: 1147-1159. https://doi.org/10.1111/ddi.12209
- Moreno-Fuentes A, Aguirre-Acosta E, Pérez-Ramírez L. 2004. Conocimiento tradicional y científico de los hongos en el estado de Chihuahua, México. Etnobiología 4: 89-117.
- Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP. 2014. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for MaxEnt ecological niche models. Methods in Ecology and Evolution 5: 1198-1205. https://doi. org/10.1111/2041-210x.12261
- Mushroom Observer. 2019. Available at https://mushroomobserver.org/ (accessed 2019 December 17).
- Nakazawa Y, Williams RAJ, Peterson AT, Mead PS, Kugeler KJ, Petersen JM. 2010. Ecological niche modeling of *Francisella tularensis* subspecies and clades in the United States. The American Journal of Tropical Medicine and Hygiene 82: 912-918. https:// doi.org/10.4269/ajtmh.2010.09-0354
- O'Neill BC, Carter TR, Ebi K, Harrison PA, Kemp-Benedict E, Kok K, Kriegler E, Preston BL, Riahi K, Sillmann J, van Ruijven BJ, van Vuuren D, Carlisle D, Conde C, Fuglestvedt J, Green C, Hasegawa T, Leininger J, Monteith S, Pichs-Madruga R. 2020. Achievements and needs for the climate change scenario framework. Nature Climate Change 10: 1074-1084. https://doi.org/10.1038/s41558-020-00952-0
- Osland MJ, Stevens PW, Lamont MM, Brusca RC, Hart KM, Waddle JH, Langtimm CA, Williams CM, Keim BD, Terando AJ, Reyier EA, Marshall KE, Loik ME, Boucek RE, Lewis AB, Seminoff JA. 2021. Tropicalization of temperate ecosystems in North America: The northward range expansion of tropical organisms in response to warming winter temperatures. Global Change Biology 27: 3009-3034. https://doi. org/10.1111/gcb.15563
- Peterson AT, Papeş M, Soberón J. 2008. Rethinking receiver er operating characteristic analysis applications in ecological niche modeling. Ecological Modelling 213: 63-72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

- Phillips SJ, Miroslav D, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231-259. https://doi. org/10.1016/j.ecolmodel.2005.03.026
- Phillips SJ, Anderson RP, Dudík M, Schapire RE, Blair ME. 2017. Opening the black box: An open-source release of MaxEnt. Ecography 40: 887-893. https:// doi.org/10.1111/ecog.03049
- Pringle A, Vellinga EC. 2006. Last chance to know? Using literature to explore the biogeography and invasion biology of the death cap mushroom *Amanita phalloides* (Vaill. ex Fr. :Fr.) Link. Biological Invasions 8: 1131-1144. https://doi.org/10.1007/ s10530-005-3804-2
- Pringle A, Adams RI, Cross HB, Bruns TD. 2009. The ectomycorrhizal fungus *Amanita phalloides* was introduced and is expanding its range on the west coast of North America. Molecular Ecology 18: 817-833. https://doi.org/10.1111/j.1365-294X.2008.04030.x
- Ramírez-Terrazo A, Montoya A, Kong A. 2021. Conocimiento micológico tradicional en dos comunidades aledañas al Parque Nacional Lagunas de Montebello, Chiapas, México. Scientia Fungorum 51: e1321. https://doi.org/10.33885/sf.2021.51.1321
- Robles-Porras L, Ishiki-Ishihara M, Valenzuela R. 2006. Inventario preliminar de los macromicetos en los Altos de Chiapas, México. Polibotánica 21: 89-101.
- Ruan-Soto F, Mariaca-Méndez R, Cifuentes J, Limón-Aguirre F, Pérez-Ramírez L, Sierra-Galván S. 2007. Nomenclatura, clasificación y percepciones locales acerca de los hongos en dos comunidades de la Selva Lacandona, Chiapas, México. Etnobiología 5: 1-20.
- Ruan-Soto F. 2018. Recolección de hongos comestibles silvestres y estrategias para el reconocimiento de especies tóxicas entre los tsotsiles de Chamula, Chiapas, México. Scientia Fungorum 48: 1-13. https://doi. org/10.33885/sf.2018.48.1179
- Shepard GH, Arora D, Lampman A. 2008. The grace of the flood: Classification and use of wild mushrooms among the highland Maya of Chiapas. Economic Botany 62: 437-470. https://doi.org/10.1007/s12231-008-9044-5
- Thuiller W, Lafourcade B, Engler R, Araújo MB. 2009. BIOMOD-a platform for ensemble forecasting of species distributions. Ecography 32: 369-373. https:// doi.org/10.1111/j.1600-0587.2008.05742.x
- UN. 1992. Rio Declaration on Environment and Development. Report of the United Nations Conference on Environment and Development A/CONF.151/26

(vol. I). Available at: https://www.un.org/en/development/desa/population/migration/generalassembly/ docs/globalcompact/A_CONF.151_26_Vol.I_Declaration.pdf (accessed 2019 December 17).

- Urban MC. 2018. Escalator to extinction. Proceedings of the National Academy of Sciences 115: 11871-11873. https://doi.org/10.1073/pnas.1817416115
- Ureta C, Martínez-Meyer E, Perales HR, Álvarez-Buylla ER. 2012. Projecting the effects of climate change on the distribution of maize races and their wild relatives in Mexico. Global Change Biology 18: 1073-1082. https://doi.org/10.1111/j.1365-2486.2011.02607.x
- Ureta C, Ramírez-Barahona S, Calderón-Bustamante Ó, Cruz-Santiago P, Gay-García C, Swingedouw D, Defrance D, Cuervo-Robayo AP. 2022. Evaluation of animal and plant diversity suggests Greenland's thaw hastens the biodiversity crisis. Communications Biology 5: 985. https://doi.org/10.1038/s42003-022-03943-3

- Vellinga EC, Wolfe BE, Pringle A. 2009. Global patterns of ectomycorrhizal introductions. The New Phytologist 181: 960-973. https://doi.org/10.1111/j.1469-8137.2008.02728.x
- Villarreal L, Pérez-Moreno J. 1989. Los hongos comestibles silvestres de México, un enfoque integral. Micología Neotropical Aplicada 2: 77-114.
- Wolfe BE, Richard F, Cross HB, Pringle A. 2010. Distribution and abundance of the introduced ectomycorrhizal fungus Amanita phalloides in North America. The New Phytologist 185: 803-816. https://doi.org/10.1111/ j.1469-8137.2009.03097.x
- Wolfe BE, Pringle A. 2012. Geographically structured host specificity is caused by the range expansions and host shifts of a symbiotic fungus. The ISME Journal 6: 745-755. https://doi.org/10.1038/ismej.2011.155
- Wollan AK, Bakkestuen V, Kauserud H, Gulden G, Halvorsen R. 2008. Modelling and predicting fungal distribution patterns using herbarium data. Journal of Biogeography 35: 2298-2310. https://doi.org/10.1111/ j.1365-2699.2008.01965.x

SUPPLEMENTARY MATERIAL

Table SI. Variables with greater contribution to the model under the different climatic scenarios evaluated (baseline and climate change).

	Baseline scenario (1970-2000)	2050 (2041-2060) SSP5-8.5	2070 (2061-2080) SSP5 8.5	
	Precipitation of coldest	Precipitation of coldest	Precipitation of coldest	
	quarter	quarter	quarter	
	BIO19	BIO19	BIO19	
	Precipitation of warmest	Precipitation of warmest	Precipitation of warmest	
	quarter	quarter	quarter	
	BIO 18	BIO 18	BIO 18	
	Min temperature of coldest	Min temperatura of coldest	Min temperatura of coldes	
	month	month	month	
	BIO6	BIO6	BIO6	
	Annual precipitation	Annual precipitation	Annual precipitation	
oclimatic	BIO12	BIO12	BIO12	
riables	Precipitation of driest	Max temperature of	Max temperature of	
	quarter	warmest month	warmest month	
	BIO17	BIO5	BIO5	
	Max temperature	Precipitation of	Temperature seasonality	
	of warmest month	driest quarter	(stantard desviation)	
	BIO5	BIO17	BIO4	
	Temperature seasonality	Temperature seasonality	Precipitation of	
	(standard deviation)	(standard deviation)	driest quarter	
	BIO4	BIO4	BIO17	
	Precipitation of driest	Precipitation of	Precipitation of	
	month	driest month	driest month	
	BIO14	BIO14	BIO14	



Fig. S1. Climatic novelty type 1 (new range of climatic variables) between North America under the baseline scenario and climate change scenarios (2050 and 2070). No type 2 climatic novelty (new combinations of climatic variables) was found.

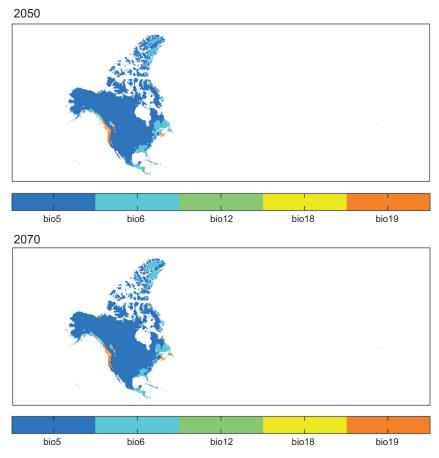


Fig. S2. Variables that contribute to climatic novelty type 1 (new range of climatic variables) between North America under the baseline scenario and under climate change scenarios (2050 and 2070).

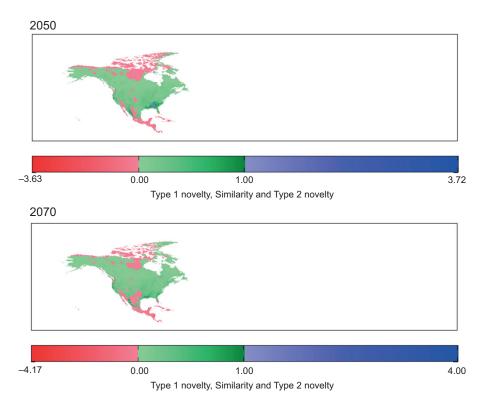


Fig. S3. Climatic novelty type 1 (new range of climatic variables) and type 2 (new combinations of climatic variables) between Europe under the baseline scenario and North America under climate change scenarios (2050 and 2070).

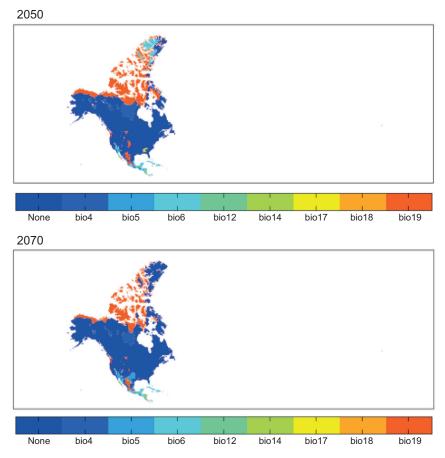


Fig. S4. Variables that contribute more to climatic novelties of type 1 (new range of climatic variables) and type 2 (new combinations of climatic variables) between Europe under the baseline scenario and North America under climate change scenarios.