Fundación Miguel Lillo
Tucumán
Argentina



# *Hannibal ad portas*: predicting the potential distribution of the exotic wood decay fungus *Coniophora olivacea*, new in Patagonia

## *Hannibal ad portas*: prediciendo la distribución potencial del hongo exótico degradador de madera *Coniophora olivacea*, nuevo en Patagonia

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## ABSTRACT

*Coniophora olivacea* has been traditionally considered as an important decay agent of building timbers of broadleaf and conifer woods, and causes significant damage on doors, window frames and other wood structures exposed to the environment. A more restricted role as tree pathogen has been also reported in cold climates. Studies of the predicted distribution of potentially invasive species are a useful tool to focus management efforts. Maximum-Entropy models allow predictions based on climatic and altitudinal layers as well as on previous data on the occurrence of species. The aim of this work is to report the presence of this wood decay fungus for the first time in Patagonia, and also to predict the potential spread pattern of this species using Maximum-Entropy.

**Keywords** — Maxent; biological invasion; brown rot; *Nothofagus*.

➤ Ref. bibliográfica: Moro Cordobés, F.; Almonacid, P.; Troncoso, O.; Romano, G.; Kuhar, F. 2023. *Hannibal ad portas*: predicting the potential distribution of the exotic wood decay fungus *Coniophora olivacea*, new in Patagonia. *Lilloa 60* (2): 149-169. doi: https://doi.org/10.30550/j.lil/1801
➤ Recibido: 1 de junio 2022 – Aceptado: 3 de agosto 2023 – Publicado en línea: 22 de agosto 2023.
➤ URL de la revista: http://lilloa.lillo.org.ar

## RESUMEN

*Coniophora olivacea* se ha considerado tradicionalmente un importante degradador de madera en obra de coníferas y latifoliadas, y también se reportan daños en puertas, marcos de ventanas y otras estructuras de madera expuestas a la intemperie. Un rol más restringido como patógeno forestal se ha citado en climas fríos. Los estudios que predicen la distribución de especies potencialmente invasoras son una herramienta para focalizar los esfuerzos de manejo de las mismas. Los modelos de Máxima Entropía permiten predicciones basadas en capas altitudinales y climáticas, así como también en datos preexistentes sobre la distribución de las especies. El objetivo de este trabajo es reportar la presencia de este degradador por primera vez en Patagonia, y estudiar sus patrones de propagación usando modelos de Máxima Entropía orientados a predecir su comportamiento.


**Palabras clave** — Maxent; invasión biológica; pudrición castaña; *Nothofagus*.

## INTRODUCTION

The genus *Coniophora* (Coniophoraceae, Boletales) is a widespread brown-rot wood decay fungus occurring in building timber as well as in natural environments, mostly in temperate regions (Kauserud *et al.*, 2007). *Coniophora arida* and *C. olivacea* have been recorded on dead wood of diverse tree species, both conifer and hardwood timber, and are distributed in northern and southern temperate zones worldwide. *Coniophora olivacea* has also been reported on living *Picea* spp. in North America. Both *C. arida* and *C. olivacea* are common in coniferous forests (Ginns, 1982). Together with *C. puteana*, they cause economically important losses in several ways; they frequently cause decay of living trees and have been observed indoors on construction materials (Kauserud *et al.*, 2007). Chee *et al.* (1998) report significant weight losses of wood in solid-state cultures of *C. olivacea*. Da Costa *et al.* (1967) also mention the capability of vigorous attack of this species on a very wide range of timbers under different uses, including hardwood trees such as *Eucalyptus marginata* in Western Australia. They also report that wood density was significantly affected by *Coniophora olivacea* whereas other fungal species tested did not significantly alter this parameter. Rudman (1963) proves that the sapwood of many tree species is uniformly susceptible to attack by this fungus. Although the infective role of each dissemination form is yet unknown (Edman & Jonsson, 2001), *C. olivacea* is able to produce basidiospores as well as mycelial cords (Stalpers, 1978), which suggests the possibility of infection through the soil from one log to another.

A specimen collected by the authors identified as *C. olivacea* and deposited at the CORD Herbarium (CORD FK16004) is to our knowledge the first and only record of this species in southern South America. Since the Andean Patagonia has a long history of cultivation of non-native trees species (e.g. *Pinus* spp., *Eucalyptus* spp., *Pseudotsuga menziesii*, among others), events of introduction of exotic fungal species are likely. Moreover, intense fieldwork performed in the last decades by many

mycologists aiming to assess in depth the aphyllophoroid funga of the region did not detect this species (e.g., Greslebin & Rajchenberg, 2003).

Our collection consists of a small decayed piece of wood found on soil in a mixed forest. Given the fragmentary nature of the material, the identity of the wood species of the substrate is not obvious, and intensive histochemical work is needed to accurately identify it.

Since *C. olivacea* has been shown to be capable of producing significant damage in wooden structures, reliable information is needed as a base for future management programs. Strategies aiming to restrict the dispersion of forest pathogens, such as *Phytophthora austrocedri*, have been already promoted (Giordana *et al.*, 2020), including restrictions in tourism and animal farming in certain areas or even chemical treatments (Silva *et al.*, 2016). Initiatives against the spread of *C. olivacea* as well as against other non-native species might be needed in the future, even if they do not mainly affect living trees, since wood is the dominant construction material in the region, especially in the Chilean slope of the Andes.

Given the complex and multicausal nature of biological invasions, it is difficult to predict the behavior of a newly arrived alien species in a given area is, at least, challenging (Desprez-Loustau *et al.*, 2007), especially when this behavior is also linked to plant species that might act as hosts, partners or reservoirs of the fungal entity (Dickie *et al.*, 2017). However, methods taking on account climatic and other variables produce robust models outlining the potential distribution of a species given their environmental preferences. In this line, Maximum Entropy (Maxent) models have been shown to be efficient in estimating the potential geographic distributions of species by merging presence-only data with environmental information (Phillips *et al.*, 2006; Yuan *et al.*, 2015).

An additional challenge regarding the identification of *C. olivacea* is the presence of distinct evolutionary clades within this species (Kauserud *et al.*, 2007). Since this diversity is morphologically cryptic, only molecular methodologies can place a specimen in this scheme. Studies taking into account this hidden diversity and aiming to find different behaviors (e.g. in degradation, dispersal, infectivity) need available material associated with reliable information on the specimen.

The aim of this work is to provide reliable information on the identity, host and potential distribution of *C. olivacea*, reported here as new for Patagonia, so future decisions on non-native species management can be made on a solid basis.

## MATERIALS AND METHODS

### Sequences and molecular analyses

DNA of the vouchered specimen was extracted with the GenElute Plant Genomic DNA Miniprep Kit (SigmaAldrich) following the manufacturer's instructions. The rDNA ITS1-5.8S-ITS2 region (ITS) was amplified using the primers ITS1F/ITS4 White *et al.*, 1990; Gardes & Bruns, 1993). The PCR reaction was performed with the REDExtract-N-Amp PCR ReadyMix (SigmaAldrich) for both regions under the

following conditions: an initial denaturing step at 95 ºC for 4 min, 36 cycles of 30 s at 94 ºC, 45 s at 55 ºC and 70 s at 72 ºC and a final extension for 10 min at 72 ºC. The amplified DNA fragment was purified and sequenced in Macrogen (Seoul, South Korea) using the primer ITS4 for ITS. This newly generated sequence was uploaded to GenBank with the accession number ON832657. Internal Transcribed Spacer sequences of the most similar taxa identified to species were queried in GenBank NCBI (http://www.ncbi.nlm.gov) using the MEGABLAST option (see Table S1). Sequences of specimens of the genus *Leucogyrophana* were recovered from GenBank and used to root the tree.

The sequences were aligned with L-INS-i strategy as implemented in MAFFT 7.0 (Katoh & Standley, 2013) and analyzed without additional editing. Nucleotide substitution models were chosen with jModelTest 2.1 (Darriba *et al.*, 2012), under the Akaike information criterion (AIC). Maximum likelihood (ML) analysis was performed in PHYML (Guindon *et al.*, 2010). Bootstrap values of the most likely tree were calculated after 1,000 repetitions with 10 random addition sequences and the topologies were produced using TBR swapping. B/MCMC analyses were conducted with MrBayes (Huelsenbeck & Ronquist, 2001) with 7,000,000 generations starting with a random tree and running four simultaneous chains. The first 100,000 generations were discarded as burn-in. TRACER1 (http://evolve.zoo.ox.ac.uk/software.html/tracer/) was used to verify that stationarity was achieved after the first 100,000 generations.

## Wood identification and characterization of the damage

Transverse, tangential and radial sections (10 $\mu$m thick) were made using a Leica Hn 40 sledge microtome and stained with cotton blue, after bleaching the wood with hydrogen peroxide 30% for 1.30 h, rinsing with distilled water 3 to 4 times, and rinsing before mounting in lactoglycerol. Ten slides of each sample were mounted and 10 unstained slides were prepared as control. Observations were made under a light microscope Leica DM500 and photomicrographs were obtained with a Canon EOS Rebel T3i digital camera. Wood library samples and the InsideWood database (http://insidewood.lib.ncsu.edu) were used for comparative study and to determine the species identity of the wood substrate.

The slides (at least 5 for each section of the procedures of noninfected and infected wood) were stained using specific procedures mentioned by Krishnamurthy (1988) for localizing lignin, carbohydrates, and other phenolics. Lignin was revealed as red using Wiesner's reagent for five minutes and mounted on a drop of 6N HCl. Toluidine blue was used to contrast lignin and polyphenols (turquoise green), carbohydrates (lilac) and oils (without color), and rinsed with water (Rivera Nava *et al.*, 1999).

## Occurrence data, climatic data, and niche modeling

Ecological niche model (ENM) was employed to infer the potential distribution of *C. olivacea* in the world, with a special focus on Patagonia. Geographical coordinates of curated registers of this species were recorded from Global Biodiversity Information Facility (GBIF website: www.gbif.org) and also from BLAST queries of ITS sequences in public databases included in the phylogenetic analyses (Table S2). Records before 1950 were eliminated since climatic data before is not systematically curated. Records without documented authoritative identification were also discarded. To avoid an autocorrelation spatial effect in the ENM, the points located closer than 50 km from each other were eliminated using the R package "Wallace" v1.0.6.1 (Kass *et al.*, 2018) implemented in R v3.6.1. The final database contained 113 records distributed on every continent except Antarctica (Table S2).

A set of 19 bioclimatic variables layers and one elevation layer were obtained from the WorldClim 2 database (http://www.worldclim.org) at 2.5 arc-min (i.e. ca. 5 km) resolution covering the entire planet (Hijmans *et al.*, 2005). In order to minimize biased fitting of the models produced by the covariance between variables, Pearson's correlation was performed to eliminate correlated environmental and elevation variables using R v3.6.1. After we excluded correlated variables ($r > 0.7$), we selected six climatic variables (Fig. S1): Bio1 (annual mean temperature), Bio2 (mean diurnal range), Bio4 (annual temperature range), Bio11 (precipitation of driest month), Bio12 (annual precipitation), Bio15 (precipitation seasonality) and the elevation variable. MaxEnt was run under default settings, including auto-features, a maximum of 500 iterations, 100 replicates to ensure reliable results, and 10,000 randomly sampled background points, with a regularization multiplier of 1 and a convergence threshold of $10^{-5}$. K-fold cross-validation was used to test the performance of the model. To do this, occurrence data were randomly split into a number of equal-size groups, and models are created after resampling the set. The left-out folds were then used for evaluation. Logistic output models were produced and uploaded to ASCII in raster format and then imported to the QGIS "Geographic Information System" Version 3.4.12 (2019). The average model was geographically projected dividing the probability of occurrence into five categories: values below the threshold were considered absent, "low" threshold–0.25, "medium" 0.25–0.5, "high" 0.5–0.75, and "very high" $> 0.75$. The area under the "receiver operating characteristic (ROC) curve" (AUC) values (Peterson *et al.*, 2008; Elith & Leathwick, 2009) were used to evaluate the fitness of the prediction. Variable importance to ENMs was evaluated based on the permutation value, percent contribution, jackknife resampling, and the response curves produced by MaxEnt (Phillips *et al.*, 2017).

# RESULTS

## Molecular identification

The analyses performed to support the morphological identification of the voucher FK16004 as *Coniophora olivacea* (Fr.) P. Karst. (Fig. 1) and also strongly suggest that

this material is affiliated with group 4 within the scheme proposed by Kauserud *et al.* (2007). This group consists of materials found in British Columbia (Canada) and the UK, and Kauserud *et al*. (2007) conclude that this lineage probably has a wider boreal distribution. But more profound studies and a wider sampling is needed before proposing these localities as the origin of the introduced strain. Group 5 has not been recovered from the dataset since no available sequences representing it were retrieved from public databases.

## Identification of the substrate and effect of the degradation

The woody substrate presented the following characteristics: In cross-section, diffuse porosity was observed, with solitary and grouped vessels colonized by abundant hyphae. Sectors without fibers or parenchymal rays (disintegrated tissue) were observed. In the radial section, rays of reddish coloration and with contents were

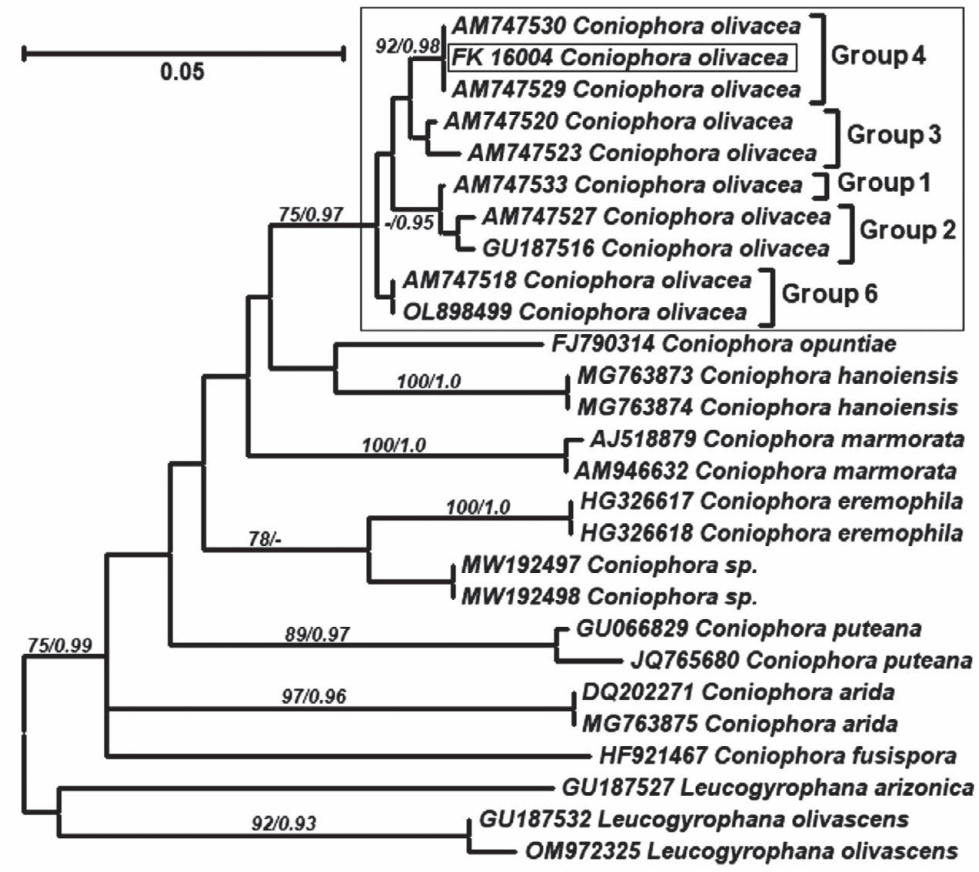


**Fig. 1.** Maximum likelihood tree showing significant bootstrap support (>75%) and significant Bayesian PP (>0.95). Intraspecific groups indicated in *C. olivacea* correspond to the cryptic clades defined by Kauserud *et al.* (2007). Group 5 was not recovered due to the lack of representative sequences.

**Fig. 1.** Árbol de Máxima verosimilitud con valores significativos de bootstrap (>75%) y PP Bayesianaas (>0.95). Los grupos intraespecíficos indicados en *C. olivacea* corresponden a los clados crípticos definidos por Kauserud *et al*. (2007). El grupo 5 no está representado debido a la falta de secuencias.

observed as well as vessels with abundant hyphae. Tangential sections made evident that rays are almost exclusively uniseriate. Vessel elements with oblique septa and opposite, scalariform intervessel pits, and with a large number of hyphae were also observed. These anatomical characteristics are coincident with *Nothofagus dombeyi* (Mirb.) Oerst wood, which has diffuse porosity, solitary and grouped vessels, in radial, multiple, short and long series (Rivera, 1988). In tangential section, *N. dombeyi* presents oblique septa, and in radial section, simple perforation plates bordering each other, with subterminal, opposite (often scalariform) intervessel pits with circular to elliptical areolae. Rays are almost exclusively uniseriate, with procumbent cells (Tortorelli, 2009).

In transverse sections, the noninfected wood tested positive for lignin, where the fibers and rays are stained to a pink/red color (Fig. 2A), while in the wood colonized by *C. olivacea* no positive reaction to lignin was detected. The fibers showed thin and deformed walls, and some showed cellular contents. The rays showed ocher colors with some reddish contents (Fig. 2B). In tangential longitudinal sections of noninfected wood, the fibers and walls of the vessels were stained to reddish/pink, evincing the presence of lignin (Fig. 2C). The wood showed a brownish coloration as well as no positive reaction for lignin (Fig. 2D).

Fibers of native (noninfected) tissues in the cross-section showed lignin presence, as evinced by the blue color, indicative of this compound, whereas the rays showed a green coloration (a weaker reaction for the presence of lignin) with dark contents. The deposits in some vessels displayed a pink reaction indicating the presence of carbohydrates (Fig. 2E). In the tangential longitudinal section, the walls of the vessels showed intervascular pits stained with color blue as well as fibers, indicating the presence of lignin (Fig. 2G).

The cross-section of the infected wood showed fibers with thinner cell walls and rays with enlarged and ocher-colored contents that evince an advanced state of degradation. The vessels were observed to be translucent (white) due to the loss of carbohydrates and the absence of other contents (Fig. 2F). The situation was similar in the tangential section, where deformed vessels were also observed (Fig. 2H).

## EMN of *C. olivacea* and potential distribution in Patagonia

The potential distribution model of *C. olivacea* exhibited a high predictive power, as shown by the AUC ($\mu$: 0.902; SD: 0.114). The maps obtained from ENM showed how the habitat suitability is distributed globally (Fig. S3), including in the Patagonia region (Fig. 3). In general, suitable areas were located in Europe, North and South America, Australia, and East Asia. The model also predicted suitable areas in Argentina and Chile, which can represent geographic regions with an adequate combination of climatic and elevation conditions for the establishment of *C. olivacea* (Fig. 3). The areas with high suitability values (> 0.5), occupied approximately 629,053 km$^2$ of the total area of Argentina and Chile (Fig. 3). According to this model, the main variables explaining the presence of the species were Bio12 (annu-

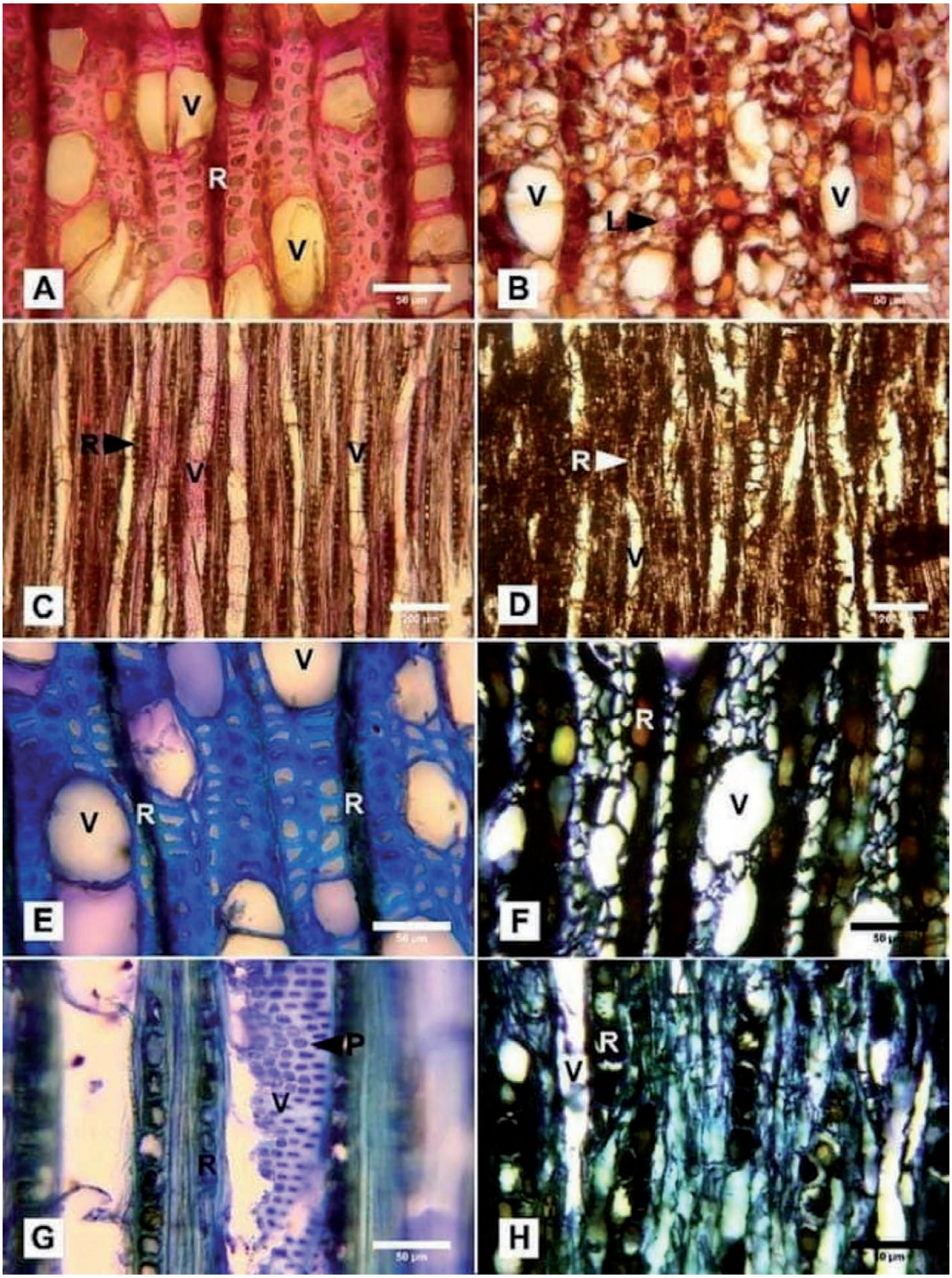


**Fig. 2.** Histochemistry of *Nothofagus dombeyi* uninfected wood (A, C, E, G) and infected by *C. olivacea* (B, D, F, H). A-D) stained with phloroglucinol. A) Cross-section with fibers and rays showing a positive reaction (pink) to lignin. B) Thin, degraded walls without pink coloration (negative reaction to lignin) and rays with large cells and reddish-brown contents. Only a few fibers with lignin contents (L) are observed. C) Tangential longitudinal section of the vessel walls and fibers showing the presence of lignin. D) Negative reaction for lignin indicating the action of the wood decay fungi. E-H) Detail of the cross-section stained with toluidine blue, where: E: the fibers and rays with dark contents are observed along with some pink vessels indicating the presence of carbohydrates. F) Thin, deformed and dark-colored walls. Ocher rays with dark contents deformed (enlarged) cells and translucent vessels due to the degradation of carbohydrates. G) Tangential longitudinal section of ➤

non-infected wood where fibers and intervascular pits appear stained in blue, indicating the presence of lignin. The rays show a greenish coloration (a weaker reaction for lignin) with darker deposits. H) Infected wood with the dark fibers of thin walls and rays showing enlarged cells of dark cellular contents. (L) = lignin; (V) = vessels; (R) = rays; (P) = intervascular pits.

**Fig. 2.** Histoquímica de madera no infectada de *Nothofagus dombeyi* (A, C, E, G) e infectada por *C. olivacea* (B, D, F, H) teñidas con floroglucinol. A) Sección transversal con fibras y radios mostrando reacción positiva (rosa) a lignina. B) Paredes delgadas, degradadas, sin coloración rosa (negativo para lignina) y radios de células grandes con contenidos castaño-rojizos. Solo se observan unas pocas fibras con contenido de lignina (L). C) Sección longitudinal de las fibras y paredes de los vasos mostrando presencia de lignina. D) Reacción negativa a la lignina indicando la acción de hongos degradadores. E-H) Detalle de secciones transversales teñidas con azul de toluidina en las que, E: se observan fibras y radios con contenidos oscuros se observan junto con algunos vasos en rosa que indica presencia de carbohidratos. G) Sección longitudinal tangencial de madera no infectada donde las fibras y las punteaduras intervasculares aparecen teñidas de azul debido a la presencia de lignina. Los vasos muestran coloración verdosa (una reacción más débil a la lignina) con depósitos oscuros. H) Madera infectada con las fibras de paredes delgadas junto con radios que muestran células de contenido celular oscuro.

al precipitation) and Bio1 (annual mean temperature) contributing together with 81.6% (Table S3). Regarding the permutation importance, determined by random permutations of the values of each variable among the training points and background data, Bio12 and Bio1 also had the maximum influence on the model and contributed 82.6% (Table S3). The result of the jackknife test showed Bio1 has the most useful information by itself and the most information that is not present in other variables (Table S4). In general, suitability was high in areas with an annual mean temperature (Bio1) between 0 °C and 10 °C, and precipitation values (Bio12) in the range of 500-1,500 $mm^3$ (Fig. 4). The potential distribution extends in areas with low-temperature variation throughout the day (Bio2), and low-temperature change over the course of the year (Bio4) (Fig. S2); and in areas where the coldest temperatures are between -10 °C and 0 °C (Bio11) and low precipitation seasonality (Bio15) (Fig. S4). The most suitable areas are found below 1,000 m.a.s.l. with a mean annual temperature of around 10 °C (Fig. S5).

## DISCUSSION

The highest habitat suitability (> 0.8) for *C. olivacea* seems be limited to humid forests in latitudes higher than 35° on the Chilean slope of the Andes. On the Argentinean slope, areas of high suitability are more restricted, and limited to humid valleys in the provinces of Chubut, Santa Cruz and Tierra del Fuego. The rain seasonality seems to be decisive, slightly lowering the habitat suitability in the rest of the Andean Patagonia. This variable has shown to be also very influential, explaining the distribution of agaricoid fungal species in this region (Romano *et al.*, 2017). However, the whole Andean Patagonia displays an also alarming suitability value above 0.6, in a region with widespread use of wood as main construction material and where wood production is one of the most important economic activities.

This high suitability supports the recognition of this record as an alien species. The chances of this species staying unnoticed despite the huge sampling efforts in the last decades are very low; especially considering the intensive campaigns looking

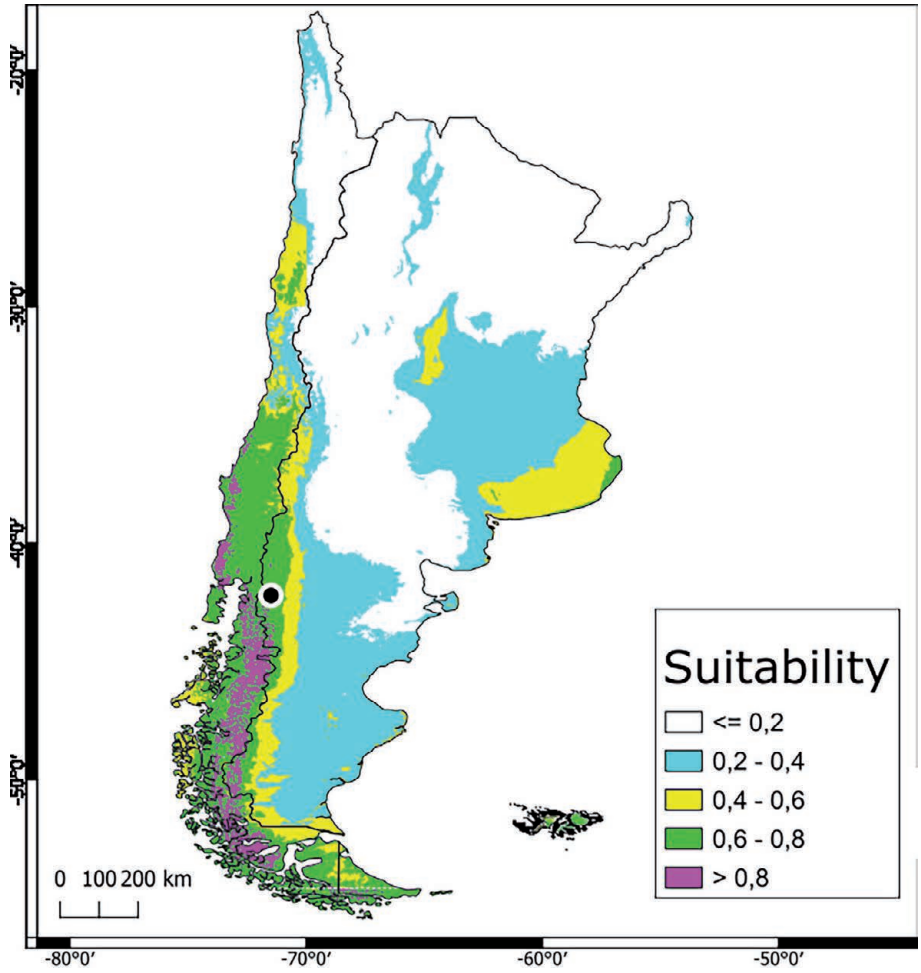


**Fig. 3.** Distribution of suitable habitat of *C. olivacea* in Argentina and Chile. The suitability value represents the predicted distribution probability (in logistic value) for climatic and elevation layers used in the niche modeling. Specimen of *C. olivacea* collected in Patagonia marked with a black dot.

**Fig. 3.** Distribución de hábitat idóneo para *C. olivacea* en Argentina y Chile. Los valores de idoneidad representan la distribución de probabilidad predicha (en valores logísticos) para las capas climáticas y de elevación usadas en el modelado de nicho. El especimen de *C. olivacea* colectado en Patagonia se marca con un punto negro.

for corticioid fungi in this region (Gallo *et al.*, 2021). Also, the fact that the location of the collection studied has a long history of forestry and forest management speaks for a recent introduction.

An important subject to discuss here is the potential role of *C. olivacea* as a wood pathogen. There are some articles showing its role as a "butt rotter" in temperate and cold forests (Worrall & Nakasone, 2009) and also as a branch and stem rotter (Aref'ev, 1991). Although it is too early to suggest that this species might act as a pathogen in Patagonia, the fact that the Patagonian collection is associated with a native tree species, together with the high habitat suitability shown, indicates that this possibility should be considered. Evidence of delignification was found in the substrate of the studied voucher despite the fact that *C. olivacea* is a brown rot species. This suggests that attack by *C. olivaceae* may be a secondary colonization on a previously decayed material. Assays in living trees under controlled conditions

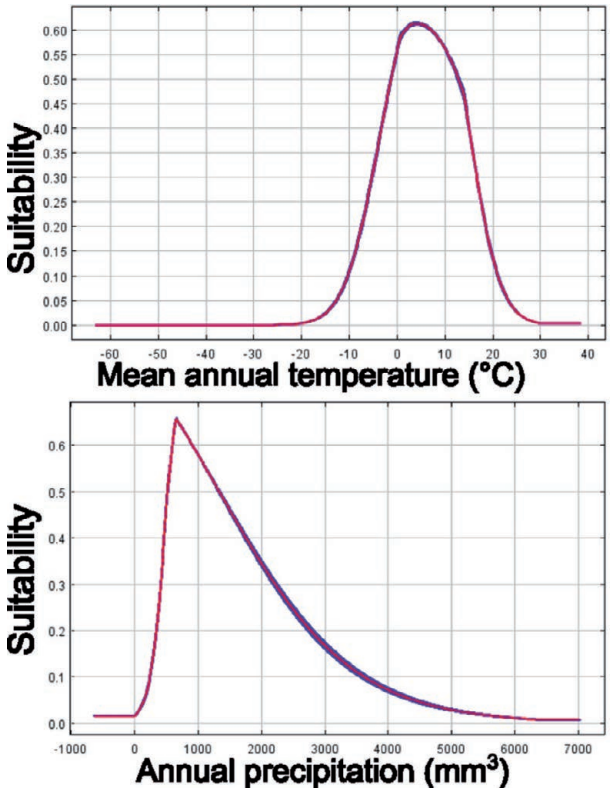


**Fig. 4**. Response curves of the most important environmental variables in modeling habitat distribution for *C. Olivacea.* Mean annual temperature (Bio1) and Annual precipitation (Bio12). The suitability value represents the predicted distribution probability on a logistic scale.

**Fig. 4.** Curvas de respuesta de las variables más importantes en el modelado de distribución de hábitat para *C. olivacea.* Temperatura anual media (Bio1) y precipitación anual (Bio12). El valor de idoneidad representa la distribución de probabilidad predicha en escala logística.

would be a potential way of assessing the latter. Furthermore, a more intense inspection of living trees in the areas surrounding the original location would provide invaluable information on this matter. The verification of potential pathogenicity on native trees would require immediate actions restricting the spread of this decayer, given the wide range of wood species where it can grow (Da Costa *et al.*, 1961).

Finally, genotyping of more collections would allow analyses that take into account the intraspecific diversity proposed by Kauserud *et al.* (2007). Such analyses are currently unviable given the number of registers needed to perform a supported prediction of the distributional range.

## ACKNOWLEDGEMENTS

This work was supported by FONCyT (Grant PICT 2018 – 3781 to F.K.) and CONICET. The authors also thank Alejandro Bringas (CORD Herbarium), and the University of Patagonia San Juan Bosco (Esquel, Argentina) for their assistance. A special acknowledgment goes to Alina Greslebin, Andrés de Errasti, and Gabriela Gonzalez for proofreading early versions of the manuscript.

## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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## SUPPLEMENTARY MATERIAL

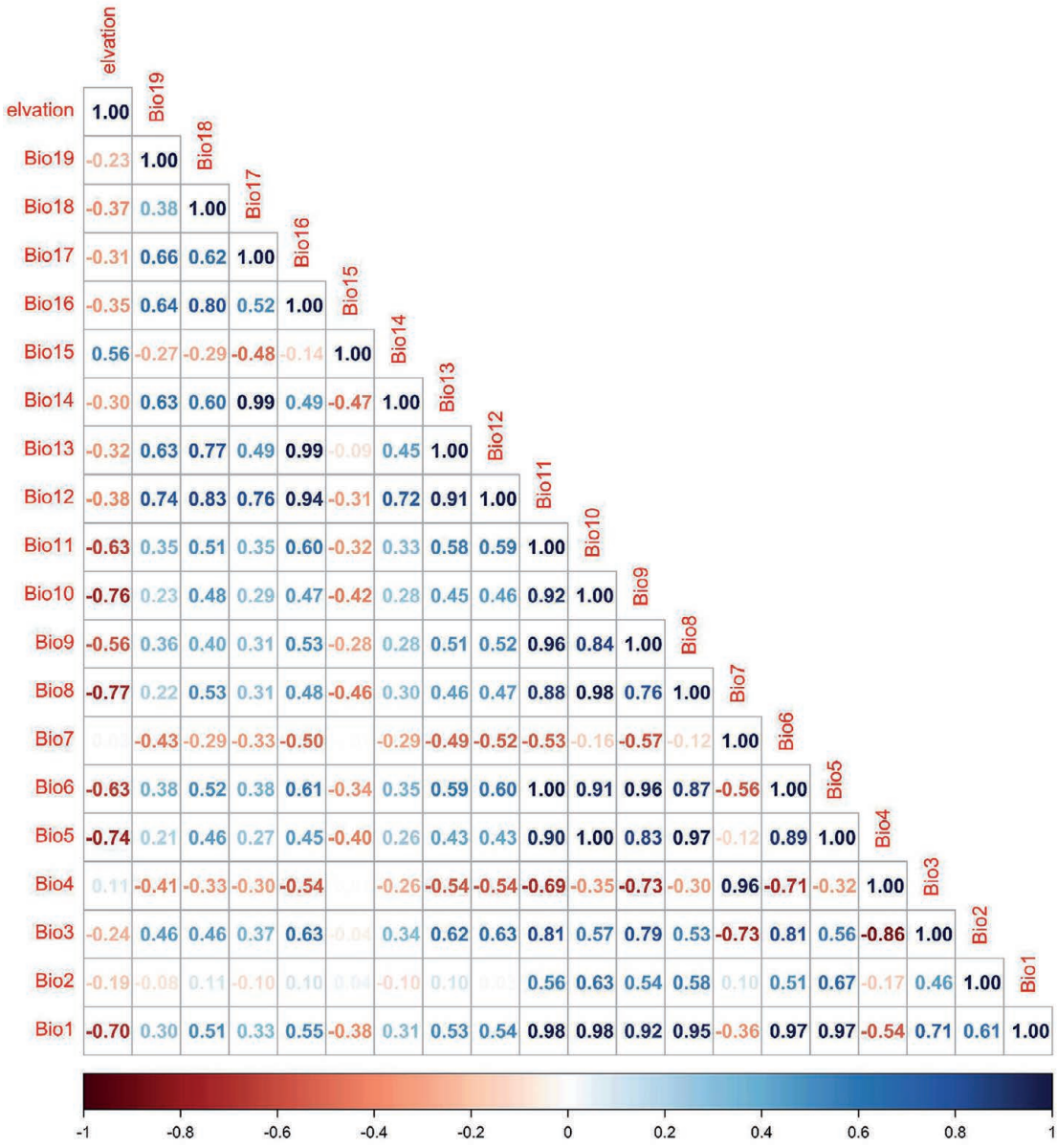


**Fig. S1.** Covariance matrix of bioclimatic and elevation layers calculated using Pearson's correlation coefficient.

**Fig. S1.** Matriz de covarianza de las capas bioclimáticas y de elevación calculadas usando el coeficiente de correlación de Pearson.

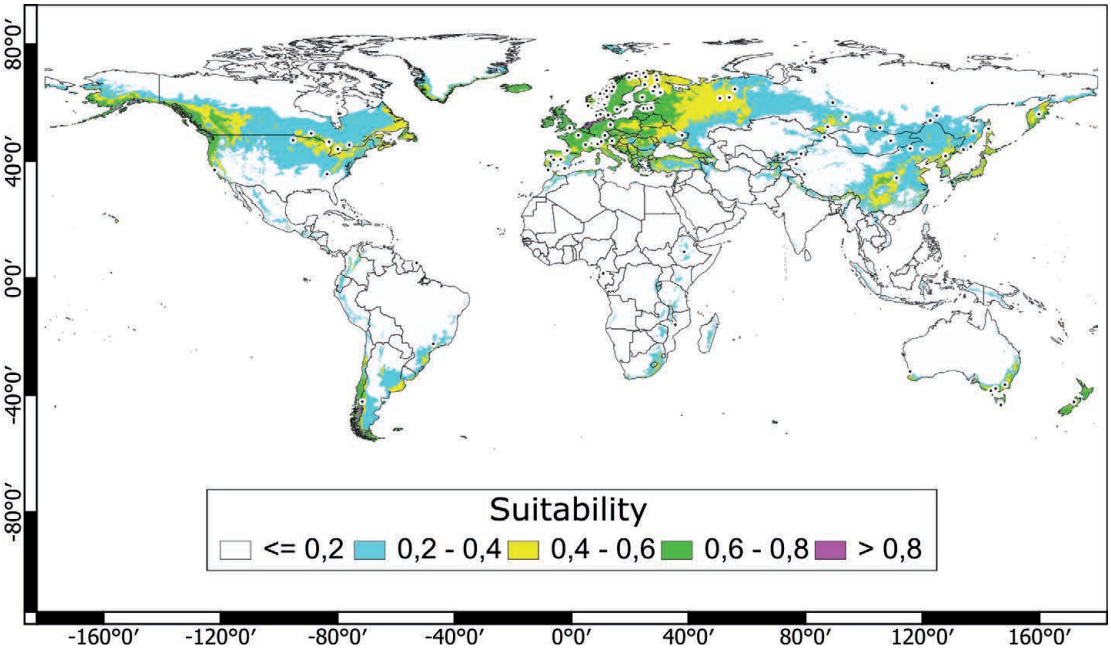


**Fig. S2**. Distribution of suitable habitat of *C. olivacea* worldwide. The suitability value represents the predicted distribution probability (in logistic value) for climatic and elevation layers used in the niche modeling. Specimens of *C. olivacea* are marked with a black dot.

**Fig. S2.** Distribución mundial de hábitat idóneo para *C. olivacea*. El valor de idoneidad representa la distribución de probabilidad predicha (en valor logístico) para las capas climáticas y de elevación.

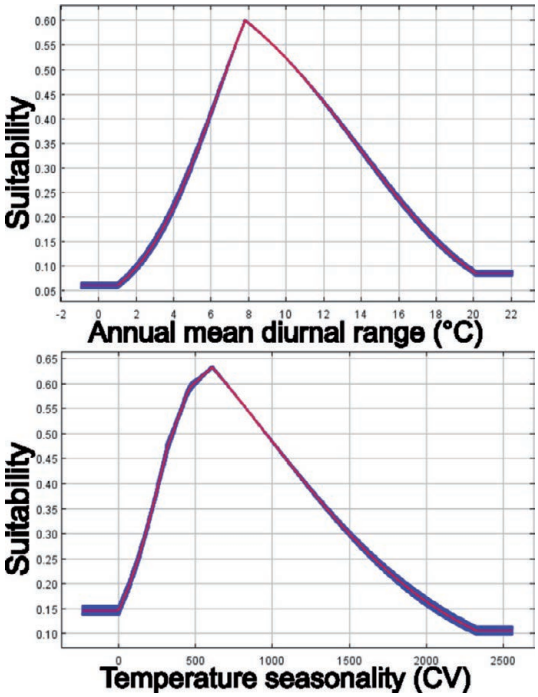


**Fig. S3**. Response curves of annual mean diurnal range (Bio2) and temperature seasonality (Bio4) in modeling habitat distribution for *C. olivacea*. The suitability value represents the predicted distribution probability (in logistic value).

**Fig. S3.** Curvas de respuesta de media anual de rango diurno (Bio2) y estacionalidad de la temperatura (Bio4) en el modelado de distribución de hábitat para *C. olivacea*. El valor de idoneidad representa la distribución de probabilidad (en escala logística).

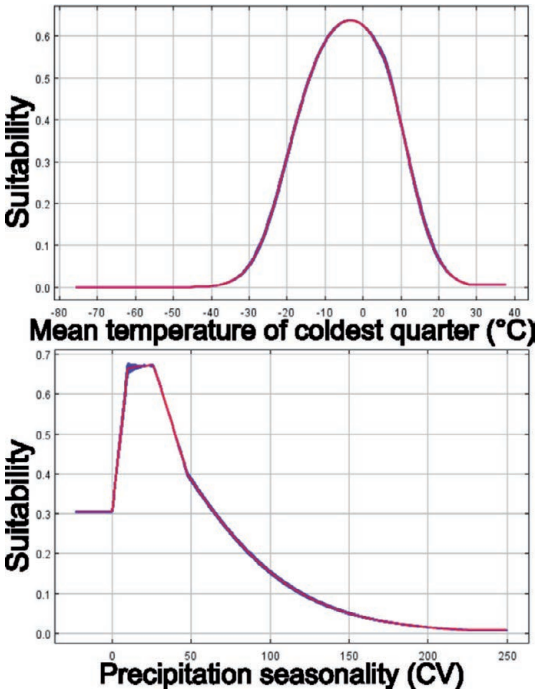


**Fig. S4**. Response curves of the mean temperature of the coldest quarter (Bio11) and precipitation seasonality (Bio15) in modeling habitat distribution for *C. olivacea*. The suitability value represents the predicted distribution probability (in logistic value).

**Fig. S4.** Curvas de respuesta de la temperatura media del trimestre más frío (Bio11) y estacionalidad de la precipitación (Bio15) al modelar la distribución de hábitat de *C. olivacea*. El valor de idoneidad representa la distribución de probabilidad predicha (en escala logística).

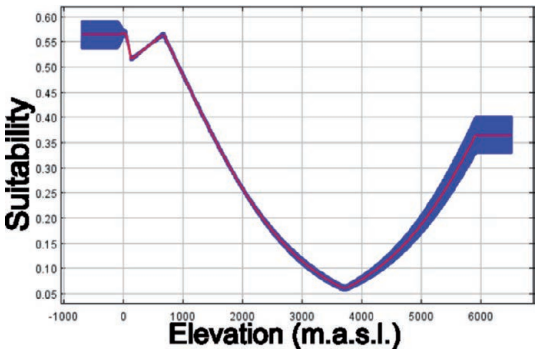


**Fig. S5**. Response curve of the elevation layer in modeling habitat distribution for *C. olivacea*. The suitability value represents the predicted distribution probability (in logistic value).

**Fig. S5.** Curva de respuesta de la capa de elevación al modelar la distribución de hábitat de *C. olivacea*. The suitability value represents the predicted distribution probability (in logistic value).

**Table S1.** GenBank Accession numbers of the sequences used in the tree, voucher numbers, and country of origin.

**Tabla S1.** Números de identificación de GenBank de las secuencias utilizadas en el árbol, números de ejemplar de fungario, y país de origen.

| GenBank | Species | Voucher | Origin |
|---|---|---|---|
| AJ518879 | *Coniophora marmorata* | P158 | Germany |
| AM747518 | *Coniophora olivacea* | MUCL 20566 | Germany |
| AM747520 | *Coniophora olivacea* | 82/34/3 | Norway |
| AM747523 | *Coniophora olivacea* | FP100334 | USA |
| AM747529 | *Coniophora olivacea* | DAOM 216045 | Canada |
| AM747530 | *Coniophora olivacea* | FPL1 | UK |
| AM747533 | *Coniophora olivacea* | MD204 | USA |
| AM946632 | *Coniophora marmorata* | FPRL 410 | UK |
| AM747527 | *Coniophora olivacea* | FP105383 | USA |
| ON832657 | *Coniophora olivacea* | FK16004 | Argentina |
| DQ202271 | *Coniophora arida* | AFTOL-ID 698 | USA |
| FJ790314 | *Coniophora opuntiae* | AH31855 | Spain |
| GU187516 | *Coniophora olivacea* | FP104386 | USA |
| GU187527 | *Leucogyrophana arizonica* | RLG-9902 | USA |
| GU187532 | *Leucogyrophana olivascens* | HHB-11134 | USA |
| HF921467 | *Coniophora fusispora* | 15702Tell | Spain |
| HG326617 | *Coniophora eremophila* | 19021Tell | Spain |
| HG326618 | *Coniophora eremophila* | MAFungi 86372 | Cape Verde |
| MG763873 | *Coniophora hanoiensis* | He5197 | Vietnam |
| MG763874 | *Coniophora hanoiensis* | He5202 | Vietnam |
| MG763875 | *Coniophora arida* | He4658 | Vietnam |
| MW192497 | *Coniophora sp.* | He6920 | Vietnam |
| MW192498 | *Coniophora sp.* | He6926 | Vietnam |
| OL898499 | *Coniophora olivacea* | MUCL 20566 | Germany |
| OM972325 | *Leucogyrophana olivascens* | S.D.Russell 54 | USA |
| GU066829 | *Coniophora puteana* | LMSA1.03.047 | France |
| JQ765680 | *Coniophora puteana* | ISOL01 | Sweden |

**Table S2 (1 of 2).** Source, coordinates, and identity of the specialist who determined the specimen of locations used in niche modeling of *C. olivacea*.

**Tabla S2 (1 de 2).** Fuente, coordenadas e identidad del especialista que determinó los especímenes de las locaciones usadas en el modelado de nicho de *C. olivacea*.

| Source | Identifier | Identified by | Latitude | Longitude |
|---|---|---|---|---|
| GBIF | 2853840061 | N. Nguyen | -43.3667 | -122.0550 |
| GBIF | 2853817742 | Leif Ryvarden | -42.6833 | -95.1651 |
| GBIF | 1803055872 | Larsen, J.M. | -42.3250 | -89.0226 |
| GBIF | 2468717113 | Leif Ryvarden | -37.8167 | -83.5569 |
| GBIF | 2872775370 | Weresub, L.K. | -37.5167 | -83.0383 |
| GBIF | 1929804531 | Cain, R.F. | -36.4931 | -82.8524 |
| GBIF | 78480752 | Weresub, L.K. | -36.4800 | -79.8667 |
| GBIF | 78480725 | Weresub, L.K. | -33.3650 | -75.9713 |
| GBIF | 3110699572 | G. Gruhn | -31.9610 | -52.9281 |
| GBIF | 31921821 | Penteado, VL | -31.9610 | -47.2314 |
| GBIF | 78480990 | M.T.Telleria | -22.4872 | -7.9800 |
| GBIF | 3128717799 | M.T.Telleria | -15.9754 | -7.5600 |
| GBIF | 1046448598 | M.T.Telleria | 8.9713 | -6.8700 |
| GBIF | 1046448588 | S. Pérez Gorjón | 30.2496 | -6.0500 |
| GBIF | 1046448584 | N. Rodríguez Ramos | 37.0300 | -5.7000 |
| GBIF | 78480692 | Pérez-Daniëls, P. | 37.5900 | -4.8209 |
| GBIF | 78480750 | De Esteban J. | 37.7573 | -4.4358 |
| GBIF | 78480751 | M.Dueñas | 37.9300 | -3.6800 |
| GBIF | 2640619325 | Guerra, A. | 37.9700 | -3.4882 |
| GBIF | 2640611323 | M.T.Telleria | 38.5045 | -2.8500 |
| GBIF | 3128711770 | K.Hjortstam | 40.4400 | -2.2900 |
| GBIF | 3128712088 | Riezu J.M. | 40.4400 | -2.1423 |
| GBIF | 3022691275 | Martin J. | 40.4400 | -1.4509 |
| GBIF | 1412705076 | Leif Ryvarden | 40.5900 | -0.6089 |
| GBIF | 3120315712 | Melo & Salcedo | 41.3400 | 4.8144 |
| GBIF | 3119888857 | Leif Ryvarden | 41.4100 | 5.6849 |
| GBIF | 3119941694 | Jean Keller | 41.7449 | 7.0766 |
| GBIF | 3120085534 | Keller Jean | 41.7449 | 7.0820 |
| GBIF | 3120083547 | Mykologische Gesellschaft Luzern | 42.8330 | 8.0603 |
| GBIF | 1935675408 | Tom Hellik Hofton | 43.0205 | 8.1391 |
| GBIF | 2580067375 | Even Høgholen | 43.9667 | 8.2132 |
| GBIF | 1935674992 | Finn Oldervik | 45.5582 | 8.3158 |
| GBIF | 2640622329 | Kilian Mühlebach | 45.8390 | 8.4596 |
| GBIF | 1935675508 | Gian-Felice Lucchini | 45.8390 | 8.5111 |
| GBIF | 2464714773 | Thomas Læssøe | 46.1528 | 8.6163 |
| GBIF | 2464715470 | Geir Gaarder, B. Bredesen | 46.3825 | 8.9995 |
| GBIF | 2464715186 | Eleno Zenone | 46.3838 | 9.0153 |
| GBIF | 3022675674 | Geir Gaarder | 46.9750 | 9.1313 |
| GBIF | 3022678099 | Leif Ryvarden | 47.0853 | 9.3892 |
| GBIF | 3022678092 | Even Høgholen | 47.1264 | 9.4323 |
| GBIF | 125721900 | Even W. Hanssen | 47.1948 | 9.4771 |
| GBIF | 3022691280 | Gaute Mohn Jenssen | 47.3250 | 9.6800 |
| GBIF | 3022711521 | Egil Bendiksen, Klaus Høgholen | 49.0760 | 9.8276 |
| GBIF | 3022710706 | Jan Vesterholt | 49.0760 | 9.9203 |
| GBIF | 3022660912 | Baici & Horak | 49.0760 | 10.2184 |
| GBIF | 3022670965 | Leif Ryvarden | 51.1364 | 10.5434 |
| GBIF | 2332466434 | Egil Bendiksen, Klaus Høgholen | 54.6592 | 10.6756 |
| GBIF | 2592349870 | Leif Ryvarden | 54.6592 | 10.6958 |
| GBIF | 2332386590 | Hofton, Tom H. | 56.0200 | 11.3122 |
| GBIF | 2332484109 | Viacheslav Spirin | 56.0477 | 11.3900 |
| GBIF | 3022678738 | L. Ryvarden | 57.8083 | 11.6876 |
| GBIF | 2332380451 | Leif Ryvarden | 58.0167 | 11.9530 |
| GBIF | 2332484110 | Leif Ryvarden | 58.2670 | 12.0205 |
| GBIF | 2332499532 | Halvor Solheim | 58.2808 | 12.1902 |
| GBIF | 3022677158 | Thomas Læssøe | 59.0407 | 12.5515 |
| GBIF | 2332484140 | Leif Ryvarden | 59.5106 | 13.2995 |
| GBIF | 2332329295 | Leif Ryvarden | 59.6542 | 13.8343 |

**Table S2 (2 of 2).** Source, coordinates, and identity of the specialist who determined the specimen of locations used in niche modeling of *C. olivacea*.

**Tabla S2 (2 de 2).** Fuente, coordenadas e identidad del especialista que determinó los especímenes de las locaciones usadas en el modelado de nicho de *C. olivacea*.

| Source | Identifier | Identified by | Latitude | Longitude |
|---|---|---|---|---|
| GBIF | 2332330958 | Michelitsch Siegmund | 59.6696 | 13.8917 |
| GBIF | 2332484094 | L. Ryvarden | 59.7348 | 13.9566 |
| GBIF | 2332484137 | L. Ryvarden | 59.9492 | 14.4268 |
| GBIF | 2332484088 | Gro Gulden, J. Eriksson | 60.1817 | 15.5935 |
| GBIF | 2332484086 | Gunnar Kristiansen | 60.1879 | 19.7542 |
| GBIF | 2332328417 | Leif Ryvarden | 60.2405 | 21.9905 |
| GBIF | 2332484099 | Leif Ryvarden | 60.5576 | 23.7227 |
| GBIF | 2332484100 | K. Juutilainen | 60.6690 | 24.2320 |
| GBIF | 2332484097 | Erast Parmasto | 60.7622 | 24.7000 |
| GBIF | 3022710206 | Leif Ryvarden | 60.7711 | 24.7060 |
| GBIF | 2332471091 | Kulju, Matti | 60.8157 | 25.0803 |
| GBIF | 2332484085 | Leif Ryvarden | 60.9684 | 25.3705 |
| GBIF | 1052045733 | Erast Parmasto | 61.1078 | 26.0733 |
| GBIF | 2332381834 | Erast Parmasto | 61.1969 | 27.0167 |
| GBIF | 2332382904 | Erast Parmasto | 61.2661 | 27.3217 |
| GBIF | 2332382048 | Moilanen, Aki | 61.2885 | 27.6367 |
| GBIF | 2332484089 | Kulju, Matti | 61.3041 | 27.9667 |
| GBIF | 3460838722 | Kulju, Matti | 61.5546 | 28.4940 |
| GBIF | 2332444819 | Leif Ryvarden | 61.5841 | 28.9949 |
| GBIF | 773226377 | Kulju, Matti | 61.6537 | 29.2642 |
| GBIF | 3460843518 | E.Parmasto | 61.7167 | 29.7911 |
| GBIF | 2332399347 | Lehtonen Hannu | 61.7291 | 30.3716 |
| GBIF | 3441197293 | M. Kirsi | 61.7413 | 30.4114 |
| GBIF | 2332460790 | Viacheslav Spirin scr. | 61.7453 | 35.5262 |
| GBIF | 2991518006 | Alexander Ordynets | 61.7694 | 36.9845 |
| GBIF | 2332445204 | Alexander Ordynets | 63.0420 | 37.8528 |
| GBIF | 3441185087 | Leif Ryvarden | 63.0432 | 38.5651 |
| GBIF | 3022706988 | Erast Parmasto | 63.0842 | 50.7887 |
| GBIF | 3022660067 | Erast Parmasto | 63.1253 | 53.9975 |
| GBIF | 3713361932 | Ain Raitviir | 63.2220 | 55.9065 |
| GBIF | 3107784828 | Erast Parmasto | 63.9944 | 78.5390 |
| GBIF | 2332329461 | Erast Parmasto | 64.0315 | 80.3301 |
| GBIF | 3713366539 | Erast Parmasto | 64.1358 | 87.6215 |
| GBIF | 3022678766 | Erast Parmasto | 64.2939 | 89.3966 |
| GBIF | 3713359652 | Erast Parmasto | 64.6526 | 93.4100 |
| GBIF | 3107787449 | Erast Parmasto | 64.6922 | 93.8500 |
| GBIF | 3460839026 | N.L. Bougher | 64.6922 | 115.8229 |
| GBIF | 2569344336 | Erast Parmasto | 64.7388 | 123.3742 |
| GBIF | 2332484113 | Erast Parmasto | 65.2961 | 124.9180 |
| GBIF | 2332484108 | Leif Ryvarden | 65.4551 | 127.9663 |
| GBIF | 1324376586 | Erast Parmasto | 66.3129 | 134.0667 |
| GBIF | 2332458095 | Erast Parmasto | 66.7660 | 136.5833 |
| GBIF | 2332484111 | Erast Parmasto | 67.8899 | 137.5000 |
| GBIF | 3022678668 | Erast Parmasto | 68.7227 | 142.6847 |
| GenBank | AJ344112 | Olaf Schmidt et al., 2002 | 48.8569 | 2.3513 |
| GenBank | ON832657 | This Article | -42.2181 | -71.4961 |
| GenBank | AM747520 | Kauserud, H. et al., 2007 | 1.635 | 10.8741 |
| GenBank | AJ345009 | Olaf Schmidt et al., 2002 | 48.8409 | 11.4395 |
| GenBank | AM747519 | Kauserud, H. et al., 2007 | 52.5166 | 13.3833 |
| GenBank | AM747527 | Kauserud, H. et al., 2007 | 42.38 | 72.2282 |
| GenBank | GU187516 | Binder, M. et al., 2010 | 39.0276 | 76.9039 |
| GenBank | AM747528 | Kauserud, H. et al., 2007 | 35.5481 | 79.6967 |
| GenBank | AM747526 | Kauserud, H. et al., 2007 | 47.0331 | 109.2266 |
| GenBank | AM747537 | Kauserud, H. et al., 2007 | 34.3131 | 111.1993 |
| GenBank | AM747533 | Kauserud, H. et al., 2007 | 44.0384 | 120.0599 |
| GenBank | AM747531 | Kauserud, H. et al., 2007 | 53.9218 | 122.7267 |

**Table S3.** Contribution of each environmental variable used to predict the potential geographic distribution of *C. olivacea*. The values shown represent the average of 100 replicates. Values in bold indicate higher percent contribution and permutation importance.

**Tabla S3.** Contribución de cada variable ambiental usada para predecir la potencial distribución geográfica de *C. olivacea*. Los valores mostrados representan la media de cien réplicas. Los valores en negrita se corresponden con los mayores porcentajes de contribución e importancia de permutación.

| | Variable | *Coniophora olivacea* |
|---|---|---|
| n | | 100 |
| AUC ± SD | | 0.91 ± 0.09 |
| Percent Contribution (%) | Bio1 | 43.1 |
| | Bio2 | 4.5 |
| | Bio4 | 3.7 |
| | Bio11 | 7.1 |
| | Bio12 | 38.5 |
| | Bio15 | 0.4 |
| | Elv | 2.7 |
| Permutation importance (%) | Bio1 | 78.9 |
| | Bio2 | 0.5 |
| | Bio4 | 8.1 |
| | Bio11 | 7 |
| | Bio12 | 3.7 |
| | Bio15 | 0.9 |
| | Elv | 2.8 |

**Table S4.** Jackknife of regularized training gain for *C. olivacea*. Variable Bio1 contains the most useful information. Without this variable, the gain value decreases dramatically.

**Tabla S4.** Entrenamiento regularizado de ganancia de jackknife para *C. olivacea*. La variable Bio1 contiene la información más relevante. Sin ella, el valor de ganancia disminuye dramáticamente.

| Variable | With only variable | Without variable | With all variables |
|---|---|---|---|
| Bio1 | 0.99 | 1.29 | 1.37 |
| Bio2 | 0.07 | 1.34 | |
| Bio4 | 0.11 | 1.37 | |
| Bio11 | 0.87 | 1.37 | |
| Bio12 | 0.65 | 1.33 | |
| Bio15 | 0.43 | 1.37 | |
| Elv | 0.14 | 1.33 | |