Universidad de Concepción
Dirección de Postgrado
Facultad de Agronomía
Programa de Magíster en Ciencias Agronómicas

INFLUENCIA DE LAS CARACTERÍSTICAS EDAFOCLIMÁTICAS EN EL DESARROLLO Y PROPIEDADES DEL HONGO COMESTIBLE *Morchella* spp. DE LA ZONA CENTRO-SUR DE CHILE

Tesis para optar al grado de Magíster en Ciencias Agronómicas

TATIANA FRANCISCA ESCOBAR HERNÁNDEZ

CHILLÁN-CHILE
2026

Profesora Guía: Ángela Elena Machuca Herrera
Depto. de Cs. y Tecnología Vegetal
Escuela de Ciencias y Tecnologías
Universidad de Concepción

Esta tesis ha sido realizada en el Departamento de Ciencias y Tecnología Vegetal y en el Departamento de Suelos y Recursos Naturales de la Universidad de Concepción.

Profesora Guía

Dra. Ángela Machuca Herrera
Escuela de Ciencias y Tecnologías
Universidad de Concepción

Profesor Co-Guía

Dr. Erick Zagal Venegas
Facultad de Agronomía
Universidad de Concepción

Comisión Evaluadora

Dra. Valeria Velasco Pizarro
Facultad de Agronomía
Universidad de Concepción

Dr. Rodrigo Segura Segura
Facultad de Química y Biología
Universidad de Santiago

Dra. Macarena Gerding González
Facultad de Agronomía
Universidad de Concepción

Directora de Programa

Dra. Marisol Vargas Concha
Facultad de Agronomía
Universidad de Concepción

TABLA DE CONTENIDOS

ÍNDICE DE FIGURAS Y TABLAS

RESUMEN

La fructificación natural de *Morchella* spp. constituye un fenómeno ecológico altamente variable y aun insuficientemente explicado, particularmente en ecosistemas templados del hemisferio sur. Considerando que la ocurrencia de este hongo comestible responde a la interacción jerárquica entre condiciones edáficas, climáticas, estructurales y de perturbación, en este estudio se planteó como hipótesis que el desarrollo, la calidad nutricional y composición mineral de *Morchella* spp. son afectados por las características edafoclimáticas de los sitios donde fructifica en forma natural.

En este contexto, el objetivo general fue evaluar la relación existente entre *Morchella* spp. y las características edafoclimáticas de los hábitats donde fructifica de manera natural, determinando el impacto potencial de estas propiedades en la calidad del recurso fúngico. Para ello, se desarrolló un estudio en cuatro sitios representativos (36°50′–37°50′ S), que incluyeron plantaciones forestales afectadas por disturbios severos (incendio forestal y cosecha mecanizada) y relictos de bosque nativo estructuralmente estables, establecidos sobre suelos de origen granítico y volcánico.

A escala de paisaje y micrositio, se caracterizaron variables climáticas mensuales durante una ventana temporal de 25 meses centrada en el evento de fructificación, junto con propiedades físicas, químicas y biológicas del suelo, y atributos estructurales de la vegetación. Los datos fueron integrados mediante

enfoques multivariados, principalmente análisis de componentes principales (PCA), con el fin de identificar gradientes ambientales asociados a la presencia y ausencia de fructificación, así como diferencias entre ambientes y especies.

Los resultados demostraron que la fructificación de *Morchella* spp. ocurre de manera consistente dentro de una ventana climática acotada, caracterizada por temperaturas moderadas del suelo, incremento de la precipitación acumulada y alta humedad relativa, confirmando el rol de la sincronización climática como gatillante del evento reproductivo. En contraste, las propiedades edáficas presentaron una amplia superposición funcional entre sitios con y sin fructificación, sin una separación multivariada consistente, lo que respalda la hipótesis de que el suelo actúa como un marco ambiental predisponente, pero no como un factor determinante de la ocurrencia anual del evento.

A escala de micrositio, el régimen de perturbación y la estructura de la vegetación emergieron como factores clave en la diferenciación de los ambientes de fructificación, condicionando la ocurrencia y composición específica de *Morchella*. Los ambientes severamente perturbados se asociaron a especies oportunistas de fructificación temprana (*M. eximia* y *M. importuna*), mientras que los bosques nativos estructuralmente estables favorecieron especies de fructificación tardía (*M. tridentina* y *M. andinensis*), en concordancia con los objetivos específicos planteados.

Finalmente, el análisis de atributos de calidad de los cuerpos de fructificación, incluyendo composición proximal, contenido mineral, compuestos fenólicos y actividad antioxidante, evidenció diferencias consistentes entre especies y tipos de cobertura forestal, cumpliendo el objetivo de evaluar cómo el ambiente de fructificación influye en la calidad nutricional y funcional del recurso.

Los resultados validan la hipótesis planteada y permiten proponer un modelo conceptual integrado en el que el suelo y el clima definen la idoneidad ambiental de base, el disturbio modula la ocurrencia y diversidad específica, y la sincronización climática desencadena la fructificación de *Morchella* spp. Esta investigación aporta evidencia relevante sobre la ecología de *Morchella* spp. en ecosistemas templados de Sudamérica y establece una base científica para su manejo sustentable y conservación como recurso forestal no maderero.

SUMMARY

The natural fruiting of *Morchella* spp. is a highly variable and still insufficiently explained ecological phenomenon, particularly in temperate ecosystems in the southern hemisphere. Considering that the occurrence of this edible fungus responds to the hierarchical interaction between edaphic, climatic, structural, and disturbance conditions, this study hypothesized that the development, nutritional quality, and mineral composition of *Morchella* spp. are affected by the edaphic and climatic characteristics of the sites where it fruits naturally.

In this context, the overall objective was to evaluate the relationship between *Morchella* spp. and the edaphoclimatic characteristics of the habitats where it naturally fruits, determining the potential impact of these properties on the quality of the fungal resource. To this end, a study was conducted at four representative sites (36°50′–37°50′ S), which included forest plantations affected by severe disturbances (forest fire and mechanized harvesting) and structurally stable remnants of native forest, established on soils of granitic and volcanic origin.

At both landscape and microsite scales, monthly climatic variables were characterized over a 25-month temporal window centered on the fructification event, together with the physical, chemical, and biological properties of the soil, as well as structural attributes of the vegetation. The data were integrated using multivariate approaches, primarily principal component analysis (PCA), in order to identify environmental gradients associated with the presence and absence of fructification, as well as differences among environments and species.

The results demonstrated that *Morchella* spp. fructification occurs consistently within a restricted climatic window characterized by moderate soil temperatures, increased cumulative precipitation, and high relative humidity, confirming the role of climatic synchronization as the trigger of the reproductive event. In contrast, edaphic properties exhibited a broad functional overlap between sites with and without fructification, without a consistent multivariate separation, supporting the hypothesis that soil acts as a predisposing environmental framework rather than as a determining factor for the annual occurrence of fructification.

At the microsite scale, disturbance regime and vegetation structure emerged as key factors differentiating fruiting environments, conditioning both the occurrence and species composition of *Morchella*. Severely disturbed environments were associated with early-fruiting opportunistic species (*M. eximia* and *M. importuna*), whereas structurally stable native forests favored late-fruiting species (*M. tridentina* and *M. andinensis*), in agreement with the specific objectives proposed.

Finally, the analysis of ascocarp quality traits, including proximate composition, mineral content, phenolic compounds, and antioxidant activity, revealed consistent differences among species and forest cover types, fulfilling the objective of evaluating how the fruiting environment influences the nutritional and functional quality of the resource.

Overall, the results validate the proposed hypothesis and support an integrated conceptual model in which soil and climate define baseline environmental suitability, disturbance modulates species occurrence and diversity, and climatic synchronization triggers the fructification of *Morchella* spp. This research provides relevant ecological evidence on *Morchella* spp. in temperate ecosystems of South America and establishes a scientific basis for its sustainable management and conservation as a non-timber forest resource.

CAPÍTULO 1. *INTRODUCCIÓN GENERAL*

Morchella (nombre común). es un hongo comestible con una taxonomía compleja, debido a la diversidad de sinonimias y las constantes actualizaciones en la filogenia del género. A través de análisis moleculares multigénicos, se ha determinado que Morchella es un género con una amplia diversidad de especies, clasificadas en tres clados principales: Rufobrunnea, Esculenta y Elata (Loizides, 2017). Perteneciente a la división Ascomycota, este género es morfológicamente fácil de reconocer y diferenciable de otros hongos. Sin embargo, a pesar de los avances en los estudios filogenéticos y taxonómicos, la identificación morfológica de las especies sigue siendo un desafío debido al considerable polimorfismo, lo que ha generado controversias entre especialistas (Masaphy et al., 2010; McFarkane et al., 2005; Martinez & Gea, 2022).

El uso de morchella en la cocina gourmet ha incrementado su valor económico, situándola entre los hongos más apreciados después de las trufas (género Tuber), tanto por sus propiedades organolépticas, nutricionales como medicinales (Wu et al., 2022). En 2021, el valor de exportación mundial de morchella alcanzó los 9.600 millones de dólares, con China como el mayor exportador (Li et al., 2023). Aunque se ha documentado un cultivo artificial extensivo de morchella negra en China (16.500 ha cultivadas), las estrategias implementadas para su domesticación no han logrado una productividad estable debido a diversos factores bióticos y abióticos aún no identificados completamente (Tan et al., 2021; Wei-Ye et al., 2022; Yu et al., 2022; Zhang et al., 2023). Como resultado, la recolección del producto silvestre sigue siendo la principal fuente de obtención de morchella a nivel global, dada la imprevisibilidad y las limitaciones del cultivo artificial.

Morchella se desarrolla en nichos ecológicos específicos en regiones templadas, bajo condiciones ambientales aún no completamente identificadas (Hussain & Sher, 2021). Estos hongos ascomicetos, de crecimiento silvestre y estacional, presentan una ecología aún incierta (Larson et al., 2016; McFarlane et al., 2005). Aunque se creía que todas las especies eran saprobiontes, actualmente se reconoce una relación simbiótica con las raíces de ciertos árboles, con estructuras similares a micorrizas (Dahlstrom et al., 2000; Loizides, 2017), sugiriéndose incluso la coexistencia de ambos hábitos tróficos en una misma especie (Pilz, 2007).

En Chile, morchella se encuentra desde zonas cordilleranas hasta áreas costeras, desde la región de Valparaíso (Spegazzini, 1921) hasta la Patagonia (Gamundi, 1975). Su fructificación en algunas regiones está asociada con bosques de *Nothofagus* spp., aunque también se encuentra en terrenos perturbados, como aquellos recientemente quemados (Moreno et al., 2013; Sanz, 2022; Sanz-Rocha et al., 2023). En el centro-sur de Chile, estos hongos tienen un papel significativo para las comunidades recolectoras, debido a su alto valor comercial como producto forestal no maderero, con la mayoría de este producto destinado a la exportación, principalmente hacia Europa (Machuca et al., 2021).

Morchella puede crecer en una variedad de hábitats, desde bosques nativos prístinos hasta áreas altamente perturbadas como suelos post-incendio o post-cosecha, jardines y zonas urbanas (Masaphy & Zabari, 2013; Machuca et al., 2021; Pfister et al., 2022; Sandoval, 2017; Sanz-Rocha et al., 2023). Su ciclo de vida se desarrolla mayoritariamente en el suelo, desde el crecimiento del micelio y la formación de primordios hasta el desarrollo de los ascocarpos (Li et al., 2023). Este entorno es complejo, con gran variabilidad en sus propiedades físicas, químicas y biológicas (Aleklett et al., 2018), lo que implica que múltiples factores ambientales y edáficos influyen en su desarrollo. La identificación de diferentes roles tróficos dentro del género también complica la comprensión de los mecanismos de asimilación de nutrientes necesarios para completar su ciclo de vida y fructificación (Liu et al., 2018).

Algunas especies de *Morchella* son pioneras en la colonización de ambientes post-incendio, con una producción significativa durante el primer año tras el evento, aunque los factores desencadenantes de esta estimulación aún no se comprenden completamente (Baynes et al., 2012; Larson et al., 2016; Masaphy & Zabari, 2013). Los efectos del fuego en el suelo varían y, según su intensidad, pueden provocar la degradación del ecosistema y alterar sus propiedades, siendo las biológicas las más sensibles a la perturbación (Filialuna & Cripps, 2021;

Garrido-Ruiz et al., 2022). Se ha observado una prolífica fructificación tras estos disturbios, y los hongos de estos entornos representan un volumen considerable del consumo total. En Chile, después de los megaincendios de 2017, el volumen de exportación de morchella aumentó a 124 toneladas (Instituto Forestal, 2020; Sanz, 2022).

Una preocupación importante sobre las morchella recolectadas en ambientes perturbados es su inocuidad. La industrialización y los incendios han incrementado la concentración de metales potencialmente tóxicos en el suelo, lo que plantea una potencial amenaza a la seguridad alimentaria, dado que estos elementos no son degradables y se acumulan en el suelo, afectando a plantas y hongos (Barrio, 2017). Así, pueden entrar en la cadena trófica y, en altas concentraciones, causar problemas de salud significativos (Badshah et al., 2023a).

El contenido nutricional y mineral de los hongos depende en gran medida de las condiciones ambientales en que se desarrollan (Gómez et al., 2019; Xu et al., 2021). Algunas especies de Morchella tienen predisposición a acumular elementos metálicos y otros elementos, lo que sugiere una estrecha relación entre el contenido mineral del suelo y los cuerpos fructíferos (Alaimo et al., 2019; Badshah et al., 2023a; Badshah et al., 2023b; Li et al., 2023). No obstante, las investigaciones al respecto se han centrado principalmente en el hemisferio norte y en especies que aún no han sido descritas en Chile, sin considerar las características ambientales locales como un factor de estudio. Esto genera preguntas sobre si las condiciones edafoclimáticas, en ambientes perturbados y no perturbados, influyen en el desarrollo y la calidad de morchella recolectada en estos diferentes entornos (Li et al., 2023; Masaphy & Zabari, 2013).

La ecología de *Morchella* spp. presenta numerosos desafíos investigativos, con muchas incógnitas aún por resolver que limitan su manejo en campo y producción en condiciones controladas (Zhang et al., 2023). En años recientes, la investigación se ha enfocado principalmente en los suelos de sistemas productivos artificiales, con poca información sobre los suelos donde el hongo crece de forma natural. Esto representa una oportunidad para monitorear su desarrollo de manera integral y generar conocimientos fundamentales para un manejo sustentable y la posible domesticación del recurso (Manikandan et al., 2011; Orlofsky et al., 2021). Por lo tanto, el estudio de los ambientes de fructificación natural de morchella es crucial para comprender su ecología y desarrollar prácticas de manejo en campo, así como para explorar su domesticación en sistemas artificiales, integrando diversos factores de manera holística. Esta investigación es esencial tanto para el avance científico en el género *Morchella* como para la gestión sostenible de este valioso recurso y su importancia para las comunidades locales.

HIPÓTESIS

El desarrollo, la calidad nutricional y composición mineral de *Morchella* spp. son afectados por las características edafoclimáticas de los sitios donde fructifica en forma natural.

OBJETIVO GENERAL

Evaluar la relación existente entre *Morchella* spp. y las características edafoclimáticas de los hábitats donde fructifica de manera natural, determinando el impacto potencial de estas propiedades en la calidad del recurso fúngico.

OBJETIVOS ESPECÍFICOS

1. Caracterizar las propiedades edafoclimáticas de los hábitats donde *Morchella* spp. fructifica en ambientes perturbados y no perturbados.

2. Analizar las propiedades nutricionales y contenido mineral de *Morchella* spp. procedente de ambientes perturbados y no perturbados.

3. Relacionar las características edafoclimáticas con el desarrollo de *Morchella* spp. y con los contenidos nutricionales y minerales.

REFERENCIAS

Aleklett, K., Kiers, E. T., Ohlsson, P., Shimizu, T. S., Caldas, V. E., & Hammer, E. C. (2018). Build your own soil: exploring microfluidics to create microbial habitat structures. *The ISME journal*, *12*(2).

Alaimo, M. G., Saitta, A., & Ambrosio, E. (2019). Bedrock and soil geochemistry influence the content of chemical elements in wild edible mushrooms (Morchella group) from South Italy (Sicily). *Acta Mycologica*, *54*(1), 1122. https://doi.org/10.5586/am.1122.

Badshah, H., Khan, M., & Mumtaz, A. (2023a). Elucidating heavy metals concentration and distribution in wild edible morels and the associated soil at different altitudinal zones of Pakistan: a hearth risk implications study. *Biological Trace Element Research*, *201*(8), 4177–4190. http://doi.org/10.1007/s12011-022-03496-w.

Badshah, H., Nisa, S.U., Ali, M.A., Alwahibi, M.S., Kamal, A., Kaleem, M., Khan, A., Khan, S.M. & Mumtaz, A.S. (2023b). Bio-Concentration and Influence of Environmental Factors on Accumulation of Heavy Metals in Edible Autumn Morel (*Morchella galilaea*) of Low Elevation. *Metals*, *13*(3), 472. https://doi.org/10.3390/met13030472.

Barrio, N. (2017). Metales pesados en suelos y sus efectos sobre la salud. Universidad Complutense.

Baynes, M., Newcombe, G., Dixon, L. & Castlebury, L. (2012). A novel plant-fungal mutualism associated with fire. *Fungal Biology, 116*: 133-144.

Dahlstrom, J. L., Smith, J.E., & Weber, N.S. (2000). Mycorrhiza-like interaction by Morchella with species of the Pinaceae in pure culture synthesis. *Mycorrhiza*, *9*(5), 279-285. https://doi.org/10.1007/s005720000072.

Filialuna, O. & Cripps, C. (2021). Evidence that pyrophilus fungi aggregate soil after fire forest. *Forest Ecology and Management* 498.

Gamundí, I. J. (1975). Fungi, ascomycetes: Pezizales (Flora criptogámica de Tierra del Fuego, Vol. X–3). *Fundación para la Educación, la Ciencia y la Cultura.*

Garrido-Ruiz, C., Sandoval, M., Stolpe, N., & Sanchez-Hernandez, J. C. (2022). Fire impacts on soil and post fire emergency stabilization treatments in Mediterranean-climate regions. Chilean Journal of Agricultural Research, 82(2), 335–350. http://dx.doi.org/10.4067/S0718-58392022000200335.

Gómez, L., Martinez, N., Enríquez, I., Garza, F., Najera, J. & Quiñónez, M. (2019). Análisis proximal y de composición mineral de cuatro especies de hongos ectomicorrízicos silvestres de la Sierra Tarahumara de Chihuahua. *Revista Especializada en Ciencias Químico-Biológicas*, *22*.

Hussain, S., & Sher, H. (2021). Ecological characterization of Morel (*Morchella* spp.) habitats: A multivariate comparison from three forest types of district Swat, Pakistan. *Acta Ecologica Sinica*, *41*(1), 1–9. https://doi.org/10.1016/j.chnaes.2020.10.007.

Instituto Forestal. (2020). Boletín de exportaciones de productos forestales no madereros (N.º 35). Ministerio de Agricultura.

Larson, A. J., Cansler, C. A., Cowdery, S. G., Hiebert, S., Furniss, T. J., Swanson, M. E., & Lutz, J. A. (2016). Post-fire morel (*Morchella*) mushroom abundance, spatial structure, and harvest sustainability. *Forest Ecology and Management*, *377*, 16–25. https://doi.org/10.1016/j.foreco.2016.06.038.

Li, X., Fu, T., Li, H., Zhang, B., Li, W., Zhang, B., Wang, X., Wang, J., Chen, Q., He, X., Chen, H., Zhang, Q., Zhang, Y., Yang, R., & Peng, Y. (2023). Safe

Production Strategies for Soil-Covered Cultivation of Morel in Heavy Metal-Contaminated Soils. *Journal of Fungi, 9*(7), Article 765. https://doi.org/10.3390/jof9070765.

Liu, Q., Ma, H., Zhang, Y., & Dong, C. (2018). Artificial cultivation of true morels: current state, issues and perspectives. *Critical Reviews in Biotechnology*, *38*(2), 259–271. https://doi.org/10.1080/07388551.2017.1333082.

Loizides, M. (2017). Morels: The story so far. *Field Mycology*, *18*(2), 42–53. https://doi.org/10.1016/j.fldmyc.2017.04.004.

Machuca, A., Gerding, M., Chávez, D., Palfner, G., Oyarzúa, P., Guillén, Y., & Córdova, C. (2021). Two New Species of Morchella from Nothofagus Forests in Northwestern Patagonia (Chile). *Mycological Progress*, *20*(6), 781–795. https://doi.org/10.1007/s11557-021-01703-x.

Manikandan, K., Sharma, V., Kumar, S., Kemal, S. & Shirur, M. (2011). Edaphic conditions of natural sites of Morchella and Phellorinia. *Mushroom Research* 20(2): 117-120.

Martinez, J. & Gea, F. (2022). Contribución al conocimiento del género Morchella Dill ex Pers.: Fr. en la provincia de Albacete y áreas próximas. *Sabuco: Revista de Estudios Albacetenses, 16*, 103-130.

Masaphy, S., & Zabari, L. (2013). Observations on post-fire black morel ascocarp development in an Israeli burnt forest site and their preferred micro-sites. *Fungal Ecology*, *6*(3), 316–318. https://doi.org/10.1016/j.funeco.2013.02.005.

Masaphy, S., Zabari, L., Goldberg, D., & Jander-Shagug, G. (2010). The complexity of Morchella systematics: a case of the yellow morel from Israel. *Fungi*, *3*(2), 14-18.

McFarlane, E., Pilz, D. & Weber, N. (2005). High-elevation gray morels and other Morchella species harvested as non-timber forest products in Idaho and Montana. *Mycologist*, *19*(2), 62–68. https://doi.org/10.1017/S0269-915X(05)00203-X.

Moreno, N., Esse, C., Donoso, G., Betancourt, O., Medina, L. & Vivallo, G. (2013). Propuesta metodológica para el estudio de los factores agroecológicos que influyen en la fructificación de Morchella spp. una revisión. *Micobotánica-Jaén*, *1*.

Orlofsky, E., Zabari, L., Bonito, G., & Masaphy, S. (2021). Changes in soil bacteria functional ecology associated with Morchella rufobrunnea fruiting in a natural habitat. *Environmental Microbiology, 23*(11), 6651–6662. https://doi.org/10.1111/1462-2920.15692

Pfister, D. H., Healy, R., LoBuglio, K. F., Furci, G., Mitchell, J., & Smith, M. E. (2022). South American morels in the Elata group: mitosporic states, distributions, and commentary. *Mycological Progress*, *21*, 97. https://doi.org/10.1007/s11557-022-01846-5.

Pilz, D., McLain, R., Alexander, S., Villarreal-Ruiz, L., Berch, S., Wurtz, T. L., Parks, C. G., McFarlane, E., Baker, B., Molina, R., & Smith, J. E. (2007). Ecology and management of morels harvested from the forests of western North America (General Technical Report PNW-GTR-710). U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. https://doi.org/10.2737/PNW-GTR-710

Sandoval L. (2017). Identificación molecular de especies del hongo comestible Morchella spp. colectadas en las regiones del BioBío, Araucanía y Aysén. Tesis, Universidad de Concepción.

Sanz M. (2022). Factibilidad de domesticación de genotipos de Morchella autóctonos del centro-sur de Chile. Tesis de Magister, Universidad de Concepción.

Sanz-Rocha, M., Gerding, M, Quezada, T, Vargas, M, Chávez, D., & Machuca, A. (2023). Molecular and cultural characterization of *Morchella* spp. from disturbed environments of central-southern Chile. *Fungal Biology, 127*(3), 938-948. https://doi.org/10.1016/j.funbio.2023.01.009.

Spegazzini, C. (1921) Mycetes Chilensis. Boletín de la Academia Nacional de Ciencias, Córdoba 25: 1-24.

Tan, H., Yu, Y., Tang, J., Liu, T., Miao, R., Huang, Z., Martin, FM., y Peng, W. (2021). Build Your Own Mushroom Soil: Microbiota Succession and Nutritional Accumulation in Semi-Synthetic Substratum Drive the Fructification of a Soil-Saprotrophic Morel. *Frontiers in Microbiology*, 12.

Wei-Ye, L., Hong-Bo, G., Ke-Xing, B., Alekseevna, S., Xiao-Jian, Q. y Xiao-Dan, Y. (2022). Determining why continuous cropping reduced the production of the morel *Morchella sextelata*. *Frontiers in Microbiology 13*.

Wu, H., Chen, J., Liu, Y., Cheng, H., Nan, J., Park, H.J., Yang, L., & Li, J. (2023), Digestion profile, antioxidant, and antidiabetic capacity of *Morchella esculenta* exopolysaccharide: in vitro, in vivo and microbiota analysis. *Journal of the Science of Food and Agriculture*, *103*(9), 4401-4412. https://doi.org/10.1002/jsfa.12513.

Xu, H., Xie, Z., Guo, J., & Men, Q. (2021). Morphological changes and bioaccumulation in response to cadmium exposure in *Morchella spongiola*, a fungus with potencial for detoxification. *Canadian Journal Microbiology*, *67*(11), 789-798. https://doi.org/10.1139/cjm-2020-057.

Yu, F., Jayawardena, R., Thongklang, N., Lv, M., Zhu, X. y Zhao, Q. (2022). Morel production associated with soil nitrogen-fixing and nitrifying microorganisms. *Journal of Fungi*, *8*, 299.

Zhang, Y., Sun, S., Luo, D., Mao, P., Rosazlina, R., Martin, F. & Xu, L. (2023). Decline in Morel Production upon Continuous Cropping Is Related to Changes in Soil Mycobiome. Journal of Fungi, 9(4), 492. https://doi.org/10.3390/jof9040492.

CAPÍTULO 2. *AMBIENTES DE FRUCTIFICACIÓN NATURAL DE Morchella spp. EN LA ZONA CENTRO-SUR DE CHILE: UNA APROXIMACIÓN EDAFOCLIMÁTICA A ESCALA DE PAISAJE Y MICROSITIO.*

Escobar-Hernández, T.[1,2], Zagal, E.[3], Muñoz-Espinoza, C.[4], Ortiz, J.[3], Gerding, M.[4], Segura, R.[5], Velasco, V.[6], Chávez, D.[2], Machuca, Á[2]*.

[1] Programa de Magister en Ciencias Agronómicas, Facultad de Agronomía, Universidad de Concepción, Campus Chillán, Chile.

[2] Departamento de Ciencias y Tecnología Vegetal, Universidad de Concepción, Campus Los Ángeles, Chile.

[3] Departamento de Suelos y Recursos Naturales, Facultad de Agronomía, Universidad de Concepción, Campus Chillán, Chile.

[4] Departamento de Producción Vegetal, Facultad de Agronomía, Universidad de Concepción, Campus Chillán, Chile.

[5] Departamento de Química de los Materiales, Facultad de Química y Biología, Universidad de Santiago de Chile, Chile.

[6] Departamento de Producción Animal, Facultad de Agronomía, Universidad de Concepción, Campus Chillán, Chile.

[*] angmachu@udec.cl

Artículo para enviar a la revista Forestry.

ABSTRACT

Morchella species are among the most economically valuable wild edible mushrooms worldwide. However, the environmental drivers that regulate their natural fructification remain poorly understood, particularly in ecosystems of Southern Hemisphere. This exploratory study aimed to characterize the climatic, edaphic, and vegetation conditions associated with the natural fructification of Morchella spp. in south-central Chile across contrasting environments. Four study sites were selected along a latitudinal gradient (36°50′–37°50′ S), including post-fire and post-logging forest plantations and relic native forests developed on granitic and volcanic soils. Monthly climatic variables were analyzed over a 25-month window centered on the fructification event using principal component analysis (PCA), while soil physical, chemical, and biological properties were evaluated through multivariate approaches. Climatic PCA revealed that fructification occurred within a restricted climatic window characterized by moderate soil temperatures, increased cumulative precipitation, and high relative humidity, consistently across sites. In contrast, soil PCA indicated broad functional overlap between sites with and without fructification. This, suggest that edaphic properties act as a predisposing environmental framework rather than as direct triggers of annual fruiting. Disturbance regime and vegetation structure emerged as key microsite-level modulators, differentiating severely disturbed environments associated with early-fruiting opportunistic species (*M. eximia* and *M. importuna*) from structurally stable native forests supporting later-fruiting species (*M. tridentina* and *M. andinensis*). Overall, these results support a conceptual model in which soil and climate define baseline habitat suitability, disturbance determines species-specific occurrence, and short-term climatic synchronization triggers fructification. This study provides novel ecological insights into *Morchella* spp. fruiting dynamics in temperate South American ecosystems and establishes an empirical foundation for future research and sustainable management of this non-timber forest resource.

Keywords: Wild edible mushrooms; morel ecology; soil properties; climate variability; forest disturbance; soil–climate interactions.

1. INTRODUCCIÓN

Morchella es un género de hongos comestibles silvestres de alto valor económico y ecológico, ampliamente distribuido en regiones templadas del mundo. A pesar de los avances recientes en su clasificación filogenética gracias al uso de herramientas moleculares (Loizides, 2017), su taxonomía continúa siendo compleja, debido al elevado polimorfismo existente dentro del género. Adicionalmente, existe desconocimiento sobre los hábitos tróficos de las especies de *Morchella*, lo que dificulta la comprensión de su ecología (Masaphy et al., 2010; Martínez & Gea, 2022; McFarlane et al., 2005). Tradicionalmente considerado un hongo saprobio, morchella (nombre común) también ha sido descrito como potencialmente micorrícico en asociación con raíces de árboles leñosos (Dahlstrom et al., 2000; Loizides, 2017; Pilz et al., 2007), e incluso con un posible comportamiento endofítico (Baynes et al. 2012), lo que sugiere una notable plasticidad ecológica aún no completamente esclarecida.

A nivel global, la fructificación natural de morchella ha sido registrada en una amplia diversidad de ambientes, que incluyen bosques nativos y plantaciones forestales, suelos agrícolas, huertos frutales, parques urbanos, jardines, bordes de caminos e incluso áreas sin cobertura vegetal aparente (Hussain & Sher, 2021; Manikandan et al., 2011; Masaphy, 2011). Asimismo, su presencia ha sido documentada tanto en ecosistemas prístinos como en sitios altamente perturbados, tales como suelos post-incendios, áreas sometidas a cosecha forestal o disturbios antrópicos recientes (Masaphy & Zabari, 2013; Pfister et al., 2022; Sanz-Rocha et al., 2023). Esta amplitud de ambientes sugiere una elevada plasticidad ecológica del género y, al mismo tiempo, plantea la hipótesis de una posible especificidad especie–hábitat, donde distintas especies de *Morchella* podrían responder diferencialmente a condiciones edáficas, climáticas y de vegetación particulares.

En Chile, la fructificación de morchella de forma natural ha sido descrita desde la región de Valparaíso hasta la Patagonia (Gamundi, 1975; Spegazzini, 1921), siendo frecuente en bosques dominados por especies del género *Nothofagus* y en terrenos alterados por disturbios recientes, tanto naturales como antrópicos (Moreno et al., 2013; Sanz, 2022). Sin embargo, existen registros informales de fructificación en la zona norte de Chile (región de Arica y Parinacota). Este contexto adquiere especial relevancia biogeográfica, dado que el país alberga especies posiblemente endémicas del género (Machuca et al. 2021) y representa uno de los límites más australes conocidos para la fructificación natural de morchella a nivel mundial. La coexistencia de especies autóctonas, junto con la ocurrencia de eventos reproductivos en ambientes contrastantes, posiciona a los ecosistemas templados del sur de Chile como un escenario clave para comprender la ecología, diferenciación ambiental y potencial adaptación de este género.

Debido a su elevado valor gastronómico, la recolección de morchella constituye una actividad económica significativa para comunidades rurales del centro-sur del país, donde el recurso se destina casi en su totalidad a la exportación (INFOR, 2024; Machuca et al., 2021). Sin embargo, a pesar de su importancia ecológica, económica y biogeográfica, la caracterización de los distintos tipos de hábitats y de los factores edafoclimáticos que regulan su desarrollo en ambientes naturales de Chile ha sido escasamente abordada, particularmente en relación con el rol de los disturbios y su vínculo con la ocurrencia de especies específicas.

La mayor parte de las investigaciones recientes se ha concentrado en sistemas productivos artificiales de morchella en el hemisferio norte (Zhang et al., 2023), existiendo un marcado vacío de conocimiento respecto a los ambientes de fructificación natural, especialmente en ecosistemas australes (Li et al., 2023). Comprender cómo las condiciones físicas, químicas y biológicas del suelo, la vegetación asociada, el microclima y el régimen de perturbación interactúan para favorecer la fructificación de morchella resulta clave para avanzar en el entendimiento de su ecología, establecer estrategias de manejo sostenible en campo y generar bases científicas para su eventual domesticación (Liu et al., 2018; Manikandan et al., 2011; Orlofsky et al., 2021).

En este contexto, el presente estudio busca contribuir al conocimiento de la ecología de *Morchella* spp. en ambientes naturales de la zona centro-sur de Chile, evaluando la influencia integrada de factores edáficos, climáticos, vegetacionales y de perturbación antrópica sobre la distribución, la fructificación natural y la ocurrencia de especies del género, aportando antecedentes fundamentales para el aprovechamiento sustentable de este valioso recurso forestal no maderero.

2. MATERIALES Y MÉTODOS

2.1 Sitios de estudio

Esta investigación se desarrolló entre los meses de agosto y noviembre del año 2023, en las regiones administrativas de Ñuble, Biobío y La Araucanía, abarcando un rango latitudinal comprendido entre los 36°50' y 37°50' S, en la zona centro-sur de Chile. La investigación abarcó tres unidades geomorfológicas: precordillera andina, depresión intermedia y precordillera de la costa (Nahuelbuta), considerando suelos de origen volcánico y granítico distribuidos entre los 137 y 955 m a.s.l. (Table 1).

Dentro de estas regiones se seleccionaron cuatro sitios representativos de la fructificación natural de *Morchella* spp., con el objetivo de capturar la variabilidad ambiental (Figure 1). Dos de los sitios presentan cobertura predominante de bosque nativo, dominado por especies del género *Nothofagus*, mientras que los otros dos corresponden a plantaciones forestales de *Pinus radiata* afectadas por fuego o cosecha. Estos contrastes en tipo de vegetación y condiciones edáficas permiten evaluar la influencia de distintos factores ecológicos sobre la distribución y fructificación natural de morchella.

Table 1. General characteristics of the study sites where morels fruit naturally in south-central Chile.

Site	Administrative region	Gegraphical coordinates	Altitude (m a.s.l)	Physiographic unit	Soil parent material	Predominant land use
Cerro Cayumanqui	Ñuble	36°44'41.11"S 72°34'16.17"O	512	Central depression	Granitic	Burnt forest plantation (*P. radiata*)
Huaqui	Biobío	37°22'9.32"S 72°38'15.43"O	137	Central depression	Volcanic	Logged forest plantation (*P. radiata*)
Peralillo	Biobío	37°23'39.30"S 71°48'32.72"O	621	Andean foothills	Volcanic	Native forest relic (*Nothofagus spp.*)
Cerro Pelado	La Araucanía	37°50'52.58"S 72°53'6.98"O	955	Coastal foothills	Granitic	Native forest relic (*Nothofagus spp.*)

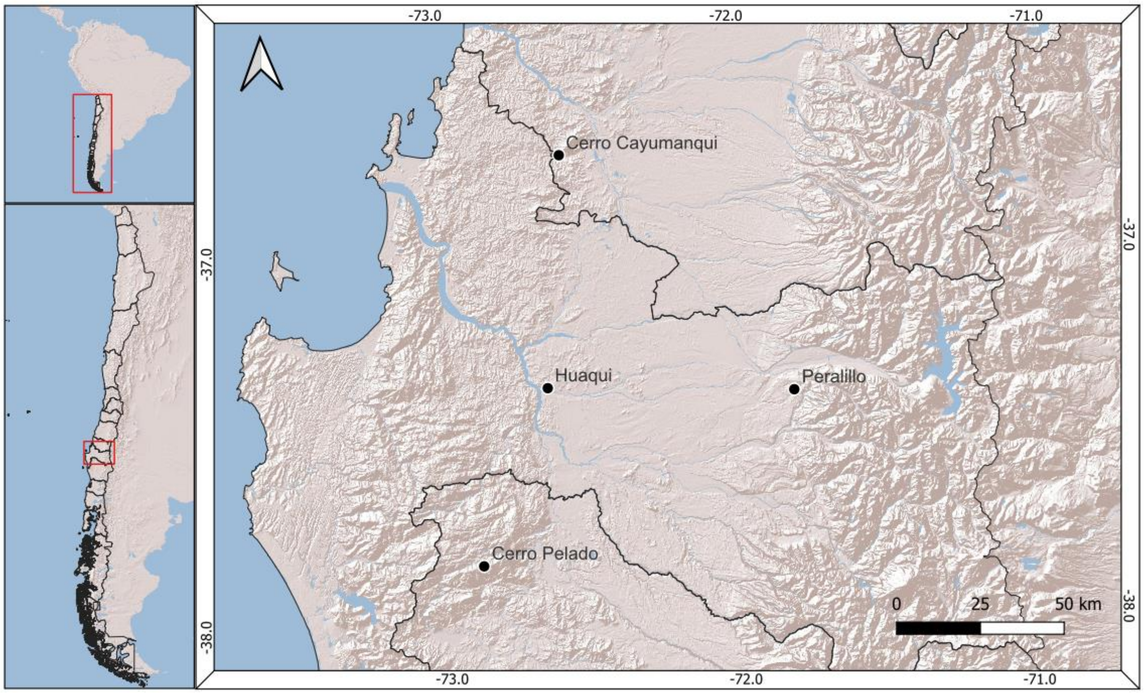

Figure 1. Geographical location of study sites where morels fruit naturally in south-central Chile. The main map shows the locations of the four study sites (Cerro Cayumanqui, Huaqui, Peralillo, and Cerro Pelado), and the red inset boxes show their relative positions on a national and regional scales. Black dots represent the study sites, and lines correspond to regional administrative boundaries.

En cada uno de los sitios de estudio se realizó un análisis ambiental a escala de paisaje, complementado con una evaluación detallada a escala de micrositio, considerando parcelas circulares de 250 m². A nivel de micrositio, se evaluaron de manera integrada las condiciones ambientales asociadas a la fructificación natural de *Morchella* spp., incluyendo variables climáticas mensuales, propiedades edáficas y la composición de la vegetación, con énfasis en la cobertura vegetal y la acumulación de hojarasca. Asimismo, se incorporó la identidad taxonómica y molecular de las especies de *Morchella* y temporalidad de su fructificación. Adicionalmente, se caracterizó el tipo y grado de perturbación antrópica dominante en cada sitio.

2.2 Recolección y análisis de datos meteorológicos

Los registros climáticos para los diferentes sitios de fructificación de morchella fueron obtenidos de estaciones automáticas de la red agroclimática del Instituto de Investigaciones Agropecuarias (INIA) y de la Dirección Meteorológica de Chile, ubicadas en las proximidades de los sitios de estudio. La información fue estandarizada a una base mensual y validada para detectar valores atípicos o faltantes. El análisis consideró la construcción de series temporales por sitio, abarcando un total de 25 meses: 12 meses previos a la fructificación, el mes de fructificación y 12 meses posteriores. Las variables climáticas consideradas incluyeron: temperatura del aire, temperatura del suelo (superficial y subsuperficial a 10 cm), humedad relativa, precipitación, radiación solar, presión atmosférica, número de días con heladas y horas acumuladas de helada.

2.3 Inventario vegetacional y evaluación estructural

Para cada sitio se realizó un inventario florístico mediante un muestreo dirigido basado en la presencia de morchella. Se establecieron parcelas circulares de 250 m^2 ($r = 8.92$ m), considerando como punto central el lugar de fructificación. La vegetación se clasificó en tres estratos: arbóreo, arbustivo y herbáceo. En el estrato arbóreo se registraron todos los individuos con diámetro a la altura del pecho (DAP) ≥ 10 cm, consignándose la identidad taxonómica de las especies presentes. Para los estratos arbustivo y herbáceo, la composición y cobertura relativa se evaluaron mediante observación directa en la parcela, complementada con el uso de cuadrantes reticulados de 1 m² en el caso del estrato herbáceo. Se realizaron registros fotográficos de la vegetación y la identificación taxonómica de las especies se efectuó en terreno.

2.4 Caracterización de suelos

2.4.1 Recolección y procesamiento

En cada uno de los sitios de estudio se delimitaron áreas de 3 m² con presencia de fructificación de morchella, donde se recolectaron muestras compuestas de suelo, conformadas por cinco submuestras de 500 g dispuestas en forma de "equis". Adicionalmente, en cada sitio se tomó una muestra compuesta de suelo control, proveniente de un área adyacente sin evidencia de fructificación. Las muestras fueron tomadas desde los primeros 20 cm de profundidad del perfil edáfico y, posteriormente, todo el material fue transportado en bolsas plásticas al laboratorio en condiciones refrigeradas (4 °C).

En el laboratorio el material se fraccionó para la realización de los análisis químicos (1 kg), análisis físicos (1 kg) y análisis biológicos (0.5 kg). Para los análisis químicos las muestras fueron homogenizadas manualmente, tamizadas a 2 mm y conservadas en bolsas plásticas a 4 °C hasta su procesamiento. Para los análisis físicos las muestras se evaluaron en su condición natural, tal como fueron recolectadas en terreno. Finalmente, para los análisis biológicos las muestras fueron homogenizadas, tamizadas a 2 mm y ajustadas a un 60 % de humedad antes de ser almacenadas en bolsas plásticas y refrigeradas a 4°C hasta su análisis.

2.4.2 Análisis químicos

Los análisis químicos de suelo se realizaron de acuerdo con Sadzawka et al. (2006) y Sadzawka (1990). El pH se determinó en solución acuosa mediante potenciometría. El contenido de materia orgánica (MO) se evaluó por colorimetría, mientras que el nitrógeno (N) total se cuantificó mediante digestión Kjeldahl. El fósforo (P) disponible se determinó mediante el método de Olsen, y los contenidos de potasio (K) y sodio (Na) se analizaron por espectrofotometría de emisión atómica (EEA). Los elementos calcio (Ca), magnesio (Mg), aluminio (Al), hierro (Fe), manganeso (Mn), zinc (Zn) y cobre (Cu) fueron determinados mediante espectrofotometría de absorción atómica (EAA) (Sadzawka,1990). Por su parte, los contenidos de azufre (S) y boro (B) se midieron por colorimetría.

2.4.3 Análisis físicos

Los análisis físicos de suelo se realizaron conforme a los procedimientos descritos por Sandoval et al. (2012). La textura se determinó mediante el método del hidrómetro. La densidad real a través del método del picnómetro y la densidad aparente utilizando el método del cilindro. La capacidad de retención de agua se determinó por el método gravimétrico, expresando el resultado en porcentaje de agua retenida. Además, se determinó la porosidad total a partir de la densidad real y aparente.

2.4.4 Análisis biológicos

Los análisis biológicos de suelos se realizaron siguiendo metodologías descritas en la literatura. Para ello, se incubaron aproximadamente 20 g de suelo fresco en frascos herméticos a temperatura constante, y la producción de CO_2 se midió a los 3, 5 y 7 días de incubación utilizando un analizador infrarrojo de gases (LI-820, LI-COR Biosciences, Lincoln, NE, USA). Los valores de respiración se expresaron como mg CO_2–C g^{-1} de suelo seco $día^{-1}$, calculados a partir de la pendiente de acumulación de CO_2 durante el período de incubación (Craine et al., 2010). La biomasa microbiana del suelo se cuantificó mediante el método de fumigación–extracción, seguido de determinación colorimétrica del carbono (C) extraído, de acuerdo con Alef & Nannipieri (1995). Se utilizaron 10 g de suelo fresco por muestra, comparando fracciones fumigadas y no fumigadas, y el C microbiano se expresó como µg C g^{-1} de suelo seco, aplicando el factor de corrección correspondiente. La actividad enzimática del suelo se evaluó mediante ensayos espectrofotométricos utilizando sustratos artificiales específicos. La actividad de fosfatasa ácida relacionada con el ciclo del fosforo (P) se determinó empleando p-nitrofenil fosfato como sustrato (Tabatabai & Bremner, 1969). La actividad de β-glucosidasa relacionada con el ciclo del C, se determinó utilizando p-nitrofenil-β-D-glucopiranósido como sustrato (Tabatabai, 1982), y la actividad de β-glucosaminidasa relacionada a los ciclos de C y N, se determinó empleando p-nitrofenil-N-acetil-β-D-glucosaminida como sustrato (Parham & Deng, 2000). En todos los casos, se incubaron 1 g de suelo húmedo con el sustrato correspondiente en buffer adecuado y a temperatura controlada, según cada metodología. La liberación de p-nitrofenol se cuantificó por espectrofotometría y la actividad enzimática se expresó como µmol de producto formado g^{-1} de suelo seco h^{-1}.

2.5 Caracterización de morchella

Cada sitio de estudio fue visitado por lo menos cinco veces durante la temporada de fructificación, para registrar a través de fotografías los cuerpos de fructificación de morchella. En cada visita se recolectaron cuerpos de fructificación representativos, seleccionando un mínimo de 10 ejemplares por sitio para estudios posteriores de identificación de especies. Cada muestra fue envasada individualmente en bolsas de papel rotuladas y conservadas a 4 °C durante el transporte hasta el laboratorio. Posteriormente, y de acuerdo con la literatura (Escobar-Hernández et al. 2025; Machuca et al. 2021; Sanz-Rocha et al., 2023) los cuerpos de fructificación fueron identificados a nivel de especie a través de análisis morfológicos, macro y microscópicos, y análisis moleculares (secuenciación ITS). Los especímenes debidamente identificados fueron depositados en el fungario del Laboratorio de Biotecnología de Hongos de la Universidad de Concepción, bajo el código UDEC-LAF.

2.6 Análisis estadísticos

Los análisis estadísticos se realizaron utilizando el software R (R Core Team 2024), con apoyo de los paquetes FactoMineR, factoextra, dplyr, ggplot2 y paquetes base de R. Las variables climáticas mensuales y las propiedades edáficas fueron analizadas mediante enfoques multivariados con el objetivo de identificar gradientes ambientales asociados a la fructificación de *Morchella spp.*. En primer lugar, se realizó un análisis de componentes principales (PCA) sobre las variables climáticas mensuales estandarizadas, considerando cada mes como una observación e incorporando un indicador binario de fructificación. Las variables climáticas más asociadas a los ejes principales se identificaron mediante la función dimdesc, seleccionándose aquellas con correlaciones significativas ($p \leq 0.05$) y altos valores absolutos de correlación ($|r|$) con los componentes retenidos. Posteriormente, se aplicó un PCA a las variables físicas, químicas y biológicas del suelo, previamente estandarizadas, con el fin de sintetizar la variabilidad edáfica entre sitios y tratamientos. En ambos análisis, los dos primeros componentes fueron retenidos para su interpretación en función de la varianza explicada, y las representaciones gráficas incluyeron elipses de confianza al 95 % para visualizar la dispersión multivariada de los grupos definidos por sitio o estado de fructificación.

3. RESULTADOS Y DISCUSIÓN

3.1 Contexto ambiental a escala de paisaje y régimen de perturbación

La fructificación natural de *Morchella* spp. fue registrada en cuatro sitios que representaron un amplio gradiente ambiental a escala de paisaje, abarcando contrastes en clima, fisiografía, material parental del suelo, cobertura vegetal y régimen de perturbación. Dos de los sitios correspondieron a plantaciones forestales de *P. radiata* ubicadas en la Depresión Central, afectadas por disturbios recientes de alta intensidad (incendio forestal y cosecha), mientras que los otros dos correspondieron a relictos de bosque nativo de *Nothofagus* spp. localizados en sectores de precordillera andina y cordillera de la costa, con disturbios antrópicos de baja intensidad (Table 1; Figure 1).

Esta heterogeneidad ambiental permitió evaluar la fructificación de morchella bajo condiciones contrastantes, distinguiendo ambientes fuertemente perturbados, donde el disturbio podría actuar como un factor gatillante, y ambientes de bosque nativo, donde la fructificación ocurrió bajo condiciones estructuralmente más estables.

3.1.1 Cerro Cayumanqui

El Cerro Cayumanqui se localiza en la transición entre la Depresión Central y la Cordillera de la Costa, bajo un clima mediterráneo con marcada estacionalidad hídrica, caracterizado por inviernos lluviosos y veranos secos. El área se desarrolla sobre sustratos graníticos, con suelos de textura liviana, excesivamente drenados y bajo contenido de MO (Centro de Información de Recursos Naturales, 2019).

La cobertura vegetal corresponde a una plantación forestal de *P. radiata* afectada por un incendio forestal en febrero de 2023, lo que generó una estructura abierta, escasa cobertura vegetal y ausencia de hojarasca durante el período de estudio.

3.1.2 Huaqui

Huaqui se ubica en la Depresión Central de la región del Biobío y presenta un clima templado con régimen mediterráneo, caracterizado por precipitaciones invernales y una estación seca estival bien definida. El relieve es plano a suavemente ondulado y se desarrolla sobre depósitos volcánicos recientes (CIREN, 2021).

La cobertura vegetal corresponde a una plantación de *P. radiata* sometida a cosecha forestal en diciembre de 2022, con presencia de residuos leñosos superficiales, canopia abierta y escaso desarrollo de los estratos arbustivo y herbáceo. Los suelos corresponden a Arenosoles, con baja capacidad de retención de agua y limitada fertilidad química.

3.1.3 Peralillo

Peralillo se localiza en la precordillera andina de la región del Biobío y presenta un clima templado lluvioso con influencia mediterránea. El área se desarrolla sobre materiales volcánicos y volcano-sedimentarios, con predominio de suelos derivados de cenizas volcánicas de tipo andisol (CIREN, 2021).

La vegetación corresponde a un relicto de bosque nativo dominado por especies del género *Nothofagus*, con canopia semi-cerrada, mayor complejidad estructural y presencia continua de hojarasca. El uso actual del entorno incluye actividades forestales y ganaderas de baja intensidad, que generan un disturbio crónico moderado sin remoción severa del suelo. La fructificación de morchella en este sitio se registró bajo condiciones de bosque nativo relativamente conservado.

3.1.4 Cerro Pelado

Cerro Pelado se emplaza en la Cordillera de Nahuelbuta, bajo un clima templado oceánico lluvioso, con alta precipitación anual y marcada influencia orográfica. El relieve es montañoso y el sustrato geológico está dominado por granitoides paleozoicos intensamente meteorizados, que dan origen a suelos arcillosos de origen granítico (CIREN, 2021).

La vegetación corresponde a un relicto de bosque templado nativo, dominado por *Nothofagus* spp., con una alta tasa de renuevo y hojarasca continua. El sitio presenta disturbios antrópicos de baja intensidad, asociados principalmente al tránsito humano y de animales domésticos, sin evidencia de remoción reciente del suelo. La fructificación de morchella se registró bajo condiciones de bosque nativo maduro y estructura vegetal compleja.

En conjunto, los sitios de estudio representaron un amplio gradiente ambiental a escala de paisaje, abarcando diferencias marcadas en clima, fisiografía, material parental y cobertura vegetal. Cerro Cayumanqui y Huaqui se caracterizaron por ambientes asociados a plantaciones forestales en la Depresión Central, desarrollados sobre suelos de origen granítico y volcánico, respectivamente, mientras que Peralillo y Cerro Pelado correspondieron a relictos de bosque nativo ubicados en sectores de precordillera andina y de la costa. Esta heterogeneidad ambiental proporcionó un marco adecuado para evaluar la fructificación natural de *Morchella* spp. bajo condiciones contrastantes.

3.2 Estructura vegetacional, perturbación y ocurrencia de *Morchella* spp. en los micrositios

La ocurrencia de *Morchella* spp. a escala de micrositio mostró una asociación clara con el tipo e intensidad del disturbio, así como con la estructura de la vegetación y la acumulación de hojarasca (Table 2; Figure 2). En los sitios Cerro Cayumanqui y Huaqui, la fructificación no estuvo asociada a la condición de plantación forestal per se, sino a la ocurrencia de eventos de perturbación recientes y severos, correspondientes a un incendio forestal y a una cosecha mecanizada, respectivamente. Este patrón concuerda con la clasificación de varias especies del clado Elata como morchellas “fenicoides” o pirofílicas (Carpenter & Trappe, 1985; Greene et al., 2010), cuya fructificación puede incrementarse tras disturbios térmicos o por remoción física del sustrato (Greene et al., 2010; Larson et al., 2016; Pilz et al., 2007).

En Cerro Cayumanqui la fructificación se registró bajo condiciones de estructura vegetal altamente abierta, con ausencia de estratos arbustivos y herbáceos desarrollados y eliminación casi total de la hojarasca. Morchella fructificó sobre el material carbonizado, en la mayoría de los casos completamente desprovisto de vegetación, y los ascocarpos también emergieron desde pequeñas depresiones o cavidades generadas por la combustión de raíces y de la materia orgánica superficial. Esta fructificación es consistente con reportes a escalas <7 m en morchellas post-fuego, asociadas a suelos con cobertura orgánica escasa o inexistente y proximidad a material leñoso carbonizado (Larson et al., 2016). En concordancia, Masaphy & Zabari (2013) han mostrado que este tipo de perturbación puede favorecer la formación de ascocarpos al reducir la competencia microbiana y aumentar la disponibilidad de nutrientes inorgánicos derivados de cenizas. Los ascocarpos recolectados en este sitio correspondieron exclusivamente a la especie *Morchella eximia* (> 99% de similitud), identificada a través de secuenciación de la región ITS (Escobar-Hernández et al. 2025), lo que respalda la interpretación de una ecología especializada en escenarios post-incendio, ya que estudios han documentado a *M. eximia* como una especie dominante en ambientes quemados (Machuca et al., 2021; Pfister et al., 2022; Pildain et al., 2014). La fructificación de esta especie ocurrió tempranamente en la temporada, durante el invierno (agosto–inicios de septiembre), lo que sugiere una respuesta oportunista al disturbio térmico y a la liberación transitoria de recursos tras el incendio (Masaphy & Zabari, 2013; Pilz et al., 2007).

Por su parte, el sitio Huaqui correspondió a una plantación de *P. radiata* recientemente cosechada, con presencia de abundantes residuos leñosos superficiales, canopia abierta y escaso desarrollo de la vegetación acompañante. En este ambiente postcosecha se encontró exclusivamente la especie identificada como *Morchella importuna* (100% de similitud) (Escobar-Hernández et al. 2025). Esta especie fructificó asociada a micrositios perturbados por remoción mecánica del suelo, sobre tocones y residuos de cosecha. Este resultado concuerda con la ecología descrita para *M. importuna* como especie ruderal y saprófita frecuente en ambientes antropogénicos y suelos físicamente perturbados, incluyendo áreas con aportes de sustratos lignocelulósicos (Alli et al., 2025; Kuo et al., 2012; Loizides, 2017). En particular, se ha reportado que la perturbación mecánica combinada con cobertura de madera puede incrementar la densidad de ascocarpos, potencialmente al favorecer la humedad superficial y proveer carbono accesible para el micelio (Masaphy & Zabari, 2013). Al igual que en Cerro Cayumanqui, la fructificación invernal sugiere que especies ruderales pueden capitalizar pulsos tempranos de recursos y condiciones hídricas favorables antes del restablecimiento de una cobertura vegetal competitiva.

En contraste, los sitios Peralillo y Cerro Pelado correspondieron a relictos de bosque nativo dominados por especies del género *Nothofagus*, con canopia semi-cerrada, mayor complejidad estructural y presencia continua de hojarasca. En estos ambientes sólo se encontraron las especies identificadas como *Morchella tridentina* (100% de similitud) y *Morchella andinensis* (>99 % de similitud) (Escobar-Hernández et al. 2025), con coexistencia de ambas especies en Cerro Pelado y presencia exclusiva de *M. tridentina* en Peralillo. Es importante destacar que, si bien en el sitio Cerro Pelado se registró la coexistencia de ambas especies de *Morchella*, esto no implica una fructificación mixta. En terreno, las especies se encuentran espacialmente segregadas, formando parches diferenciados y bien delimitados, sin superposición aparente en sus áreas de fructificación. A diferencia de las especies asociadas a plantaciones perturbadas, estas especies presentaron una fenología más tardía, con fructificación concentrada en primavera (octubre–noviembre). Cabe destacar que en estos sitios no se encontraron morchellas entre agosto y septiembre, e históricamente no existen registros de aparición de cuerpos de fructificación del hongo en otras épocas que no sea la primavera (comunicación personal con los recolectores y dueños de predios). La vegetación arbustiva y herbácea en los sitios de bosque nativo estuvo dominada por especies perennes y tolerantes a sombra, y la capa de hojarasca presentó espesores variables entre 2 y 7 cm, configurando micrositios relativamente estables desde el punto de vista microclimático. En términos biogeográficos, *M. tridentina* se reconoce como una especie cosmopolita, con amplia distribución, mientras que *M. andinensis* presenta distribución más restringida (Chile - Argentina) y una asociación consistente con el bioma andino-patagónico, lo que refuerza una diferenciación ecológica dentro del género (Machuca et al., 2021; Pfister et al., 2022; Pildain et al., 2014).

De esta forma, en este estudio las especies *M. eximia* y *M. importuna* solo se encontraron asociadas a sitios de plantación forestal con disturbios severos, en tanto *M. tridentina* y *M. andinensis* sólo se encontraron en sitios de bosque nativo con bajos grados de perturbación, reforzando la idea de una estrecha relación entre grado de disturbio y ocurrencia especie-específica de morchella. Por otro lado, se observó segregación temporal en la fructificación, con especies oportunistas fructificando en invierno y especies vinculadas a bosques nativos concentrando su fructificación en primavera, sugiriendo una estrategia reproductiva vinculada a condiciones ambientales más estables y a la acumulación progresiva de humedad y MO. En conjunto, estos resultados indican que la fenología en *Morchella* depende de la identidad específica y del contexto ambiental local (Lobos & Icarte, 2021; Masaphy & Zabari, 2013; Pilz et al., 2007).

Cabe destacar que las características de la vegetación descritas corresponden al micrositio de fructificación y a su entorno inmediato, reflejando condiciones locales de cobertura, estructura vertical y acumulación de hojarasca bajo las cuales se registró el desarrollo de los cuerpos de fructificación. Las especies vegetales indicadas (Table 2) corresponden a aquellas con mayor cobertura relativa en dichos micrositios y no necesariamente representan la composición florística completa del sitio de estudio.

Table 2. Vegetation structurea, litter layer and disturbance regime associated with the natural fructification of *Morchella* spp. at each study site in south-central Chile.

Site	Vegetation type	Dominant tree species	Canopy condition[b]	Dominant shrub species	Dominant herbaceous species	Litter layer[c]	Type of disturbance	*Morchella* species associate
Cerro Cayumanqui	Forest plantation	*Pinus radiata* (burned debris)	Open	-	*Fallopia convolvulus* *Trifolium repens*	Absent	Forest fire	*M. eximia*
Huaqui	Forest plantation	*Pinus radiata* (logged debris)	Open	-	*Carduus pycnocephalus* *Rumex acetosella*	Absent–very thin (<1 cm)	Logging	*M. importuna*
Peralillo	Native forest relic	*Nothofagus dombeyi* *Nothofagus obliqua* *Podocarpus salignus*	Semi-closed	*Rosa rubiginosa* *Crataegus monogyna*	*Trifolium repens* *Acaena ovalifolia*	Present (4 – 7 cm)	Forestry and livestock influence	*M. tridentina*
Cerro Pelado	Native forest relic	*Nothofagus dombeyi* *Nothofagus obliqua*	Semi-closed	*Barberis darwinii*	*Acaena ovalifolia* *Poa annua*	Present (2 – 4 cm)	Human and animal traffic	*M. tridentina* and *M. andinensis*

[a] Vegetation attributes were determined based on the relative cover at the fructification microsite and its immediate surroundings.

[b] This refers to the degree of canopy closure at the fructification microsite.

[c] When present, the litter thickness corresponded to the average depth (cm) measured at the fructification microsite and its immediate surroundings.


A1
A2
B1
B2
C1
C2
D1
D2
E1
E2

Figure 2. Fruiting environments of morels (left) and their associated species (right) in south-central Chile. (A1) Post-fire forest plantation in Cerro Cayumanqui site, and (A2) *M. eximia*. (B1) Logged forest plantation in Huaqui site, and (B2) M. importuna. (C1) Relic of native forest in Peralillo site, and (C2) *M. tridentina*. (D1) Relic of native forest in Cerro Pelado site, and (D2) *M. andinensis*. (E1) Relic of native forest in Cerro Pelado site, and (E2) *M. tridentina*. The images show the relationship between habitat conditions and the presence of specific Morchella species recorded during the fruiting season.

3.3 Propiedades edáficas asociadas a la fructificación de *Morchella* spp.

La información general de clasificación y características edáficas de los sitios de estudio se resume en la Table 3. Estos antecedentes entregan un marco descriptivo de referencia para la interpretación posterior del análisis multivariado de las propiedades físicas (Table S1, material suplementario), químicas (Table S2, material suplementario) y biológicas del suelo (Table S3, material suplementario), permitiendo contextualizar la variabilidad edáfica observada entre los distintos ambientes de fructificación.

Table 3. General soil properties and classification of study sites.

Site	Soil series	Soil order	Texture class	Slope (%)
Cerro Cayumanqui	San Esteban	Ultisol	Clay loam	50
Huaqui	Arenales	Arenosol	Loam	2
Peralillo	Collipulli	Andisol	Sandy loam	20
Cerro Pelado	San Esteban	Inceptisol	Sandy loam	30

El análisis de componentes principales (Figure 3), realizado sobre el conjunto de variables edáficas estandarizadas, permitió sintetizar la variabilidad del suelo entre sitios, temporadas y tratamientos asociados a la presencia y ausencia de fructificación de *Morchella* spp. Los dos primeros componentes explicaron el 63.5 % de la varianza total, con un 45.4 % atribuible al PC1 y un 18.1 % al PC2.

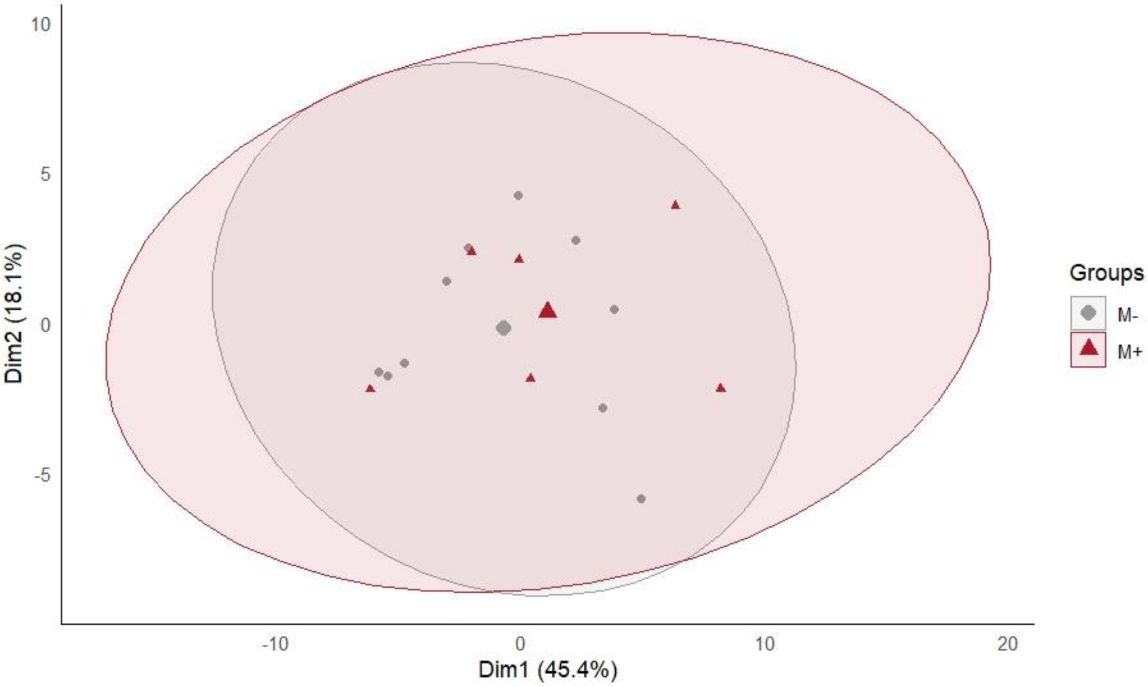

Figure 3. Projection of soil samples in the space defined by the first two components of principal component analysis (PCA), constructed from physical, chemical, and biological variables of the soil. The symbols represent individual samples, and the colors indicate treatment according to the fruiting history of *Morchella* spp. (M+ and M−). The ellipses show the 95% confidence intervals.

El PC1 estuvo principalmente asociado a variables relacionadas con el estado físico–hídrico y el funcionamiento biológico del suelo, incluyendo contenido de humedad, capacidad de retención de agua, punto de marchitez, MO, C orgánico, respiración basal y actividad enzimática (β-glucosidasa) (Figure S2, material suplementario). Este eje representó un gradiente funcional vinculado a la disponibilidad de agua y a la actividad microbiana del suelo. El PC2 estuvo dominado por variables de carácter químico y nutricional, tales como K intercambiable y disponible, capacidad de intercambio catiónico, saturación de bases, Ca y Mg intercambiables, saturación de Al, nitratos y fracción de arcilla (Figure S3, material suplementario), describiendo un gradiente asociado al estado químico y de fertilidad del suelo.

La proyección de las muestras en el espacio definido por ambos componentes mostró una amplia superposición entre los tratamientos con (M+) y sin fructificación (M-), sin una separación multivariada clara entre grupos. Este patrón se observó de manera consistente entre sitios y temporadas, indicando que las propiedades edáficas evaluadas caracterizan un rango ambiental funcional común, pero no permiten discriminar de forma consistente la ocurrencia anual del evento de fructificación.

En conjunto, los resultados indican que las propiedades del suelo configuran un marco ambiental predisponente para la presencia de *Morchella* spp., más que actuar como un factor determinante directo de la fructificación anual. Esta interpretación coincide con estudios previos que señalan que la aparición de ascocarpos responde a la interacción entre condiciones edáficas favorables y señales ambientales específicas, más que a un único controlador aislado (Masaphy & Zabari, 2013; Mihail et al., 2007; Pilz et al., 2007). En este contexto, variables asociadas a la retención de agua, el contenido de MO y la actividad microbiana dominaron el gradiente principal, sugiriendo que la funcionalidad del suelo es más relevante que parámetros químicos puntuales considerados de forma individual (Kakakhel, 2020; Manikandan et al., 2011; Orlofsky et al., 2021).

La importancia de la estructura física del suelo y de su capacidad de retención hídrica concuerda con la ecología conocida de *Morchella* spp., tanto en ambientes post-incendio como naturales, donde la fructificación parece depender estrechamente de la dinámica del agua en el perfil del suelo y no exclusivamente de la precipitación inmediata. Estudios recientes, identifican la precipitación y la temperatura como predictores clave, destacando la interacción entre condiciones climáticas y propiedades edáficas que generan escenarios de “estrés hídrico controlado” favorables para la formación de ascocarpos (Allı et al., 2025; Mihail et al., 2007). Asimismo, se ha descrito una preferencia por suelos con buena capacidad de drenaje y fracciones arenosas significativas, que evitan el anegamiento sin comprometer la disponibilidad hídrica (Hussain & Sher, 2021).

El predominio de variables asociadas a la MO refuerza su rol como componente central en la ecología de *Morchella* spp., actuando como fuente de carbono, regulador de la humedad y modulador de la actividad biológica del suelo. Estudios previos han demostrado que contenidos intermedios de MO favorecen el crecimiento del género, tanto por su aporte energético como por su efecto en la agregación del suelo y la estabilidad del microambiente edáfico (Kakakhel, 2020; Manikandan et al., 2011). En este sentido, la profundidad de la hojarasca emerge como un factor relevante, al contribuir a la retención de humedad y a la protección del micelio frente a la desecación.

Si bien los parámetros químicos puntuales no emergieron como los principales controladores, estos deben interpretarse dentro de un marco multivariable integrado. Elementos como fósforo, magnesio, calcio y pH han sido identificados como relevantes para determinadas especies, actuando como filtros ambientales que modulan la idoneidad del hábitat (Alli et al., 2025; Hussain & Sher, 2021; Manikandan et al., 2011). De manera complementaria, evidencia reciente sugiere que *Morchella* spp. interactúa activamente con la biota del suelo, modificando la composición de comunidades bacterianas potencialmente involucradas en la adquisición de nutrientes y la inducción de la fructificación, lo que refuerza la idea de un suelo funcionalmente activo más que químicamente óptimo (Orlofsky et al., 2021; Pion et al., 2013).

Finalmente, este estudio abordó al género *Morchella* como una unidad funcional, debido a limitaciones en el tamaño muestral y en la frecuencia de ocurrencia de las especies, lo que impidió evaluaciones interespecíficas robustas. Investigaciones futuras con un mayor número de observaciones por especie y diseños muestrales dirigidos permitirán evaluar con mayor precisión la existencia de requerimientos edáficos diferenciados y nichos ecológicos específicos dentro del género.

3.4 Condición climática durante la fructificación de *Morchella* spp.

Con el fin de caracterizar el contexto climático asociado a la fructificación natural de *Morchella* spp., se analizaron series mensuales de variables meteorológicas mediante un enfoque multivariado. El análisis de componentes principales (PCA; Figure 4) permitió sintetizar la variabilidad climática entre sitios y a lo largo del tiempo, identificando los principales gradientes ambientales y la posición relativa de los meses con y sin fructificación en el espacio climático.

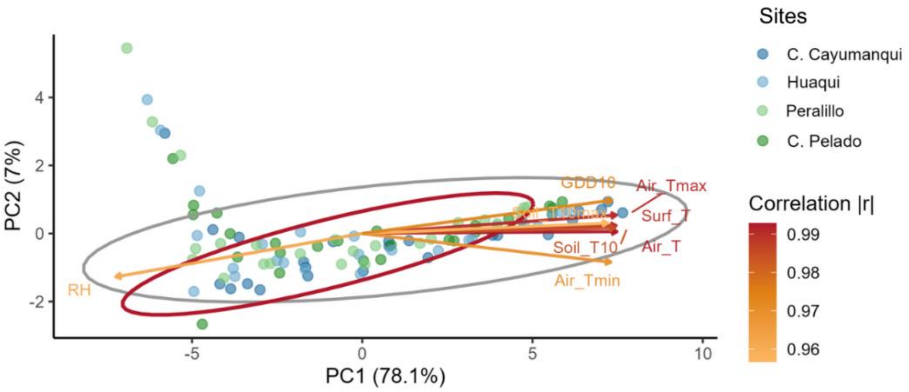

Figure 4. Principal component analysis (PCA) of monthly climate variables at the four study sites. The colored points represent months at each site. The ellipses (95%) correspond to months without (gray) and with (red) fruiting of *Morchella* spp. (red). The arrows represent the selected climate variables using dimdesc and are colored according to the magnitude of the absolute correlation (|r|) between each variable and the principal axes (PC1 - PC2).

Los dos primeros componentes explicaron el 85.1 % de la varianza total, con un 78.1 % asociado al PC1 y un 7.0 % al PC2, indicando una fuerte estructuración climática dominada por un eje principal. Los meses con fructificación se concentraron en una región acotada del espacio multivariado, mientras que los meses sin fructificación ocuparon un rango más amplio de condiciones climáticas, evidenciando la existencia de una ventana climática específica asociada al evento reproductivo.

El PC1 estuvo dominado por un gradiente térmico–energético estacional, con correlaciones positivas con la temperatura del aire, la temperatura del suelo y de la superficie, los grados día acumulados y la radiación solar, y correlaciones negativas con la humedad relativa. Este eje reflejó la transición estacional desde condiciones frías y húmedas hacia condiciones más cálidas y energéticas. El PC2 se asoció principalmente a variables relacionadas con la ocurrencia de eventos de helada, representando un gradiente de extremos térmicos. Las variables climáticas identificadas mediante dimdesc ($p \leq 0.05$) correspondieron mayoritariamente a variables térmicas y energéticas, reflejando su contribución a la estructuración del espacio climático.

La representación temporal de las variables seleccionadas (Figure 5) mostró que, en todos los sitios, la fructificación coincidió con períodos caracterizados por incrementos en la precipitación acumulada y la humedad relativa, junto con temperaturas moderadas del suelo a 10 cm de profundidad. Estos patrones se repitieron de manera consistente entre sitios, a pesar de las diferencias climáticas regionales, indicando la convergencia hacia condiciones climáticas recurrentes asociadas al evento de fructificación.

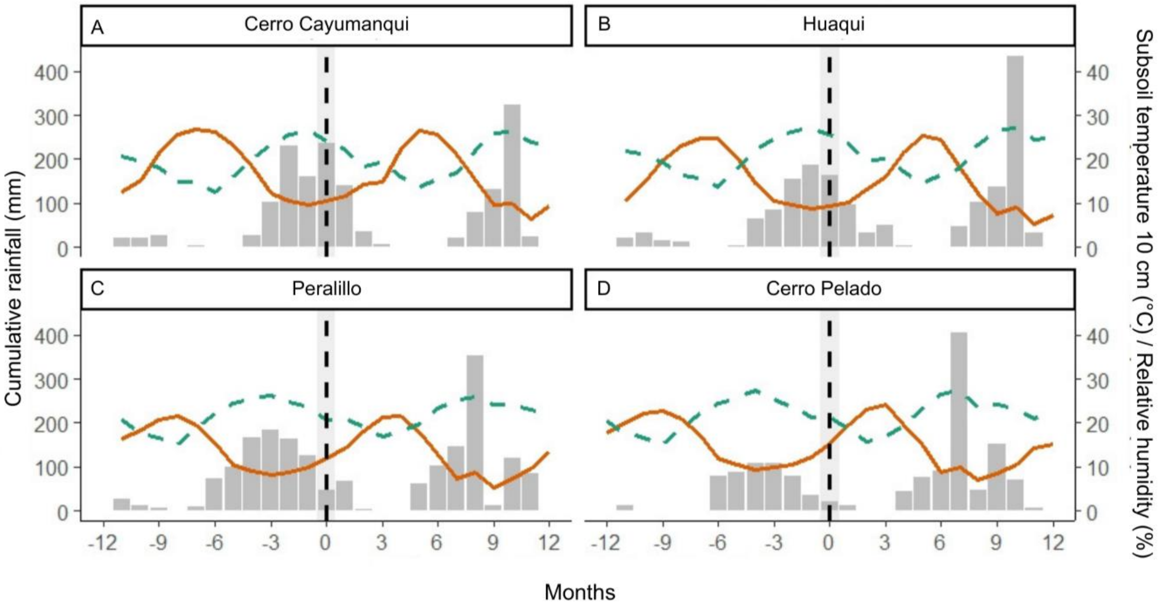

Figure 5. Temporal variation in climatic and soil conditions at the study sites: (A) Cerro Cayumanqui, (B) Huaqui, (C) Peralillo, and (D) Cerro Pelado. The gray bars represent cumulative monthly precipitation (mm). The solid orange line shows soil temperature at a depth of 10 cm (°C), and the dashed green line shows relative humidity (%RH). The time axis is expressed in months relative to fruiting, where month 0 (the dashed vertical line) indicates the time at which *Morchella* spp. fruit at each site. Negative values correspond to months before fruiting, and positive values correspond to months after fruiting.

La posición de los meses con fructificación en el espacio multivariado mostró una superposición parcial entre sitios, sugiriendo que el evento reproductivo ocurre bajo condiciones climáticas similares independientemente del contexto geográfico. En términos temporales, la fructificación se concentró mayoritariamente en períodos de transición estacional, coincidiendo con el término del invierno (en ambientes de plantación forestal perturbada) y el inicio de la primavera (en ambientes de bosque nativo) en todos los sitios evaluados.

En conjunto, los resultados confirman que la fructificación natural de *Morchella* spp. en los ecosistemas templados del sur de Chile no es un evento aleatorio, sino que responde a la interacción crítica entre condiciones ambientales acumulativas de largo plazo y estímulos climáticos gatilladores de corto plazo. El análisis multivariado reveló que la aparición de los ascocarpos se circunscribe a una ventana climática acotada, caracterizada por temperaturas edáficas específicas, alta humedad relativa y un aumento en la precipitación acumulada. Estos hallazgos concuerdan con estudios que señalan que, si bien el micelio vegetativo puede tolerar amplios rangos ambientales, la morfogénesis del cuerpo fructífero requiere umbrales térmicos y hídricos precisos (Hussain & Sher, 2021; Manikandan et al., 2011).

Específicamente, la dependencia de la temperatura del suelo observada en este estudio es consistente con el concepto de "temperatura acumulada" o grados-día necesarios para el desarrollo de los primordios. Chen (2018) demostró que la temperatura acumulada del suelo superficial (5 cm) es un indicador de referencia crítico para la demanda de energía térmica de *Morchella*, determinando las fases de diferenciación de los primordios y la maduración de los ascocarpos. Esto sugiere que las morchellas en el centro-sur de Chile requieren acumular una cantidad específica de calor edáfico después del invierno para fructificar, lo que explica la fenología primaveral observada en especies como *M. tridentina* y *M. andinensis* (Machuca et al., 2015).

Por otro lado, la precipitación actúa como un estímulo de corto plazo fundamental. Alli et al. (2025) identificaron mediante modelos de aprendizaje automático que la precipitación, junto con las temperaturas máximas y mínimas, son los predictores ambientales más importantes para el crecimiento de *Morchella*. Sin embargo, la dinámica hídrica es compleja, observaciones en otros ecosistemas indican que no solo la humedad constante es clave, sino que la fluctuación entre humedecimiento y desecación del sustrato puede actuar como un disparador fisiológico para la fructificación (Masaphy & Zabari, 2013). Asimismo, la alta humedad relativa registrada durante la fructificación es vital para prevenir la desecación de los primordios emergentes, especialmente en especies expuestas a ambientes abiertos (Orlofsky et al., 2021).

3.5 Modelo conceptual integrado: perturbación, diversidad de especies y tiempo de fructificación de morchella.

Los resultados de este estudio permiten proponer un modelo conceptual integrado para explicar la fructificación natural de *Morchella* spp. en ecosistemas templados del centro-sur de Chile, basado en la interacción entre el régimen de perturbación, las especies y la sincronización temporal de la fructificación (Figure

6). Este modelo reconoce que la ocurrencia del evento reproductivo no responde a un único factor ambiental, sino a la convergencia de procesos que operan a distintas escalas espaciales y temporales.

Conceptual model of *Morchella* spp. fructification

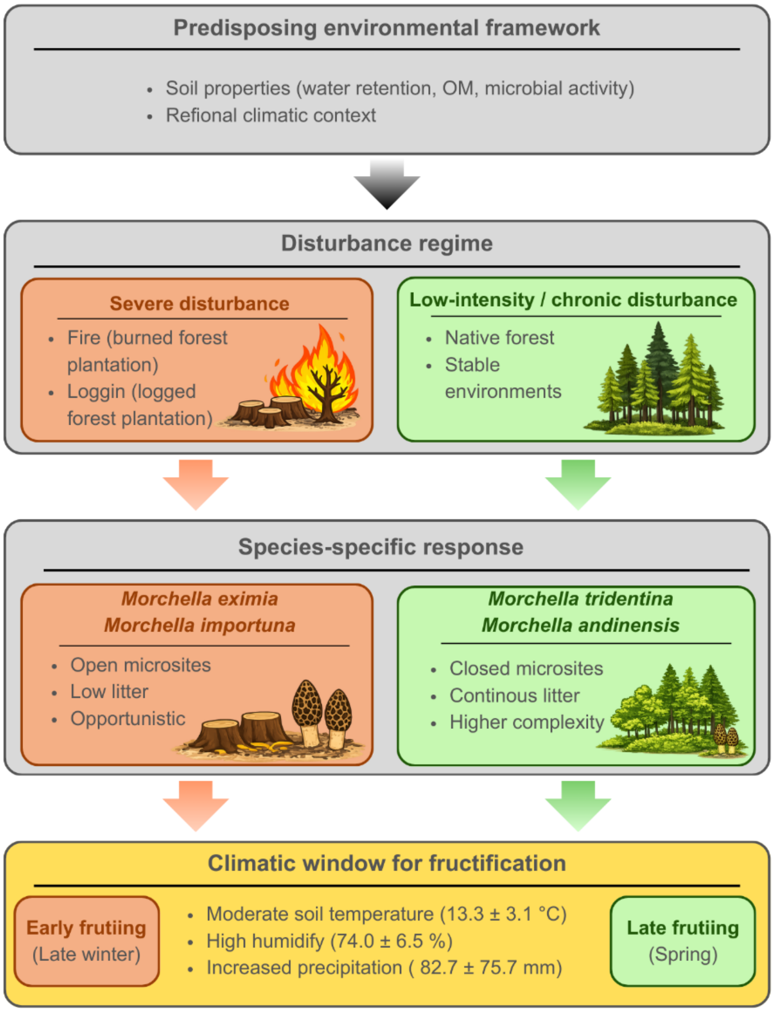

Figure 6. The diagram illustrates the hierarchical interaction between environmental predisposition, disturbance regime, species diversity, and climatic synchronization that controls the natural fructification of morels. At the landscape scale, soil functional properties and the regional climatic context establish an

environmental framework that predisposes the area to certain conditions. At the microsite scale, the disturbance regime acts as the main modulator, differentiating environments affected by severe disturbances (post-fire and post-harvest) from structurally stable native forests. These contrasting conditions favor the appearance of distinct species: *M eximia* and *M. importuna* associated with recently disturbed environments, and *M. tridentina* and *M. andinensis* associated to native forest conditions. Fruiting occurs when a short-term climatic window characterized by moderate soil temperatures, high relative humidity, and increased precipitation is met, resulting in species-specific differences in fructification timing, from early (late winter) to late (spring) fruiting.

A escala de paisaje, las propiedades edáficas y climáticas definen un marco ambiental predisponente que delimita los ambientes potencialmente favorables para el desarrollo de morchella. Los análisis multivariados de suelo y clima evidencian gradientes funcionales comunes entre sitios, asociados principalmente a la retención de agua, el contenido de materia orgánica y la actividad microbiana. Sin embargo, estas variables no explican por sí solas la ocurrencia anual de la fructificación. En este sentido, el suelo actúa como un componente estructural de base que condiciona la funcionalidad del sistema, pero cuya estabilidad relativa no determina directamente la expresión del evento reproductivo. La ausencia de una diferenciación consistente entre micrositios con y sin fructificación en el espacio edáfico multivariado refuerza la hipótesis de que la fructificación natural de *Morchella* spp. depende de la sincronización entre condiciones edáficas favorables, estímulos climáticos de corto plazo y el régimen de perturbación.

El régimen de perturbación emerge como el principal modulador del microambiente a escala de micrositio, generando condiciones contrastantes que favorecen la ocurrencia especie-específica. Los disturbios severos y recientes, como incendios forestales y cosechas mecanizadas, promueven la fructificación temprana de especies oportunistas y probablemente saprobias (Baynes et al. 2012; Dahlstrom et al., 2000; Pilz et al., 2007), tales como *M. eximia* y *M. importuna*, respectivamente, asociadas a ambientes abiertos, con escasa cobertura vegetal y mínima acumulación de hojarasca. Estas especies presentarían una estrategia reproductiva sincronizada con la fase post-disturbio aprovechando la liberación transitoria de recursos y las condiciones microclimáticas generadas tras la remoción de la cobertura vegetal.

En contraste, en ambientes de bosque nativo con disturbios de baja intensidad, la fructificación se asocia a especies como *M. tridentina* y *M. andinensis*, que ocurren bajo condiciones estructurales más estables, caracterizadas por canopia semi-cerrada, acumulación continua de hojarasca y mayor complejidad de la vegetación. Estas especies exhiben una fenología más tardía, con fructificación concentrada en primavera, lo que sugiere una dependencia de condiciones climáticas progresivamente más favorables y de procesos edáficos de mayor estabilidad temporal. Aunque el estado trófico de estas especies hasta la fecha no se conoce, podrían presentar algún tipo de asociación simbiótica (micorrícica o endofítica) con la vegetación dominante en estos ecosistemas.

La sincronización climática actúa como el gatillante final del evento reproductivo, definiendo una ventana climática acotada caracterizada por temperaturas moderadas del suelo (13.3 ± 3.1 °C), alta humedad relativa (74.0 ± 6.5 %) y aumento en la precipitación acumulada (82.7 ± 75.7mm). Esta ventana fue consistente entre sitios y especies, aunque su expresión temporal varió en función del tipo de perturbación y de la especie de *Morchella*, generando una segregación fenológica clara entre especies asociadas a disturbios severos y aquellas vinculadas a ambientes menos perturbados.

El modelo conceptual propuesto integra tres componentes clave: un marco edáfico–climático predisponente a escala de paisaje, el régimen de perturbación como modulador del microambiente y determinante de la ocurrencia especie-específica, y la sincronización climática como gatillante temporal de la fructificación. Este enfoque permite integrar la alta plasticidad ecológica del género *Morchella* con patrones consistentes de diferenciación ecológica y fenológica, y proporciona una base conceptual para futuras investigaciones que puedan incluir un gradiente latitudinal más extenso de sitios de estudio, orientadas al manejo sustentable y a la comprensión de la dinámica reproductiva de este valioso recurso forestal no maderero en ecosistemas australes.

4. CONCLUSIÓN

La fructificación natural de *Morchella* spp. en ecosistemas templados del centro-sur de Chile responde a la interacción entre un marco ambiental predisponente, el régimen de perturbación y la sincronización climática de corto plazo. Las propiedades funcionales del suelo y el contexto climático regional definen condiciones de base favorables, pero no determinan por sí solas la ocurrencia anual del evento reproductivo.

El régimen de perturbación actúa como el principal modulador de la ocurrencia especie-específica, favoreciendo especies oportunistas en ambientes post-incendio (*M. eximia*) y post-cosecha (*M. importuna*), y especies asociadas a condiciones estructuralmente más estables en bosques nativos (*M. andinensis* y *M. tridentina*). La fructificación ocurre dentro de una ventana climática acotada, común a todos los sitios, aunque su expresión temporal difiere entre especies, generando una segregación fenológica clara entre fructificación temprana y tardía.

Los resultados apoyan un modelo conceptual en el que el suelo actúa como un componente estructural de fondo, el disturbio determina la identidad de las especies y el clima sincroniza el momento de la fructificación, aportando bases relevantes para la comprensión ecológica y el manejo sustentable de *Morchella* spp. en ecosistemas australes.

Este estudio constituye una aproximación exploratoria a un fenómeno ecológico escasamente documentado en ecosistemas templados del hemisferio sur. En este contexto, los resultados presentados establecen una base empírica inicial para la comprensión de los ambientes de fructificación natural de *Morchella* spp., y proporcionan un marco conceptual que permite orientar investigaciones futuras. La integración de variables climáticas, edáficas y de vegetación abre nuevas líneas de investigación orientadas a profundizar en los mecanismos que regulan la fructificación, con implicancias directas para el manejo sustentable, la conservación del recurso y el desarrollo de estrategias de domesticación adaptadas a condiciones ambientales locales.

REFERENCIAS

Alef, K. & Nannipieri, P. (1995). Methods in applied soil microbiology and biochemistry. *Academic Press*.

Alli, H., Güler Dincer, N., & Pekmezci, A. (2025). Machine Learning-Based Insights into Environmental Determinants of Morchella importuna Growth in Muğla, Türkiye. Life, 15(12), 1806. https://doi.org/10.3390/life15121806.

Baynes, M., Newcombe, G., Dixon, L., Castlebury, L., & O'Donnell, K. (2012). *A novel plant–fungal mutualism associated with fire*. *Fungal Biology, 116*(1), 133–144. https://doi.org/10.1016/j.funbio.2011.10.008.

Chen, X.-H. (2018). Impact of ≥0°C accumulated temperature on the growth development of *Morchella importuna*. *Mycosystema*, *37*(12), 1717–1722.

Centro de Investigación de Recursos Naturales.- CIREN (2019). Comuna Quillón: Recursos Naturales.

Centro de Investigación de Recursos Naturales.- CIREN (2021). Recursos Naturales Comuna de Los Sauces.

Centro de Investigación de Recursos Naturales.- CIREN (2021). Recursos Naturales Comuna de Quilleco.

Centro de Investigación de Recursos Naturales.- CIREN (2021).Recursos Naturales Comuna de Laja.

Craine, J., Fierer, N. & McLauchlan, K. Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nature Geosci* **3**, 854–857 (2010). https://doi.org/10.1038/ngeo1009.

Dahlstrom, J. L., Smith, J.E., & Weber, N.S. (2000). Mycorrhiza-like interaction by Morchella with species of the Pinaceae in pure culture synthesis. *Mycorrhiza*, 9(5), 279-285. https://doi.org/10.1007/s005720000072.

Escobar-Hernández, T., Segura, R., Muñoz-Espinoza, C., Sanz-Rocha, M., Zagal, E., Velasco, V., Elso, M., Guillén, Y., Gerding, M., Chávez, D., & Machuca, Á. (2025). Quality traits of the Morchella mushrooms harvested from forest plantations and native forests in south-central Chile [Manuscript submitted for publication]. *Food Chemistry*.

Gamundí, I. J. (1975). Fungi, ascomycetes: Pezizales (Flora criptogámica de Tierra del Fuego, Vol. X–3). *Fundación para la Educación, la Ciencia y la Cultura.*

Greene, D. F., Hesketh, M., & Pounden, E. (2010). Emergence of morel (*Morchella*) and pixie cup (*Geopyxis carbonaria*) ascocarps in response to the intensity of forest floor combustion during a wildfire. *Mycologia*, *102*(4), 766–773. https://doi.org/10.3852/09-178.

Hussain, S., & Sher, H. (2021). Ecological characterization of Morel (Morchella spp.) habitats: A multivariate comparison from three forest types of district Swat, Pakistan. *Acta Ecologica Sinica*, *41*(1), 1–9. https://doi.org/10.1016/j.chnaes.2020.10.007.

Instituto Forestal. (2024). Boletín de exportaciones de productos forestales no madereros (N.º 43). Ministerio de Agricultura.

Kakakhel, S. F. B. (2020). Physical and Chemical Characteristics of Morels (Morchella Species) Habitat in Mankial Valley, District Swat, Khyber Pakhtunkhwa, Pakistan. *The International Journal of Science & Technoledge, 8*(6). https://doi.org/10.24940/theijst/2020/v8/i6/ST2006-005.

Kuo, M., Dewsbury, D. R., O’Donnell, K., Carter, M. C., Rehner, S. A., Moore, J. D., Moncalvo, J. M., Canfield, S. A., Stephenson, S. L., Methven, A. S., & Volk, T. J. (2012). Taxonomic revision of true morels (*Morchella*) in Canada and the United States. *Mycologia*, *104*(5), 1159–1177. https://doi.org/10.3852/11-375.

Larson, A. J., Cansler, C. A., Cowdery, S. G., Hiebert, S., Furniss, T. J., Swanson, M. E., & Lutz, J. A. (2016). Post-fire morel (*Morchella*) mushroom abundance, spatial structure, and harvest sustainability. *Forest Ecology and Management*, *377*, 16–25. https://doi.org/10.1016/j.foreco.2016.06.038.

Li, X., Fu, T., Li, H., Zhang, B., Li, W., Zhang, B., Wang, X., Wang, J., Chen, Q., He, X., Chen, H., Zhang, Q., Zhang, Y., Yang, R., & Peng, Y. (2023a). Safe Production Strategies for Soil-Covered Cultivation of Morel in Heavy Metal-Contaminated Soils. *Journal of Fungi,* *9*(7), Article 765. https://doi.org/10.3390/jof9070765.

Liu, Q., Ma, H., Zhang, Y., & Dong, C. (2018). Artificial cultivation of true morels: current state, issues and perspectives. *Critical Reviews in Biotechnology*, *38*(2), 259–271. https://doi.org/10.1080/07388551.2017.1333082.

Lobos, I., & Icarte, J. (2021). Agregación de valor del hongo morchella que fructifica en el Territorio Patagonia Verde, Región de Los Lagos, Chile (Boletín INIA N° 443). Instituto de Investigaciones Agropecuarias.

Loizides, M. (2017). Morels: The story so far. *Field Mycology*, *18*(2), 42–53. https://doi.org/10.1016/j.fldmyc.2017.04.004

Machuca, A., Córdova, C., Gómez, C., Gerding, M., & Silva, F. (2015). Factores microambientales relacionados con el desarrollo y diversidad de Morchella spp. en bosques de Nothofagus de la Patagonia Aysenina (Informe Final Proyecto 077/2013). Fondo de Investigación del Bosque Nativo; Universidad de Concepción.

Machuca, A., Gerding, M., Chávez, D., Palfner, G., Oyarzúa, P., Guillén, Y., & Córdova, C. (2021). Two new species of *Morchella* from *Nothofagus* forests in Northwestern Patagonia (Chile). *Mycological Progress*, *20*, 781–795. https://doi.org/10.1007/s11557-021-01703-x.

Manikandan, K., Sharma, V. P., Kumar, S., Kamal, S., & Shirur, M. (2011). Edaphic conditions of natural sites of Morchella and Phellorinia. *Mushroom Research*, *20*(2), 117–120.

Martinez, J. & Gea, F. (2022). Contribución al conocimiento del género Morchella Dill ex Pers.: Fr. en la provincia de Albacete y áreas próximas. *Sabuco: Revista de Estudios Albacetenses, 16*, 103-130.

Masaphy, S. (2011). Diversity of fruiting patterns of wild black morel mushroom. In Proceedings of the 7th International Conference on Mushroom Biology and Mushroom Products (ICMBMP7) (pp. 165–169).

Masaphy, S., & Zabari, L. (2013). Observations on post-fire black morel ascocarp development in an Israeli burnt forest site and their preferred micro-sites. *Fungal Ecology*, *6*(3), 316–318. https://doi.org/10.1016/j.funeco.2013.02.005.

Masaphy, S., Zabari, L., Goldberg, D., & Jander-Shagug, G. (2010). The complexity of Morchella systematics: a case of the yellow morel from Israel. *Fungi*, *3*(2), 14-18.

McFarlane, E., Pilz, D. & Weber, N. (2005). High-elevation gray morels and other Morchella species harvested as non-timber forest products in Idaho and Montana. *Mycologist*, *19*(2), 62–68. https://doi.org/10.1017/S0269-915X(05)00203-X.

Mihail, J. D., Bruhn, J. N., & Bonello, P. (2007). Spatial and temporal patterns of morel fruiting. *Mycological Research*, *111*(3), 339–346. https://doi.org/10.1016/j.mycres.2007.01.007.

Moreno, N., Esse, C., Donoso, G., Betancourt, O., Medina, L. & Vivallo, G. (2013). Propuesta metodológica para el estudio de los factores agroecológicos que influyen en la fructificación de Morchella spp. una revisión. *Micobotánica-Jaén*, *1*.

Orlofsky, E., Zabari, L., Bonito, G., & Masaphy, S. (2021). *Changes in soil bacteria functional ecology associated with Morchella rufobrunnea fruiting in a natural habitat. Environmental Microbiology,* *23*(11), 6651–6662. https://doi.org/10.1111/1462-2920.15692

Pfister, D. H., Healy, R., LoBuglio, K. F., Furci, G., Mitchell, J., & Smith, M. E. (2022). South American morels in the Elata group: mitosporic states, distributions, and commentary. *Mycological Progress*, *21*(97). https://doi.org/10.1007/s11557-022-01846-5

Pildain, M. B., Visnovsky, S. B., & Barroetaveña, C. (2014). Phylogenetic diversity of true morels (*Morchella*), the main edible non-timber product from native Patagonian forests of Argentina. *Fungal Biology*, *118*(9–10), 755–763. https://doi.org/10.1016/j.funbio.2014.05.004

Pilz, D., McLain, R., Alexander, S., Villarreal-Ruiz, L., Berch, S., Wurtz, T. L., Parks, C. G., McFarlane, E., Baker, B., Molina, R., & Smith, J. E. (2007). Ecology and management of morels harvested from the forests of western North America (General Technical Report PNW-GTR-710). U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. https://doi.org/10.2737/PNW-GTR-710

Pion, M., Spangenberg, J. E., Simon, A., Bindschedler, S., Flury, C., Chatelain, A., Bshary, R., Job, D., & Junier, P. (2013). Bacterial farming by the fungus Morchella crassipes. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1773), 20132242. https://doi.org/10.1098/rspb.2013.2242

Sadzawka, R. (1990). *Métodos de análisis de suelos*. Instituto de Investigaciones Agropecuarias.

Sadzawka, A., Carrasco, M., Grez, R., Mora, M., Flores, H., & Neaman, A. (2006). *Métodos de análisis recomendados para los suelos de Chile*. Instituto de Investigaciones Agropecuarias.

Sandoval, M., Dörner, J., Seguel, O., Cuevas, J., & Rivera, D. (2012). *Métodos de análisis físicos de suelos*. Publicaciones Departamento de Suelo y Recursos Naturales, Universidad de Concepción.

Sanz-Rocha, M., Gerding, M, Quezada, T, Vargas, M, Chávez, D., & Machuca, A. (2023). Molecular and cultural characterization of *Morchella* spp. from disturbed environments of central-southern Chile. *Fungal Biology, 127*(3), 938-948. https://doi.org/10.1016/j.funbio.2023.01.009.

Sanz M. (2022). Factibilidad de domesticación de genotipos de Morchella autóctonos del centro-sur de Chile. Tesis de Magister, Universidad de Concepción.

Spegazzini, C. (1921) Mycetes Chilensis. Boletín de la Academia Nacional de Ciencias, Córdoba 25: 1-24.

Tabatabai, M. A. (1982). Soil enzymes. In A. L. Page (Ed.), Methods of soil analysis. Part 2: Chemical and microbiological properties (2nd ed., Agronomy Monograph No. 9, pp. 903–947). American Society of Agronomy.

Tabatabai, M. A., & Bremner, J. M. (1969). Use of p-nitrophenyl phosphate for the assay of soil phosphatase activity. *Soil Biology and Biochemistry, 1*, 301–307. https://doi.org/10.1016/0038-0717(69)90012-1.

Zhang, Y., Sun, S., Luo, D., Mao, P., Rosazlina, R., Martin, F. & Xu, L. (2023). Decline in Morel Production upon Continuous Cropping Is Related to Changes in Soil Mycobiome. *Journal of Fungi*, *9*(4), 492. https://doi.org/10.3390/jof9040492.

MATERIAL SUPLEMENTARIO

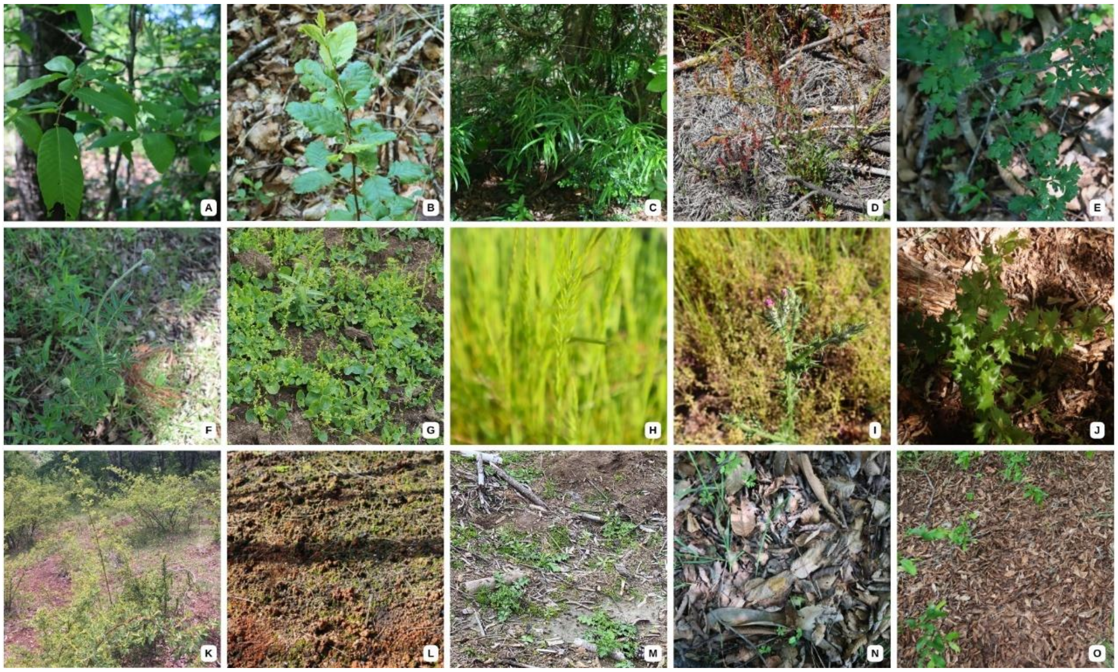

Figure S1. Representative plant species and soil surface conditions observed at the study sites during the morchella fructification period.

(A) *Nothofagus dombeyi*; (B) *Nothofagus obliqua*; (C) *Podocarpus salignus*; (D) *Rumex acetosella*; (E) *Crataegus monogyna*; (F) *Acaena ovalifolia*; (G) *Fallopia convolvulus*; (H) *Poa annua*; (I) *Carduus pycnocephalus*; (J) *Barberis darwinii*; (K) *Rosa rubiginosa*; (L) Soil cover of Cerro Cayumanqui; (M) Soil cover of Huaqui; (N) Soil cover of Peralillo; (O) Soil cover of Cerro Pelado. Photographs (aug–nov 2023).

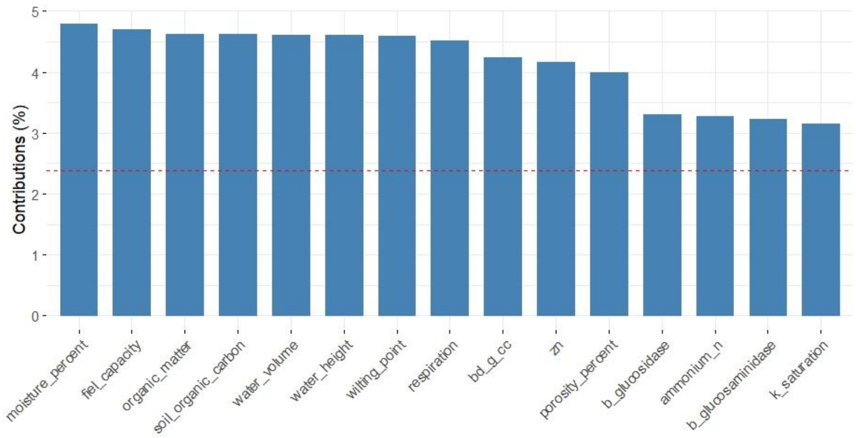

Figure S2. Contribution of variables to the first principal component (PC1).

Relative contribution (%) of the 15 soil variables with the highest contribution to the construction of the first principal component (PC1) of the principal component analysis (PCA). The dashed line indicates the expected contribution by chance (100/p), where *p* corresponds to the total number of variables included in the analysis. Variables exceeding this threshold are considered the main contributors to the variability explained by PC1.

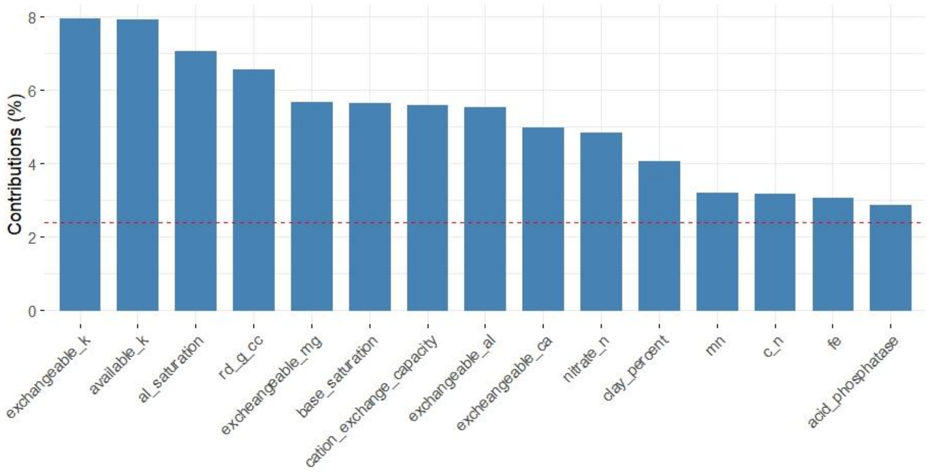

Figure S3. Contribution of variables to the second principal component (PC2).

Relative contribution (%) of the 15 soil variables with the highest contribution to the construction of the second principal component (PC2) of the principal component analysis (PCA). The dashed line represents the expected contribution by chance (100/p). Variables with contributions above this value indicate a greater influence on the definition of the chemical–nutritional gradient represented by PC2.

Table S1. Physical properties of the soil at the study sites

Site	Treatment	Sand	Silt	Clay	Texture	BD	RD	PT	FC	WP	AW	VWC	WHC
C. Cayumanqui	M-	40.40	24.20	35.40	Clay loam	1.35	2.54	46.85	23.21	13.33	9.88	13.34	2.67
	M+	42.70	26.80	30.50	Clay loam	1.32	2.56	48.44	31.35	18.67	12.68	16.74	3.35
Huaqui	M-	64.20	27.90	7.90	Sandy loam	1.38	2.52	45.24	14.89	9.17	5.72	7.89	1.58
	M+	82.00	13.30	4.70	Loamy sand	1.53	2.48	38.31	18.84	11.22	7.62	11.66	2.33
Peralillo	M-	50.70	33.50	15.80	Loam	0.95	2.47	61.54	73.59	48.48	25.11	23.85	4.77
	M+	52.30	25.70	22.00	Sandy clay loam	0.97	2.52	61.51	76.01	45.60	30.41	29.50	5.90
C. Pelado	M-	59.80	21.60	18.70	Sandy loam	1.05	2.50	58.00	44.22	28.26	15.96	16.76	3.35
	M+	71.20	17.00	11.80	Sandy loam	1.19	2.54	53.15	33.42	20.05	13.37	15.91	3.18

This table presents the physical properties of surface soils at the study sites, including particle-size distribution [sand, silt, and clay contents; %], textural class, bulk density (BD, g cm^{-3}), particle density (PD, g cm^{-3}), total porosity (TP, %), soil water retention parameters [field capacity (FC, %), wilting point (WP, %), and available water (AW, %)], volumetric water content (VWC, m^{3} m^{-3}), and water holding capacity (WHC, mm). Values correspond to means derived from five soil subsamples collected at each site and treatment.

Table S2. Chemical properties of the soil at the study sites

Site	Treatment	pH	OM	SOC	C/N	N-NO3	N-NH4	N avail	P Olsen	K avail	K exch	Ca exch	Mg exch	Na exch	SB	Al exch	CICE	Al sat	K sat	Ca sat	Mg sat	Fe avail	Mn avail	Zn avail	Cu avail	B avail	EC

C. Cayumanqui	M-	6.36	2.92	1.69	0.11	6.5	9.4	15.9	4.8	172.7	0.44	5.24	1.72	0.04	7.44	0.01	7.46	0.19	5.94	70.25	23.03	50.4	44.4	0.2	1.4	0.1	0.1
	M+	6.45	2.87	1.66	0.10	9.3	7.8	17.1	8	260.6	0.67	8.1	2.07	0.05	10.9	0.01	10.91	0.13	6.12	74.28	18.98	32	20	0.2	0.6	0.2	0.1
Huaqui	M-	6.34	3.54	2.05	0.30	1.9	4.9	6.8	9.9	141.8	0.36	3.23	0.58	0.06	4.24	0.01	4.25	0.34	8.55	75.96	13.72	19	1.1	0.2	0.3	0.4	0.1
	M+	6.41	2.83	1.64	0.30	1.6	3.8	5.4	16.9	105.8	0.27	2.28	0.65	0.05	3.25	0.01	3.26	0.44	8.32	69.73	19.91	22.2	0.9	0.2	0.1	0.3	0.1
Peralillo	M-	5.86	18.84	10.93	0.42	11.4	14.4	25.9	4	97.88	0.25	4.66	1.07	0.03	6.01	0.02	6.03	0.37	4.16	77.18	17.72	42.4	8.4	0.6	1.2	0.3	0.1
	M+	6.15	18.62	10.80	0.22	38.2	11.2	49.4	2.8	274.6	0.7	17.06	2.55	0.04	20.9	0.01	20.91	0.07	3.37	84.17	12.19	38.4	13.2	0.7	1	0.4	0.1
C. Pelado	M-	6.03	15.5	8.99	0.33	19.7	7.3	27	16.9	302.5	0.78	11.8	1.44	0.05	14.07	0.01	14.08	0.1	5.51	83.8	10.22	54.2	17.8	0.5	0.4	0.6	0.1
	M+	6.23	13.41	7.78	0.33	17.9	5.6	23.4	17.5	297.5	0.76	10.48	1.21	0.03	12.49	0.01	12.51	0.12	6.1	83.84	9.66	30	5.4	0.6	0.5	0.5	0.1

This table summarizes the chemical properties of surface soils at the study sites, including soil pH (unitless), organic matter (OM, %), soil organic carbon (SOC, %), carbon-to-nitrogen ratio (C:N), nitrate (NO_3–N, mg kg^{-1}), ammonium

(NH_4–N, mg kg⁻¹), available nitrogen (N_avail, mg kg⁻¹), Olsen phosphorus (P_Olsen, mg kg⁻¹), available potassium (K_avail, mg kg⁻¹), exchangeable cations [K_exch, Ca_exch, Mg_exch, Na_exch; cmol(+) kg⁻¹], sum of exchangeable bases (SB, cmol(+) kg⁻¹), cation exchange capacity (CEC, cmol(+) kg⁻¹), exchangeable aluminum (Al_exch, cmol(+) kg⁻¹), aluminum and base saturation (Al_sat, K_sat, Ca_sat, Mg_sat; %), micronutrients (Fe, Mn, Zn, Cu, B; mg kg⁻¹), and electrical conductivity (EC, dS m⁻¹). Values correspond to means derived from five soil subsamples collected at each site.

Table S3. Biological properties of the soil at the study sites

Site	Treatment	MBC	BR	BGN	BG	AP
C. Cayumanqui	M-	8.37 ± 0.79	0.93 ± 0.05	0.48 ± 0.09	0.23 ± 0.04	2.25 ± 0.04
	M+	8.92 ± 1.02	1.15 ± 0.14	0.95 ± 0.12	0.30 ± 0.14	1.53 ± 0.34
Huaqui	M-	10.75 ± 0.43	1.73 ± 0.07	1.34 ± 0.10	1.97 ± 0.93	1.82 ± 0.09
	M+	6.87 ± 0.72	0.89 ± 0.1	0.84 ± 0.32	2.99 ± 0.15	2.04 ± 0.01
Peralillo	M-	17.31 ± 1.53	4.57 ± 0.24	0.97 ± 0.08	6.45 ± 0.12	0.00 ± 0.00
	M+	16.45 ± 0.47	6.38 ± 1.78	7.02 ± 0.11	8.02 ± 0.05	1.67 ± 0.01
C. Pelado	M-	27.01 ± 1.96	4.15 ± 0.32	6.64 ± 0.12	6.17 ± 0.24	0.66 ± 0.01
	M+	6.89 ± 0.73	2.36 ± 0.09	5.37 ± 0.52	6.28 ± 0.11	2.59 ± 0.02

This table shows the biological properties of surface soils at the study sites, including microbial biomass carbon (MBC, µg C g⁻¹ dry soil), basal soil respiration (BR, mg CO_2 g⁻¹ day⁻¹), and enzymatic activities related to carbon, nitrogen, and phosphorus cycling, namely β-glucosaminidase (BGN), β-glucosidase (BG), and acid phosphatase

(AP), all expressed as μmol g^{-1} h^{-1}. Values are presented as mean ± standard deviation of triplicate measurements and are expressed on a dry soil basis.

CAPÍTULO 3. *QUALITY TRAITS OF THE MORCHELLA MUSHROOMS HARVESTED FROM FOREST PLANTATIONS AND NATIVE FORESTS IN SOUTH-CENTRAL CHILE.*

Tatiana Escobar-Hernández[1,2], Rodrigo Segura[3], Claudia Muñoz-Espinoza[4], Mauricio Sanz-Rocha[2], Erick Zagal[5], Valeria Velasco[6], Mhartyn Elso[2], Yudith Guillén[2], Macarena Gerding[4], Daniel Chávez[2], Ángela Machuca[2]*.

[1] Programa de Magíster en Ciencias Agronómicas, Facultad de Agronomía, Universidad de Concepción, Campus Chillán, Chile.

[2] Departamento de Ciencias y Tecnología Vegetal, Universidad de Concepción, Campus Los Ángeles, Chile.

[3] Departamento de Química de los Materiales, Facultad de Química y Biología, Universidad de Santiago de Chile, Chile.

[4] Departamento de Producción Vegetal, Facultad de Agronomía, Universidad de Concepción, Campus Chillán, Chile.

[5] Departamento de Suelos y Recursos Naturales, Facultad de Agronomía, Universidad de Concepción, Campus Chillán, Chile.

[6] Departamento de Producción Animal, Facultad de Agronomía, Universidad de Concepción, Campus Chillán, Chile.

*angmachu@udec.cl

Article submitted to Food Chemistry journal.

ABSTRACT

Morels are highly valued edible mushrooms due to their ecological and nutraceutical importance. However, nutritional studies in South America are still scarce. This study evaluated the mineral, nutritional and bioactive properties of *M. eximia*, *M. importuna*, *M. tridentina*, and the endemic *M. andinensis*, which naturally fruits in forest plantations (FP) and native forests (NF) in south-central Chile. Soils differed significantly indicating varied fertility levels across morel habitats. The ascocarps of all species showed high accumulation of K and P, which were actively translocated to the pileus. Ni and Zn accumulated moderately, As was undetectable and Cd and Pb remained within safe limits. FP species had a higher total phenolic content, while NF species showed greater antioxidant activity. All species had high protein and fiber levels. A multivariate analysis revealed that the mineral composition and bioactive and nutritional properties of *Morchella* spp. are simultaneously modulated by soil and type of forest cover.

Keywords: wild edible mushroom, *Morchella andinensis*, accumulation factor, mineral composition, nutritional quality, bioactivity.

1. INTRODUCTION

The genus *Morchella* comprises ascomycete fungi highly valued for their gastronomic appeal (Loizides, 2017; Tietel & Masaphy, 2018), nutritional composition, and bioactive potential (Li et al., 2023b; Meng et al., 2019; Wu et al., 2023; Xu et al., 2025). Commonly known as morels, these edible mushrooms are prized for their distinctive flavor, texture, and rich profile of bioactive compounds. This has made them a valuable fungal resource with potential applications in the food, nutraceutical, and pharmaceutical industries (Li et al., 2023b; Qiu et al., 2024; Sambyal & Singh, 2021; Tian et al., 2025; Xu et al., 2022).

Interest in morels has recently grown due to increasing commercial demand (Belbase et al., 2025; Li et al., 2023a; Liu et al., 2018). However, the origin of the fruiting bodies, or ascocarps, is particularly important, as those of wild origin develop in heterogeneous natural environments and may better reflect the interaction between the fungus and soil conditions (Hussain & Sher, 2021). In contrast, the available substrates and nutrients in cultivation systems are largely controlled (Fu et al., 2025; Liu et al., 2018; Xu et al., 2021; Xu et al., 2022; Zhang et al., 2024). This distinction is crucial when evaluating the presence of specific potentially toxic metallic elements, as the risk and magnitude of metal bioaccumulation can vary considerably between wild and cultivated morels (Alaimo et al., 2019; Gursoy et al., 2009; Zhang et al., 2019).

Edible wild mushrooms are known for their ability to absorb minerals from their growing environment (Badshah et al., 2023a; Gałgowska & Pietrzak-Fiećko, 2020; Zhang et al., 2024), including essential elements such as sodium (Na), potassium (K), calcium (Ca), manganese (Mn), zinc (Zn), copper (Cu), and iron (Fe) (Khan et al., 2023; Qiu et al., 2024; Zhang et al., 2024), which are necessary for metabolism. Also, non-essential or potentially toxic elements such as cadmium (Cd), lead (Pb), arsenic (As), and chromium (Cr) (Gursoy et al., 2009; Zhang et al., 2024), hazardous for human health (Badshah et al., 2023b; Mohammad et al., 2015; Qin et al., 2024). This ability gives fungi biotechnological potential for the bioremediation of contaminated environments (Dinakarkumar et al., 2024; Malik et al., 2021). However, it also raises concerns about the nutritional quality of ascocarps intended for human consumption (Bucurica et al., 2024; Li et al., 2023b; Zhang et al., 2024).

Various physiological mechanisms are involved in the metal absorption and accumulation in fungi, including biosorption in cell walls (Boulaiche et al., 2019; Papadaki et al., 2019; Tamjidi et al., 2023, active incorporation through membrane transporters (Liu et al., 2020; Xu et al., 2021), and differential translocation between the stipe and pileus of the ascocarps (Qiu et al., 2024; Robinson et al., 2021). The determination of parameters such as the accumulation factor (AF) and translocation factor (TF) allows one to assess the efficiency with which fungi absorb elements from the soil and redistribute them internally (Ab Rhaman et al., 2022; Alaimo et al., 2019; Zhang et al., 2024). This provides insight into their nutrition and detoxification strategies.

Furthermore, the presence and accumulation of metals have been recorded in *Morchella* species collected in mountainous regions and in soils with anthropogenic influences or particular characteristics (Badshah et al., 2023b; Bucurica et al., 2024; Hussain & Sher, 2021; Salihovic et al., 2022). However, most of these studies have focused on the Northern Hemisphere and often lack precise taxonomic identification of the analyzed species, difficulting the result comparisone. In the Southern Hemisphere, particularly in Chile, morels are mainly harvested from the wild because artificial cultivation has not yet been developed commercially (Machuca et al., 2014; Machuca et al., 2021). Large quantities of morels are harvested in areas with high levels of anthropogenic disturbance, as well as in more preserved forests with native vegetation. Most of the harvest is exported, while a small amount is allocated for local consumption (Instituto Forestal, 2024). However, information about the quality of the harvested product is still scarce, and a lack of data integrating the nutritional composition and presence of metals in the ascocarps of formally identified *Morchella* species.

In this context, the aim of this study is to evaluate some quality attributes of the ascocarps of the *Morchella* spp. collected from native forests and forest plantations in south-central Chile which exhibit varying degrees of anthropogenic disturbance, in order to determine the possible influence of the environment on their quality. These results should provide the scientific data necessary for a comprehensive assessment of this valuable edible resource and help identify any potential risks associated with its consumption. Furthermore, the results should provide a foundation for the sustainable and safe management of this resource by promoting best practices for harvesting and habitat conservation.

2. MATERIALS AND METHODS

2.1 Study sites

Four sites were selected in south-central Chile (latitude 36.7°-37.8°S), with a temperate Mediterranean climate, where natural fruiting of the morel has been reported. These sites represent different types of vegetation cover and disturbance conditions. Two sites are relict native forests, dominated by species of the genus *Nothofagus*: Peralillo (Pe) and Cerro Pelado (CPe) sites. Two other sites correspond to *Pinus radiata* forest plantations, which have been harvested or affected recently by fires: Huaqui (Hu) and Cerro Cayumanqui (CCa) sites, respectively. Thus, the study sites exhibit a variety of disturbances and physical characteristics allow for the wide distribution of *Morchella* spp. (Figure 7; Supplementary Table S4).

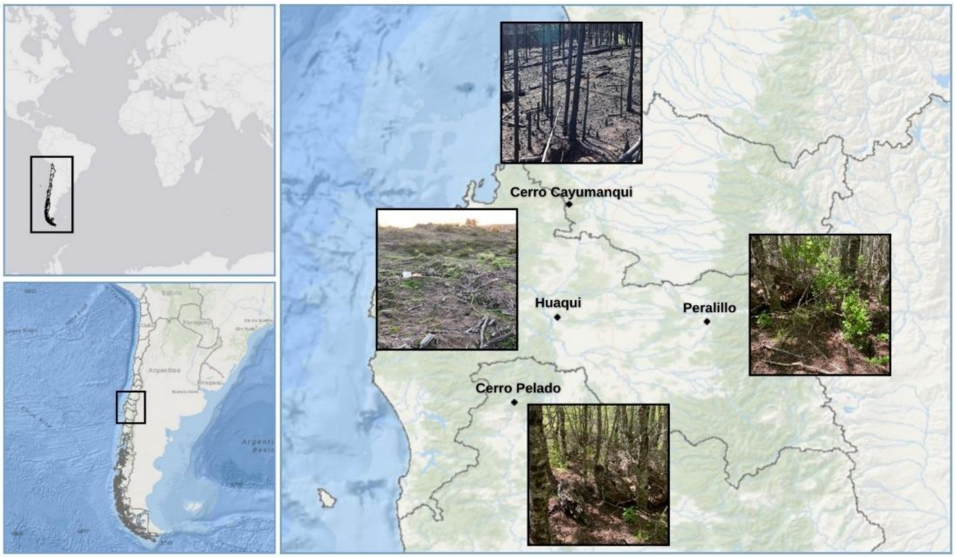

Figure 7. Geographical location and visual characteristics of the four *Morchella* spp. natural fruiting sites in south-central Chile correspond to forest plantations disturbed by fire (Cerro Cayumanqui) or logging (Huaqui), and native forests (Peralillo and Cerro Pelado). The images provide overviews of the environmental conditions at each study site.

2.2. Sampling

2.2.1. Collection of ascocarps and soils

The *Morchella* ascocarps were harvested between August and November during the 2023 and 2024 seasons. At each study site, 3 m^2 plots were demarcated. Fresh ascocarps were collected from these plots, individually packaged in paper bags, and transported to the laboratory at 4°C, where they were carefully cleaned of any soil or leaf litter.

For the soil samples, 50 g of soil were extracted from the base of each specimen. Three independent soil samples, corresponding to three different specimens, were collected at each site. In addition, within each plot, composite soil samples were collected from the surface layer (0–20 cm) in an “X” pattern. Each sample consisted of five 500 g subsamples. All soil samples were packaged in plastic bags and transported to the laboratory under refrigerated conditions (4°C).

2.2.2. Sample preparation

From each site, approximately 250 g of fresh morels were collected, and a composite sample (200 g) was obtained for proximate analysis (item 2.8). Additionally, individual samples (n = 3) were reserved for mineral content analysis (item 2.4), phenol content analysis, antioxidant activity analysis (item 2.7) and species molecular identification. To prepare the ascocarps, the samples were dehydrated and freeze-dried. Then, they were ground to a particle size of 1 mm and stored at room temperature in hermetically sealed containers with silica gel. The soil samples were homogenized and dried in an oven at 105 °C for 24 h. Then, the composite samples were sieved to a size of 2 mm and stored at 4 °C until processing. For mineral determination, the samples were sieved to 0.63 μm and stored in hermetically sealed containers with silica gel until analysis.

2.2.3. Species identification

All morel specimens collected in the field were identified based on micro and macroscopic morphological descriptions of the fresh ascocarps (Machuca et al., 2021; Sanz-Rocha et al., 2023), and representative ascocarps from each morphological group were analyzed using molecular techniques. Approximately 100 mg of dry pileus tissue were suspended in 250 µL of TL buffer (E.Z.N.A. Tissue DNA Kit, Omega), following the manufacturer's instructions. The ITS region (ITS1–5.8S–ITS2) was amplified by PCR using the ITS1 and ITS4 universal primers (White et al., 1990), according to the conditions described by Machuca et al. (2021). The PCR products were sequenced by AUSTRAL-Omics (Valdivia, Chile). The sequences obtained were edited, aligned, and compared with reference sequences available in GenBank using the Geneious v2025.0.1 software. A maximum likelihood phylogenetic tree was constructed in MEGA v5.2 software (Kumar et al., 2018), using the GTR+I+G model and evaluating the robustness of the tree with 1000 bootstrap replicates. In addition, a BLAST search was performed to confirm the identity and phylogenetic similarity of the sequences obtained. A voucher specimen of each identified species was deposited in the fungarium of the Fungal Biotechnology Laboratory at the University of Concepción, under the UDEC-LAF code.

2.3. Physical and chemical analysis of soils

The soils were characterized by determining their pH, organic matter (OM) content, carbon/nitrogen (C/N) ratio, and cation exchange capacity (CEC). The sand, silt, and clay fractions were also quantified to establish the textural class. Chemical analyses were performed according to the methods described by Sadzawka et al. (2006) and Sadzawka (1990), while physical analyses were performed according to the procedures reported by Sandoval et al. (2012).

2.4. Analysis of essential and non-essential mineral elements

For the analysis of mineral elements, the ascocarps and soil samples were mineralized, for which sieved samples (0.63 µm) of 0.2 g of ascocarps and dry soil were weighed. Then, acid digestion was performed in Teflon bombs, adding 8 mL of 65% HNO_3 and 2 mL of 30% H_2O_2, using a microwave digestion system (Milestone Ethos Easy) for 90 min at 200°C. After cooling, the samples were filtered through 0.45 µm filters and then gauged to 25 mL with ultrapure water (Milli-Q). Ca, Cu, Fe, K, Na, P, and Zn were determined in the mineralized samples using flame atomic absorption spectrometry (FAAS) on an Analytik Jena AnovA 350 (Cu, Fe, and Zn) and on a Thermo Scientific ICE 3000 Series instrument (Ca, K, Na, and P). The calibration curves were made using standards at four different concentrations, manually adjusted for each element based on the linear response range of the device. Analytical quality was verified in all cases by evaluating the coefficient of determination ($R^2 > 0.95$). Meanwhile, As, Cd, Co, Cr, Mn, Ni, and Pb were determined using a Thermo Scientific ICE 3500 Series graphite furnace atomic absorption spectrometer (GF-AAS) under the manufacturer's optimal conditions. For these analyses, an external standard of 50 g L^{-1} was used for each element, and calibration curves were made, and the linearity was confirmed using the coefficient of determination ($R^2 > 0.95$). Three categories were established to analyze the mineral elements found in soils and ascocarps: i) major essential elements: Ca, K, Na, P (g kg^{-1}); ii) essential trace elements: Co, Cr, Cu, Fe, Mn, Ni, Zn (mg kg^{-1}); and iii) trace elements potentially harmful to health: As, Cd, Pb (mg kg^{-1}).

2.5. Accumulation factor (AF)

The accumulation factor of mineral elements by *Morchella* spp. was calculated as the ratio of the element concentration in the ascocarps to its concentration in the corresponding soil, using the following formula (1) (Olowoyo et al., 2010):

$$AF = \frac{Concentration\ of\ the\ element\ in\ the\ ascocarps\ (m\ kg^{-1})}{Concentration\ of\ the\ element\ in\ the\ soil\ (mg\ kg^{-1})} \qquad (1)$$

AF values > 1 indicates that the ascocarps are actively accumulating the element from the soil, while AF < 1 suggests that the ascocarps are excluding or absorbing it in smaller proportions (Murtić et al., 2024).

2.6. Translocation factor (TF)

To determine the translocation factor, samples of the pileus and stipe of morel ascocarps were analyzed separately. Then, the translocation factor of mineral elements in *Morchella* spp. was calculated as the ratio of the pileus concentration to the stipe concentration using the following formula (2) (Dimitrijević et al., 2021):

$$TF = \frac{Concentration\ of\ the\ element\ in\ pileus\ (mg\ kg^{-1})}{Concentration\ of\ the\ element\ in\ the\ stipe\ (mg\ kg^{-1})} \quad (2)$$

TF values > 1 indicate that the ascocarp actively translocates the element from the stipe to the pileus, whereas TF < 1 indicates a reduced element mobilization (Badshah et al., 2023b).

2.7. Analysis of total phenols and antioxidant activity

2.7.1. Total phenols

Dried and ground samples of the ascocarps were weighed to 0.2000 g into 50 mL Falcon tubes and then 10 mL of 70% acetone was added. The suspension was placed in an ultrasonic bath for 30 min, after which it was centrifuged at 4400 rpm for 30 min at 4°C. The supernatant was recovered and stored in an ice bath for later total phenols analysis. The Folin-Ciocalteu reagent was used to quantify total phenols in the extracts according Slinkard and Singleton (1977). The results were expressed as tannic acid equivalents per gram of dry material (mg TAE g^{-1} DM).

2.7.2. Antioxidant activity

The antioxidant activity was determined using a methanolic extract of the dried and ground ascocarps. Then, 7.5 mg of the sample was weighed and processed according to the methodology of Hatano et al. (1998). The mixture was kept in an ultrasonic bath for 24 hours at 4°C in darkness. Afterward, it was centrifuged at 4,400 rpm for 30 min at 4°C, and the supernatant was recovered and stored in ice bath until analysis. Antioxidant activity was determined using the stable 2,2-diphenyl-1-picrylhydrazyl (DPPH) free radical, following the methodology of Gursoy et al. (2009). The results were expressed in terms of percentage inhibition of the DPPH free radical (I%), calculated according to the following formula (3):

$$I\% = \frac{A\ control - A\ sample}{A\ control} \times 100 \qquad (3)$$

2.8. Proximate composition

To determine the proximate composition, composite samples (200 g of fresh material) of ascocarps were collected from native forest sites (Cerro Pelado and Peralillo) and forest plantation sites (Huaqui and Cerro Cayumanqui). These procedures followed the official methodologies of the Association of Official Analytical Chemists (1997). Moisture content (MC) was determined by drying the samples in an oven at 105°C until they reached a constant weight. The MC was then calculated using the following formula (4):

$$MC\ (\%) = \frac{Weight\ fresh - Weight\ dry}{Weight\ fresh} \times 100 \qquad (4)$$

The following parameters were quantified: crude protein (CP) using Kjeldahl (method 991.20), crude fiber (CF) by digestion (method 926.09), total ash (TA) by muffle furnace calcination (method 942.05), and (EE) by Soxhlet extraction (method 920.39C). The non-nitrogen extract (NNE) content was calculated by difference according to the following formula (5):

$$NNE\ (\%) = 100 - (CP\ (\%) + EE\ (\%) + CF\ (\%) + TA\ (\%)) \qquad (5)$$

The metabolizable energy (E) was calculated using Atwater's equation (1910) (6):

$$E\ (kcal\ 100\ g^{-1}) = 4 \times CP\ (\%) + 9 \times EE\ (\%) + 4 \times NFE\ (\%) \qquad (6)$$

2.9. Statistical analysis

All the analyses were performed in triplicate, and results were expressed as the mean ± standard deviation. Statistical analysis was performed using the R software (R Development Core Team, 2024), with a significance level of $p < 0.05$. Assumptions of normality and homogeneity of variances were verified for each data set. An analysis of variance (ANOVA) was performed on variables that accomplished these assumptions, followed by an LSD (least significant difference) multiple comparison test. When statistical assumptions were not met, transformations and nonparametric tests were applied. The Cr values used to determine the TF were transformed using log(x+1) to meet the assumptions required for the ANOVA. Variables that did not reach normality, such as the Cu and Ni content in ascocarps, and the As, Cd, Co, Cu, Ni, Na, and Pb content for determining AF and As for determining TF, were analyzed using the nonparametric Kruskal-Wallis test, followed by Dunn's multiple comparison test. A principal component analysis (PCA) was also performed with 21 variables related to ascocarp quality using the R statistical software and the FactoMineR library. Then, to identify the most contributing variables, a correlation analysis was performed between the variables and the first two components derived from PCA. The analysis selected the variables that were significantly correlated ($p < 0.05$) (Muñoz-Espinoza et al., 2016).

3. RESULTS AND DISCUSSION

Although morels are commercially cultivated in countries such as China (Liu et al., 2023), wild harvesting remains the primary method of acquiring and consuming them in many other countries. In Chile, *Morchella* spp. can be found in pristine native forest ecosystems such as those in Patagonia (Machuca et al., 2021; Pfister et al., 2022). However, it can also be found outside of Patagonia in forest plantations (FP) and native forests (NF) that have experienced varying degrees of anthropogenic disturbance (Sanz-Rocha et al., 2023). Most of the morels harvested in Chile are mainly exported to European markets. Only a small portion is sold for consumption in local markets (Instituto Forestal, 2024). Due to the economic importance of this export resource, this study evaluated the quality attributes of *Morchella* spp. ascocarps harvested from different forest environments in south-central Chile to determine the possible influence of the environment on the quality of the resource.

3.1. Study sites

The study sites where *Morchella* spp. fruited differed in their degree of disturbance (Supplementary Table S1). The FP sites showed the most altered environments. Cerro Cayumanqui (CCa) was affected by an extended fire in February 2023, and

Huaqui (Hu) was subjected to logging for timber harvest in December 2022. In contrast, the NF sites, Peralillo (Pe) and Cerro Pelado (CPe), represent relicts that, despite conserving native vegetation, are surrounded and have been partially invaded by exotic plantations, mainly in the case of Pe site. The soils at these study sites (NF and FP) also showed contrasting physical and chemical properties (Table 4).

Table 4. Physical and chemical characteristics of soils at the different study sites where *Morchella* spp. fruits naturally in south-central Chile.

Site	pH	OM (%)	C/N	CEC (cmol$^+$ kg^{-1})	Sand (%)	Silt (%)	Clay (%)	Textural class
Burned forest plantation (CCa)	6.50	2.87	0.10	10.91	42.70	26.80	30.50	Clay loam
Logged forest plantation (Hu)	6.40	2.83	0.30	3.26	82.00	13.30	4.70	Loamy sand
Native forest (Pe)	6.20	18.62	0.22	20.91	52.30	27.70	22.00	Sandy clay loam
Native forest (CPe)	5.90	11.37	0.54	8.11	62.40	21.50	16.10	Sandy loam

The values correspond to composite samples (n = 5) from each study site. CCa: Cerro Cayumanqui, Hu: Huaqui, Pe: Peralillo, CPe: Cerro Pelado.

The pH of the soil was similar and slightly acidic at all sites, mainly at site CPe (5.90) in NF. The carbon-nitrogen ratio (C/N) was also similar at all sites, and particularly low values (0.10) were observed at the CCa site in FP. In contrast, organic matter (OM) content and cation exchange capacity (CEC) parameters showed the greatest differences between sites. The OM content varied widely, ranging from over 10% at the NF sites to 2.8% at the FP sites.In the case of CEC, the highest value was observed at the Pe site in NF (20.91 cmol^{+} kg^{-1}) and the lowest at the Hu site in FP (3.26 cmol^{+} kg^{-1}). These parameters (OM and CEC) are indicators of superior fertility and greater nutrient retention, associated with the accumulation of leaf litter and a lower degree of disturbance (Food and Agriculture Organization of the United Nations, 2017; Gerke, 2022; Voltr et al., 2021). This is consistent with observations at NF sites. In contrast, sites of harvested or burned forest plantation (FP) had low OM content and CEC, suggesting lower soil quality and reduced nutritional support capacity (Certini, 2005; Ulery et al., 2017).

Differences in soil texture were observed among the sites related to varying proportions of sand, silt, and clay. The FP sites were notable for having soils with higher sand (Hu) and clay (CCa) content. These results indicated that the study sites have contrasting soil conditions, ranging from lighter soils with low water retention (Hu) to finer soils with greater retention capacity (CCa). These results showed that morels can fruit under a wide range of soil conditions, demonstrating remarkable ecological plasticity in response to different soil qualities and textures.

3.2. *Morchella* species

This study used morphological descriptions and sequencing of the ITS region (Machuca et al. 2021; Sanz-Rocha et al. 2023) to confirm the identification of four

Morchella species from the Elata clade in south-central Chile (Supplementary Table S5; Figure S4; Figure S5). Each species was associated with a particular site, and there was no overlap in their distribution. At the FP sites, all the specimens analyzed from the fire-affected site (CCa) showed 99.7-100% similarity to *M. eximia*. This is consistent with the strictly pyrophilic nature of *M. eximia* described in the literature, which requires fire events to trigger the production of fruiting bodies (Du et al., 2015; Loizides, 2017; Pfister et al., 2022). Conversely, the specimens from the logged forest plantation (Hu) showed 100% similarity to *M. importuna*, which suggests an affinity of this species for highly disturbed environments. Depending on their location, the NF specimens exhibited 100% similarity with *M. tridentina* (Pe) and between 99.84-100% similarity with *M. andinensis* (CPe) (Supplementary Table S5). These results are consistent with previous studies describing the presence of these *Morchella* species in less disturbed environments dominated by *Nothofagus* spp. (Machuca et al., 2021; Pfister et al., 2022; Pildain et al. 2014). Although knowledge of species diversity is key scientific significance, it should be noted that morels are currently marketed and exported as a single product without differentiation by species or harvesting environment.

3.3. Soils mineral content

The soils at the sites where *Morchella* spp. fruited in south-central Chile varied significantly in the concentration of major, essential, and potentially toxic elements

(Table 5). In most cases, the levels of analyzed mineral elements were significantly higher in soils at FP sites than at NF sites. This difference reflects the influence of anthropogenic disturbance and the edaphic origin of the study sites (Garrido-Ruiz et al., 2022; Hussain & Sher, 2021; Zhang et al., 2024).

Table 5. Element contents in soils at the different study sites where *Morchella* spp. fruits in south-central Chile.

Element	Burned forest plantation (CCa)	Logged forest plantation (Hu)	Native forest (Pe)	Native forest (CPe)
Major essential elements (g Kg^{-1})				
Ca	1.42 ± 0.09 b	7.58 ± 0.24 a	1.03 ± 0.03 c	1.56 ± 0.01 b
K	5.75 ± 0.13 a	0.78 ± 0.07 c	0.53 ± 0.00 d	2.13 ± 0.02 b
Na	21.42 ± 20.79 a	5.29 ± 0.05 ab	0.57 ± 0.01 b	0.21 ± 0.03 b
P	0.54 ± 0.03 d	0.65 ± 0.02 c	1.71 ± 0.06 a	0.94 ± 0.08 b
Essential trace elements (mg Kg^{-1})				
Co	7.33 ± 0.03 a	5.67 ± 0.22 b	7.18 ± 0.03 a	3.88 ± 0.00 c
Cr	22.56 ± 0.73 a	12.40 ± 0.61 c	15.62 ± 0.11 b	7.13 ± 0.52 d
Cu	0.03 ± 0.00 b	0.03 ± 0.00 b	0.05 ± 0.00 a	0.01 ± 0.00 c
Fe	44.84 ± 2.33 a	25.67 ± 2.84 c	46.77 ± 0.71 a	31.95 ± 0.81 b
Mn	21.85 ± 0.55 a	20.99 ± 0.08 ab	20.56 ± 0.74 b	18.62 ± 0.06 c
Ni	7.03 ± 0.54 b	12.03 ± 0.35 a	6.56 ± 0.32 b	1.30 ± 0.01 c
Zn	0.08 ± 0.04 ab	0.02 ± 0.00 c	0.09 ± 0.00 a	0.05 ± 0.00 bc
Trace elements potentially harmful to health (mg Kg^{-1})				
As	9.95 ± 1.08 a	1.25 ± 0.29 c	4.38 ± 0.27 b	2.00 ± 0.77 c
Cd	0.34 ± 0.01 b	0.28 ± 0.00 c	0.56 ± 0.05 a	0.27 ± 0.00 c
Pb	8.48 ± 1.46 a	1.60 ± 0.02 d	5.45 ± 0.03 ac	4.03 ± 0.18 c

Values correspond to the mean ± standard deviation (n = 3). Different letters in the row indicate significant differences ($p < 0.05$). CCa: Cerro Cayumanqui, Hu: Huaqui, Pe: Peralillo, CPe: Cerro Pelado.

As for the major essential elements (g Kg^{-1}), the highest levels of calcium (Ca), potassium (K), and sodium (Na) were found in the soils at the FP sites. The highest level of K was found in the burned FP site, while the highest levels of Ca and Na were found in the logged FP site. High variability was observed for Na, with the maximum value found at the burned FP site. On the other hand, the NF sites had the lowest concentrations of Ca, K, and Na, but the highest levels of phosphorus (P). This was especially remarkable at the Pe site, where the levels were significantly higher than at the other sites (Table 5).

Contrasting patterns were recorded regarding the trace elements (mg Kg^{-1}) in the soils of the PF and NF sites. The highest contents of cobalt (Co) and iron (Fe) were detected at the burned FP site and Pe site (NF). These values were significantly higher than those at the other sites. The highest content for chromium (Cr) was detected at the burned FP site, followed by Pe site (NF). Meanwhile, the highest content of nickel (Ni) was detected at the logged FP site. The manganese (Mn) content was high and similar across sites, whereas the zinc (Zn) and copper (Cu) content was low and similar as well.

In terms of potentially toxic trace elements the levels of arsenic (As) and lead (Pb) were significantly higher in the soils at the burned FP site, followed by the NF sites. Meanwhile, the highest cadmium (Cd) content was detected at the NF site (Pe) (Table 5).

Harvested FP had the highest Ca and Ni contents, which may be linked to the removal of vegetation cover and exposure of the mineral horizon. Consistent with the literature, burned FP had high concentrations of K, Cr, As, and Pb, indicating that fires can mobilize nutrients and metals immediately, albeit temporarily (Alcañiz et al., 2018; Garrido-Ruiz et al., 2022; Gómez-Rey & González-Prieto, 2014). Thus, the results suggest that both the type of disturbance (burning or logging) and the intrinsic characteristics of the soil determine the availability of nutrients and metals (Zhang et al., 2024), directly affecting the ecology of *Morchella* spp. and its fruiting capacity (Hussain & Sher, 2021).

3.4. Ascocarp mineral content

As a quality trait of the ascocarps of *Morchella* spp. collected from the various study sites, the mineral composition was assessed in terms of essential and potentially toxic non-essential elements. The ascocarps collected at the FP and NF sites showed significant variations in the concentration of essential and potentially toxic mineral elements. For most elements, the highest concentrations were detected in the ascocarps of species harvested from the FP site that were burned (*M. eximia*) or logged (*M. importuna*) (Table 6).

Table 6. Element contents in morchella ascocarps harvested from forest plantations (*M. eximia* and *M. importuna*) and native forests (*M. tridentina* and *M. andinensis*) in south-central Chile.

Element	*M. eximia*	*M. importuna*	*M. tridentina*	*M. andinensis*
		Major essential elements (g Kg^{-1})		
Ca	0.38 ± 0.17 b	0.71 ± 0.08 a	0.23 ± 0.02 b	0.76 ± 0.05 a
K	34.72 ± 0.90 b	29.56 ± 0.66 c	30.66 ± 1.14 c	42.03 ± 0.49 a
Na	0.48 ± 0.23 ab	0.64 ± 0.16 a	0.23 ± 0.09 b	0.32 ± 0.01 b
P	16.22 ± 0.57 a	12.05 ± 0.79 b	12.78 ± 0.03 b	15.52 ± 0.13 a
		Essential trace elements (mg Kg^{-1})		
Co	0.27 ± 0.07 bc	0.42 ± 0.08 a	0.20 ± 0.07 c	0.28 ± 0.05 b
Cr	14.33 ± 2.59 a	13.88 ± 3.19 a	5.63 ± 2.60 b	4.13 ± 2.23 b
Cu	0.03 ± 0.00 a	0.01 ± 0.00 bc	0.01 ± 0.00 ac	0.01 ± 0.00 b
Fe	0.54 ± 0.07 b	0.77 ± 0.05 a	0.24 ± 0.06 c	0.21 ± 0.08 c
Mn	14.28 ± 0.50 ab	13.74 ± 0.37 bc	11.81 ± 2.24 c	16.78 ± 1.48 a
Ni	20.57 ± 9.99 a	7.44 ± 2.41 b	7.62 ± 2.49 b	10.07 ± 4.78 b
Zn	0.09 ± 0.01 a	0.07 ± 0.03 a	0.09 ± 0.04 a	0.09 ± 0.03 a
		Trace elements potentially harmful to health (mg Kg^{-1})		
As	0.00 ± 0.00 a	0.00 ± 0.00 a	0.00 ± 0.00 a	0.00 ± 0.00 a
Cd	1.13 ± 0.11 a	0.46 ± 0.14 d	0.65 ± 0.13 c	0.90 ± 0.04 b
Pb	0.51 ± 0.00 b	1.83 ± 0.64 a	0.37 ± 0.07 b	0.80 ± 0.63 b

Values correspond to the mean ± standard deviation (n = 3). Different letters in the row indicate significant differences ($p < 0.05$).

The general trend in the concentration of major elements in *Morchella* ascocarps was K > P >> Ca ≈ Na. Among the species, *M. importuna* and *M. andinensis* showed the highest Ca content, whereas K, the most abundant macronutrient in all species, was significantly higher in *M. andinensis*. In addition, *M. importuna* had also the highest Na concentration, followed by *M. eximia*, which together with *M. andinensis* had the highest P concentrations (Table 6).

Trace elements showed the general trend Ni > Mn > Cr >> Fe > Co > Zn > Cu in the *Morchella* ascocarps (Table 6). Among the FP species, *M. eximia* exhibited the highest concentrations of Cu and Ni, while *M. importuna* had the highest concentrations of Co and Fe. Both species had significantly higher Cr content in their ascocarps than the other species. The NF species *M. andinensis* showed the highest concentration of Mn in its ascocarps, followed by *M. eximia*, though the difference was not significant. Zn was the only trace element that showed no significant differences among the different *Morchella* species.

Regarding potentially toxic elements, the Cd concentration was significantly higher in *M. eximia*, while the Pb concentration was higher in *M. importuna*; both species were found in FP. However, the Pb concentration was also high in *M. andinensis* from NF (Table 6). Under the analytical conditions of this study, none of the *Morchella* species had detectable concentrations of As in their ascocarps. This is despite the fact that significant quantities of As and Pb were found in the soils of the study sites, at much higher concentrations than Cd, mainly at the burned FP site. However, As was not detected in the ascocarps of any of the *Morchella* species under our analysis conditions. This absence is particularly relevant from a nutritional point of view, considering that As is one of the most toxic and highest-risk metalloids in wild fungi, having been detected in other edible species such as *Amanita caesarea* or *Boletus edulis* (Bucurica et al., 2024; Falandysz & Borovička, 2013; Salihovic et al., 2022).

The determination of mineral element accumulation in the *Morchella* ascocarps using the accumulation factor (AF) revealed significant differences between species, depending on the element type (Figure 8). All *Morchella* species from FP and NF showed a high accumulation of K and P (AF >> 1), while Ca and Na accumulation was limited (AF < 1) (Figure 2A). In the case of K, the marked accumulation (AF 6 - 58) showed the general trend *M. tridentina* > *M. importuna* > *M. andinensis* > *M. eximia*. Despite having lower AF values than K, P was also present in large quantities (AF 7.5–30) in the ascocarps of the different species, following the trend *M. eximia* > *M. importuna* > *M. andinensis* > *M. tridentina* (Figure 8A). The results suggest that morels may act as superaccumulators of macronutrients with a notably species-specific accumulation capacity. Thus, although the contents of these elements (K and P) were not the highest in the soil, the intrinsic capacity of the species enabled them to accumulate these elements in their ascocarps. This behavior is consistent with previously reported studies in other edible fungi such as *B. edulis* and *Cantharellus cibarius*, where K and P also accumulated significantly, which would be related to their physiological relevance (Falandysz & Borovička, 2013; Kalač, 2016; Zhang et al., 2019). On the other hand, the accumulation of these elements highlights their nutritional importance. Both elements play key roles in the human body (Kalač, 2016; Valverde et al., 2015), such as electrolyte balance, muscle function, and blood pressure regulation in the case of K, and bone and tooth formation in the case of P (National Institutes of Health, 2022a,b; Whitney & Rolfes, 2016). In contrast, the low accumulation of Ca and Na (AF <1) in the ascocarps of all species suggests the presence of exclusion mechanisms or low ionic mobility, consistent with the osmotic and homeostatic regulatory strategies described for ectomycorrhizal fungi (Alaimo et al., 2019; Zhang et al., 2019). The low Ca content in morels agrees with reports on most edible fungi, where this element is generally found in low levels due to its limited mobility and poor intracellular accumulation capacity (Gałgowska & Pietrzak-Fiećko, 2020; Gursoy et al., 2009; Vieira et al., 2016). Although low Ca content reduces its contribution to the diet, this characteristic is considered physiologically normal within the group of edible fungi (Falandysz & Borovička, 2013; Kalač, 2016). Nevertheless, a low concentration of sodium is a positive attribute from a nutritional point of view since it is desirable in human nutrition and contributes to regulating blood pressure and water balance (Khan et al., 2023; Mohammad et al., 2015; NIH, 2022c; Valverde et al., 2015). These results confirm that, although morels are not a significant source of Ca, their low Na content and high K and P content reinforce their value as a healthy, functional food.

A significant accumulation (AF > 1) of Ni and Zn was observed among the essential trace elements. The high Ni accumulation (AF 3–6.8) following the trend

M. andinensis > *M. tridentina* > *M. eximia*. *M. importuna* was the only species that showed limited Ni accumulation (AF 0.62) in its ascocarps. The AF values for Zn were lower than those observed for Ni; however, Zn accumulated in the ascocarps of all the species (AF 1.4 - 2.9) (Figure 8B). Although Ni plays an important physiological role at low concentrations, excess Ni can be toxic to the human body (Miles & Chang, 2004; Dighton, 2003). However, the concentrations detected in *Morchella* spp. remain within safe consumption ranges (Badshah et al., 2023b; Qin et al., 2024; Food and Agriculture Organization of the United Nations and World Health Organization, 2021), so moderate levels could contribute to essential micronutrient intake without posing a health risk. The other trace elements exhibited a limited (Cr, Cu, and Mn) to very limited (Co and Fe) accumulation in the ascocarps of the different *Morchella* species (Figure 8B). This is similar to reports regarding other wild edible mushrooms (Falandysz & Borovička, 2013; Isildak et al., 2004; Turkekul et al., 2004). In the case of Fe, one of the most abundant elements in the soils at the study sites, the lowest accumulation values (AF 0.05) were observed, suggesting an active exclusion or very limited absorption. This could be related to the low bioavailability of Fe in its ferric state (Kalač, 2016; Liu et al., 2017).

Regarding potentially harmful elements, the AF values indicated the accumulation of Cd and Pb (AF > 1) (Figure 8C). The Cd exhibited a significant accumulation in all species (AF 1.6–3.5), in the order *M. andinensis* ≈ *M. eximia* > *M. tridentina* >

M. importuna. For Pb, only *M. importuna* showed accumulation of this element (AF 1.15), while the other species had limited accumulation in their ascocarps (≤ 0.19). These results are consistent with those reported for other species in the genus, such as *M. esculenta, M. galilaea*, and *M. conica*, in which a greater accumulation of Cd than for Pb has also been observed (Badshah et al., 2023b; Kalač & Svoboda, 2000; Qin et al., 2024; Vieira et al., 2016). Cd accumulation appears to be a common trait in the genus *Morchella*, possibly due to its ability to synthesize chelating compounds such as chitin, melanins, and polysaccharides, which immobilize metals and reduce their intracellular toxicity (Alaimo et al., 2019; Gadd, 2007). Several authors have suggested that low concentrations of Cd could even play an ecological role in wild fungi by acting as a defense mechanism against insects or microorganisms predation, a phenomenon also observed in plants (Falandysz & Borovička, 2013; Falandysz et al., 2017). The Cd concentrations recorded in *Morchella* did not exceed the permissible limits established by the FAO/WHO (2021) for human consumption, maintaining levels within safe margins and ensuring its safety. Thus, the accumulation patterns of essential and non-essential elements in *Morchella* ascocarps suggest a strategy involving a significant accumulation of essential elements (K, P, Zn, Ni), selective exclusion of others (Ca, Na, Fe), and limited retention of potentially toxic elements. These patterns suggest a physiological regulatory mechanism balancing nutrition, detoxification, and environmental responses, which may be influenced by species- and habitat-specific conditions.

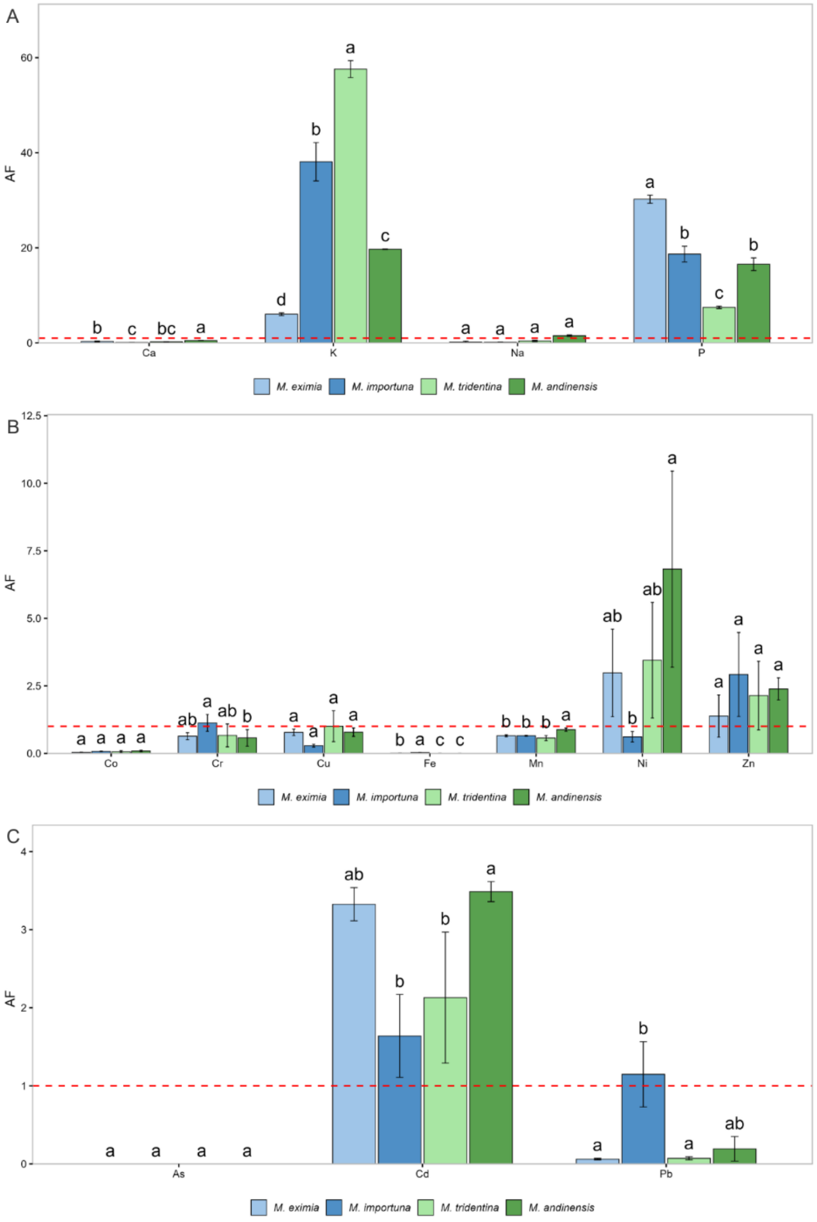

Figure 8. Accumulation factor (AF) of (A) major essential elements, (B) essential trace elements, and (C) trace elements potentially harmful in morchella ascocarps collected in forest plantations (*M. eximia* and *M. importuna*) and native forests (*M. tridentina* and *M. andinensis*) in south-central Chile. Values correspond to means ± standard deviation (n = 3). The dashed red line indicates the AF threshold = 1, signifying the accumulation of the element in the ascocarp relative to the soil.

The translocation factor (TF) of elements was only assessed in species from NF, given that *M. andinensis* is a species endemic to South America (Machuca et al., 2021; Pildain et al. 2014), making it a particularly relevant as a fungal resource of ecological and local interest. *M. tridentina* was also included in this analysis despite being a transcontinental species, to facilitate a direct comparison with *M. andinensis*, as both species fruit in the same type of NF ecosystem. The translocation of mineral elements from the stipe to the pileus differed between the two species depending on the element evaluated (Figure 9). Among the major essential elements (Figure 9A), only K and P showed active translocation to the pileus (TF > 1) in both species, with slightly higher P values (1.44) in *M. tridentina*. In the case of Ca, *M. andinensis* exhibited an almost equal distribution between the two structures, with a TF value of 0.94, which was significantly higher than the value of 0.65 obtained for *M. tridentina*. In contrast, TF values < 1 were obtained for Na in both species (0.57–0.59), indicating a preferential accumulation in the stipe. Thus, while Ca and Na exhibited limited mobility and remained in the stipe (TF < 1), K and P actively moved toward the pileus in both species (TF > 1). This is consistent with the role of K and P in respiration and reproduction processes (Liu et al., 2023; Zhang et al., 2019), and the lower mobility of Ca and Na in fungal tissues (Falandysz & Borovička, 2013; Kalač, 2016).

Regarding the essential trace elements, only Cr, Cu, and Zn showed translocation to the pileus (TF > 1), with significant differences among species (Figure 9B).

These differences could reflect physiological variations in transport efficiency and the metabolic utilization of metals (Falandysz & Borovička, 2013; Gadd, 2007; Kalač & Svoboda, 2000). For Cr, a trend toward transport to the pileus was only detected in *M. andinensis* (TF 2.24), and for Cu, this translocation occurred only in *M. tridentina* (TF 1.60). Both species showed Zn translocation of the element toward the pileus (TF > 1), with the highest values for *M. andinensis*. TF values < 1 were observed for Co, Fe, and Ni in both species, and for Mn, the values were close to one (TF ≈ 1), mainly in *M. andinensis*. Of the potentially toxic elements, only Cd showed preferential accumulation in the pileus (TF > 1), mainly in *M. tridentina* (TF 2.13) (Figure 9C). In contrast, greater retention of Pb was detected in the stipe of both species (TF < 1).

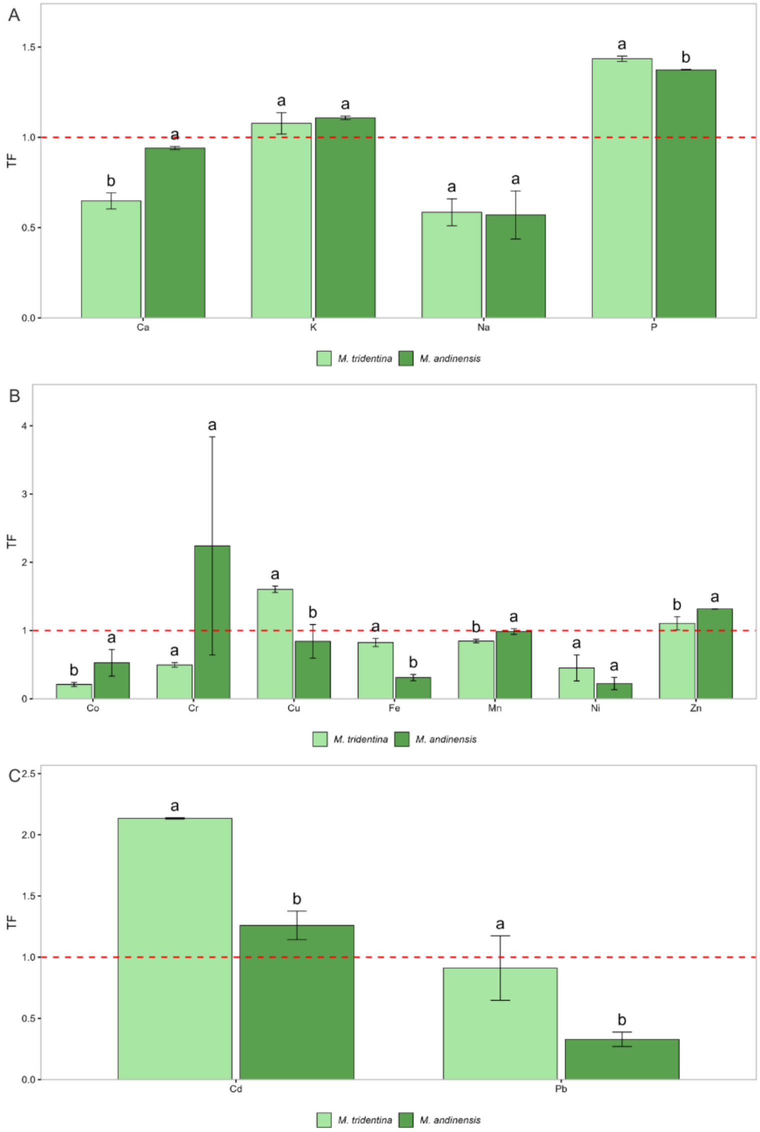

Figure 9. Translocation factors (TF) of (A) major essential elements, (B) essential trace elements, and (C) trace elements potentially harmful between pileus and stipe in *Morchella* species from native forest. Values correspond to means ± standard deviation (n = 3). The red dashed line indicates the TF threshold = 1, representing an equal distribution of the element between the structures, with values > 1 indicating greater translocation to the pileus.

Since the pileus is the most consumed part of the *Morchella* ascocarps, the fact that there is a higher accumulation of essential elements in these structures is relevant from a nutritional perspective. However, in the case of potentially toxic elements, it could pose a safety risk (Badshah et al., 2023b; Falandysz et al., 2017). Therefore, the combination of AF and TF provides an integrated perspective of mineral dynamics in *Morchella* spp., where selectivity, mobility, and accumulation adapt to physiological demands and environmental conditions. In Chile, there are no reference values for Cd or Pb in wild or cultivated edible mushrooms. Therefore, it is not possible to establish specific consumption recommendations. However, the levels detected in morels are within internationally accepted safe ranges (FAO/WHO, 2021; Falandysz et al., 2017; Kalač, 2016), meaning only high and frequent consumption would pose a risk. This emphasizes the importance of regulations and systematic monitoring to ensure the safety of wild fungal products.

3.5. Bioactivity and proximate composition of *Morchella* ascocarps

Other quality attributes measured in the morel ascocarps included biological activity, which was determined by the phenolic compound content and antioxidant activity, and nutritional quality, which was determined by proximate composition.

The total phenol content in the ascocarps showed significant differences among species from different habitat type (Figure 10A). The two species associated with FP, *M. eximia and M. importuna*, exhibited the highest total phenol values (164.4

and 183.1 mg TAE g^{-1} DM, respectively), with no significant differences between them. However, both NF species, *M. tridentina* and *M. andinensis*, presented similar levels of total phenols (109.9 and 124.8 mg TAE g^{-1} DM, respectively), lower than those of the FP species, although *M. andinensis* did not differ significantly from *M. eximia*. The antioxidant activity of ascocarps (Figure 10B), determined as DPPH radical inhibition (%), showed significant differences among species from different habitats. The ascocarps of the FP species, *M. eximia* and *M. importuna*, showed similar values of DPPH radical inhibition, with averages close to 80%, with no statistical differences between them. In contrast, ascocarps from the two NF sites exhibited greater variability. *M. andinensis* showed antioxidant activity (close to 90%) significantly higher than *M. importuna* and *M. eximia* from FP. Meanwhile, *M. tridentina* showed an intermediate value, statistically comparable to the other species.

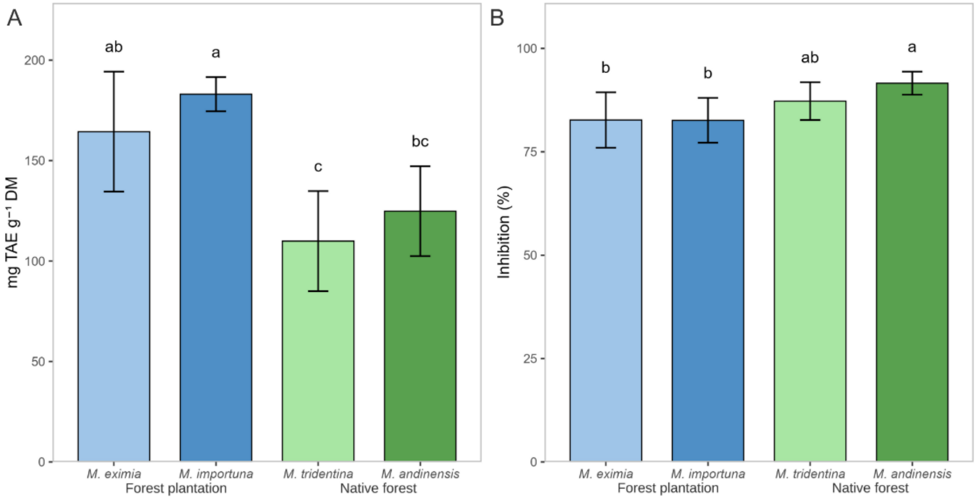

Figure 10. Total phenol content (mg TAE g-1 DM) (A) and the antioxidant activity (B) expressed as inhibition (%) of the DPPH radical by the morchella ascocarps collected from forest plantations (*M. eximia* and *M. importuna*) and native forests (*M. tridentina* and *M. andinensis*) in south-central Chile. Values correspond to the mean ± standard deviation (n = 3). Different letters above the bars indicate significant differences between species ($p < 0.05$).

These differences suggest that both the species and forest cover type could influence the bioactive potential of *Morchella* spp. (Meng et al., 2019; Taşkın et al., 2020; Tietel & Masaphy, 2018). The ascocarps collected in FP exhibited a higher total phenolic content than those collected in NF. This could be related to the more stressful environmental conditions in FP, such as lower plant diversity (Palfner & Casanova-Katny, 2019), and exposure to a highly disturbed environment, factors that stimulate the synthesis of secondary metabolites with protective functions in fungi (Barros et al., 2007; Gursoy et al., 2009; Reis et al., 2012; Tietel & Masaphy, 2018). In contrast, NF ascocarps, particularly those of *M. andinensis*, showed high antioxidant activity, suggesting the presence of antioxidants other than phenolic compounds or those with greater DPPH radical inhibitory capacity (Gursoy et al., 2009; Meng et al., 2019; Taşkın et al., 2020; Tietel & Masaphy, 2018). This pattern aligns with reports on other wild edible mushrooms, where antioxidant activity does not always correlate with phenolic content (Cheung et al., 2003; Heleno et al., 2015), but rather with the presence of polysaccharides or bioactive peptides (Badshah et al., 2021; Li et al., 2017; Qiu et al., 2024; Taşkın et al., 2020; Wu et al., 2023).

Unlike the previously described tests, the proximate composition analysis of *Morchella* ascocarps was not performed at the species level, due to limited material availability and the considerable sample volume was required for species determination. For this reason, composite samples were formed from FP ascocarps (mixture of *M. eximia* and *M. importuna*), and NF ascocarps (mixture of *M. tridentina* and *M. andinensis*). A proximate analysis of *Morchella* ascocarps showed no significant differences between FP and NF, except for moisture content, total ash, and metabolizable energy (Table 7). The ascocarps from FP-related *Morchella* spp. had a significantly higher total ash content than those from NF. Conversely, the moisture content and metabolizable energy were significantly lower in the FP than in the NF species. The crude protein content was high (around 33%) in both groups, with similar values between FP and NF. Similarly, no significant differences were observed in the ethereal extract, crude fiber, or non-nitrogenous extract.

Table 7. Proximate composition of the morchella ascocarps collected from forest plantations and native forests in south-central Chile.

		Forest plantation (*M. eximia* + *M. importuna*)	Native forest (*M. tridentina* + *M. andinensis*)
Moisture content	(%)	83.92 ± 6.23 b	89.17 ± 3.25 a
Crude protein	(% DM)	33.85 ± 2.76 a	33.72 ± 1.07 a
Crude fiber	(% DM)	16.89 ± 1.86 a	17.28 ± 1.03 a
Total ashes	(% DM)	10.41 ± 0.04 a	8.71 ± 0.80 b

Ethereal extract	(% DM)	4.43 ± 0.34 a	4.93 ± 1.13 a
Nitrogen-free extract	(% DM)	34.42 ± 0.85 a	35.36 ± 3.88 a
Energy value	(kcal 100 g^{-1})	312.91 ± 457 b	320.69 ± 1.11 a

Values correspond to the mean ± standard deviation (n = 3). DM: dry matter. Different letters in the row indicate significant differences ($p < 0.05$).

The ascocarps of *Morchella* spp. from NF and FP had a similar nutritional profile consistent with that reported for morels from other regions (Li et al., 2022b; Tietel & Masaphy, 2018), highlighting their high crude protein content (≈ 34% DM) and crude fiber (≈ 17% DM) (Meng et al., 2019; Qiu et al., 2024), along with a predominant fraction of non-nitrogenous extract (≈ 35% DM) and a low content of ethereal extract (< 5% DM) (Li et al., 2022b; Valverde et al., 2015). This balanced composition reinforces its value as a functional food and source of bioactive compounds (Jacinto-Azevedo et al., 2021; Kalač, 2016; Nitha et al., 2007; Valverde et al., 2015). On the other hand, the differences in the moisture and ash content detected between FP and NF ascocarps reflect the physiological state of the ascocarps at harvest and the influence of edaphic factors on mineral accumulation (Alaimo et al., 2019; Zhang et al., 2019). Although the proximate analysis was performed on composite samples of *Morchella* species mixed by type of forest cover, the obtained values were comparable to those described for other wild *Morchella* species, including *M. sextelata* and *M. esculenta* (Li et al., 2022b; Meng et al., 2019). This demonstrates the nutritional consistency of morels from different origins and environments. Additionally, recent comparisons between wild and cultivated morels show that the nutritional profiles of cultivated species are similar to those of wild ones (Li et al., 2023a; Li et al., 2022b). These results suggest that *Morchella* spp. has a balanced nutritional profile regardless of forest cover or geographical origin, standing out as a significant source of protein, fiber, and bioactive metabolites of nutraceutical interest (Jacinto-Azevedo et al., 2021; Li et al., 2023b; Qiu et al., 2024). Future studies of morels in south-central Chile would seek to expand the study sites and collection volumes to analyze the nutritional and bioactive potential of each species further and determine possible interspecific differences. This research may contribute to a better understanding and appreciation of this valuable export resource from the forest ecosystems of south-central Chile.

3.6. Principal component analysis (PCA)

A principal component analysis (PCA) was performed to explore the relationships between the quality traits of *Morchella* ascocarps and their association with forest cover type. This multivariate approach allows visualization of the clustering patterns among ascocarps from native forests (NF) and forest plantations (FP), as well as to identification of the variables that contributed most to their differentiation (Figure 11).

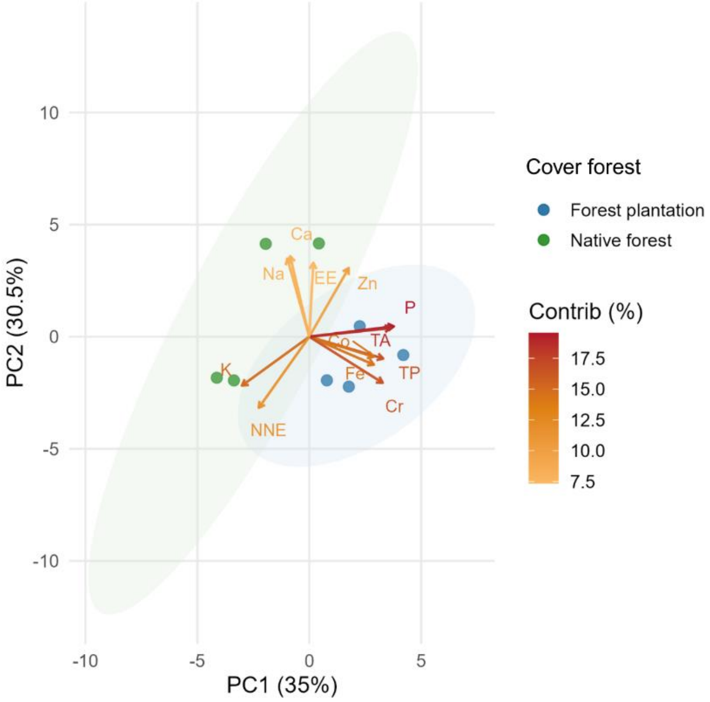

Figure 11. Principal component analysis (PCA) of the quality traits of morchella ascocarps collected from FP (blue) and NF (green). The points represent the study sites, and the ellipses indicate the 95% confidence interval for each forest cover. Arrows represent the variables included in the analysis, and their color intensity indicates their percentage contribution to the first two principal components (PC1 = 35% and PC2 = 30.5%).

PCA explained 65.5% of the total variance (PC1 = 35%, PC2 = 30.5%), revealing consistent differences between ascocarps collected in FP and NF. The variables with the highest significant correlation ($p \leq 0.05$) with the principal axes were P, total ash content (TA), Ca, Na, total phenols (TP), ethereal extract (EE), non-nitrogenous extract (NNE), Cr, Zn, K, Fe and Co. PC1 was positively associated with P, TA, TP, Cr, Fe, and Co, and negatively associated with K. This indicates that these variables primarily contributed to differentiating ascocarps from FP, which have higher concentrations of these substances. By contrast, PC2 was associated with Ca, Na, Zn, and EE, describing a pattern more representative of NF. The analysis shows that ascocarps collected in FP exhibit a more concentrated P and TA profile, while those from NF have higher Ca, Na, and Zn contents.

Taken together, the results of multivariate analysis showed that soil and type of forest cover simultaneously modulates the mineral composition, content of bioactive compounds, and nutritional properties of *Morchella* spp. The association of FP species with elements such as P, Cr, and Fe, as well as higher levels of phenolic compounds, suggests an effect of environmental disturbance on their metabolism. This is consistent with what has been described for other species of the genus under similar conditions (Taşkın et al., 2020; Tietel & Masaphy, 2018). Conversely, the relationship between NF species and K and moisture reflects a more balanced chemical profile that is favorable for organoleptic and nutritional quality (Li et al., 2022b; Meng et al., 2019). These results highlight the interaction between edaphic, forest cover and physiological factors in determining the ascocarps quality, integrating the mineral, nutritional, and bioactive attributes of the genus *Morchella* (Heleno et al., 2015; Zhang et al., 2019).

4. CONCLUSION

The results of this study demonstrate that the quality attributes of *Morchella* species that naturally fruit in south-central Chile depend largely on the type of forest cover and the characteristics of surrounding soil. Soils in forest plantation (FP) were less fertile and more disturbed, while soils in native forest (NF) were characterized by higher organic matter (OM) and cation exchange capacity (CEC). These differences in soil characteristics were reflected in variations in the mineral and bioactive composition of the morel ascocarps. However, since all study sites were in disturbed environments, future work should incorporate pristine NF sites to accurately contrast the influence of cover type on ascocarp quality.

Mineral analyses revealed that *Morchella* spp. efficiently accumulates essential macronutrients, particularly K and P, while controlling the absorption of Ca and Na, and selectively accumulating micronutrients such as Ni and Zn. Similarly, the ascocarps showed limited retention of potentially toxic elements, with no detection of As and safe levels of Cd and Pb, which highlights their safety for human consumption within the observed values.

Differences in phenolic compound content and antioxidant activity reflect the bioactive potential of species influenced by the environment, with higher phenolic content in FP ascocarps and higher antioxidant capacity in NF ascocarps. The analyzed morels had a high protein and crude fiber content, comparable to that reported for cultivated species, which confirms their nutritional and functional value.

The morel mushroom is an ecological and physiological model of resilience and efficiency, capable of integrating environmental variability into its metabolism and composition. Studying this mushroom provides valuable information for conserving its natural habitats and developing sustainable collection strategies that protect this valuable wild export resource in south-central Chile.

REFERENCES

Ab Rhaman, SMS., Naher, L., & Siddiquee, S. (2022). Mushroom Quality Related with Various Substrates Bioaccumulation and Translocation of Heavy Metals. *Journal of Fungi*, *8*(1), 42. http://doi.org/10.3390/jof8010042.

Alaimo, M. G., Saitta, A., & Ambrosio, E. (2019). Bedrock and soil geochemistry influence the content of chemical elements in wild edible mushrooms (Morchella group) from South Italy (Sicily). *Acta Mycologica*, *54*(1), 1122. https://doi.org/10.5586/am.1122.

Alcañiz, M., Outeiro, L., Francos, M., & Úbeda, X. (2018). Effects of prescribed fires on soil properties: A review. *Science of the Total Environment*, *613-614*, 944–957. https://doi.org/10.1016/j.scitotenv.2017.09.144.

Association of Official Analytical Chemists. (1997). *Official methods of analysis* (16th ed.). AOAC International.

Atwater, W. O. (1910). *Principles of nutrition and nutritive value of food* (Bulletin No. 142). U.S. Department of Agriculture.

Badshah, H., Khan, M., & Mumtaz, A. (2023a). Elucidating heavy metals concentration and distribution in wild edible morels and the associated soil at different altitudinal zones of Pakistan: a hearth risk implications study. *Biological Trace Element Research*, *201*(8), 4177–4190. http://doi.org/10.1007/s12011-022-03496-w.

Badshah, H., Nisa, S.U., Ali, M.A., Alwahibi, M.S., Kamal, A., Kaleem, M., Khan, A., Khan, S.M. & Mumtaz, A.S. (2023b). Bio-Concentration and Influence of Environmental Factors on Accumulation of Heavy Metals in Edible Autumn Morel (*Morchella galilaea*) of Low Elevation. *Metals*, *13*(3), 472. https://doi.org/10.3390/met13030472.

Badshah, S. L., Riaz, A., Muhammad, A., Tel Çayan, G., Çayan, F., Emin Duru, M., Ahmad, N., Emwas, A, & Jaremko, M. (2021). Isolation, Characterization, and Medicinal Potential of Polysaccharides of *Morchella esculenta*. *Molecules*, *26*(5), 1459. http://doi.org/ 10.3390/molecules26051459.

Barros, L., Ferreira, M.-J., Queirós, B., Ferreira, I. C. F. R., & Baptista, P. (2007). Total phenols, ascorbic acid, β-carotene and lycopene in Portuguese wild edible mushrooms and their antioxidant activities. *Food Chemistry*, *103*(2), 413–419. https://doi.org/10.1016/j.foodchem.2006.07.038.

Belbase, S., Paudel, K., Sunna, S., Das, S. & Kumar, S. (2025). *Morchella esculenta* Fr. A Growing Gold of Mountains, its Nutritive Value and Cultivation. *Current Agriculture Research Journal,* *13*(1). http://dx.doi.org/10.12944/CARJ.13.1.03.

Boulaiche, W., Hamdi, B., & Trari, M. (2019). Removal of heavy metals by chitin: Equilibrium, kinetic and thermodynamic studies. *Applied Water Science*, *9*, 39. https://doi.org/10.1007/s13201-019-0926-8.

Bucurica, I., Dulama, I., Radulescu, C., Banica, A., & Stanescu S. (2024). Heavy metals and associated risks of wild edible mushrooms consumption: transfer factor, carcinogenic risk, and health risk index. *Journal of Fungi*, *10*(12), 844. https://doi.org/10.3390/jof10120844.

Certini, G. (2005). Effects of fire on properties of forest soils: A review. *Oecologia*, *143*, 1–10. https://doi.org/10.1007/s00442-004-1788-8.

Cheung, L., Cheung, P. & Ooi, V. (2003). Antioxidant activity and total phenolics of edible mushroom extracts. *Food Chemistry*, *81*(2), 249-255. http://doi.org/10.1016/S0308-8146(02)00419-3.

Dighton, J. (2003). *Fungi in ecosystem processes*. Marcel Dekker.

Dimitrijević, M., Mitić, V., Đorđević, D., Popović, G., Krstić, N., Nikolić, J., & Stankov-Jovanović, V. (2021). Macroelements versus toxic elements in selected wild edible mushrooms of the Russulaceae family from Serbia. *Journal of the Serbian Chemical Society*, *86*(10), 927–940. https://doi.org/10.2298/JSC210210038D.

Dinakarkumar, Y., Ramakrishnan, G., Gujjula, K. R., Vasu, V., Balamurugan, P., & Murali, G. (2024). Fungal bioremediation: An overview of the mechanisms, applications and future perspectives. *Environmental Chemistry and Ecotoxicology*, *6*, 293-302. https://doi.org/10.1016/j.enceco.2024.07.002.

Du, XH., Zhao, Q., & Yang, ZL. (2015). A review on research advances, issues, and perspectives of morels. *Mycology*, *6*(2), 78-85. http://doi.org/10.1080/21501203.2015.1016561.

Falandysz, J., & Borovička, J. (2013). Macro and trace mineral constituents and radionuclides in mushrooms: Health benefits and risks. *Applied Microbiology and Biotechnology*, *97*(2), 477–501. https://doi.org/10.1007/s00253-012-4552-8.

Falandysz, J., Zhang, J., Wiejak, A., Barałkiewicz, D., & Hanć, A. (2017). Metallic elements and metalloids in *Boletus luridus*, *B. magnificus* and *B. tomentipes* mushrooms from polymetallic soils from SW China. *Ecotoxicology and Environmental Safety*, *142*, 497-502. https://doi.org/10.1016/j.ecoenv.2017.04.055.

Food and Agriculture Organization of the United Nations & World Health Organization. (2021). *Codex Alimentarius: General standard for contaminants and toxins in food and feed* (CXS 193-1995, Rev. 2021). FAO & WHO.

Food and Agriculture Organization of the United Nations. (2017). *Carbono orgánico del suelo: El potencial oculto*. FAO.

Fu, Y., Fan, M., Qin, H., Zhang, Z., Liu, S., Wu, S., Wang, Y., & Yuan, X. (2025). Interactions Between Morel Cultivation, Soil Microbes, and Mineral Nutrients: Impacts and Mechanisms. *Journal of Fungi*, *11*(6), 405. https://doi.org/10.3390/jof11060405.

Gadd, G. M. (2007). Geomycology: Biogeochemical transformations of rocks, minerals, metals and radionuclides by fungi, bioweathering and bioremediation. *Mycological Research*, *111*(1), 3–49. https://doi.org/10.1016/j.mycres.2006.12.001.

Gałgowska, M., & Pietrzak-Fiećko, R. (2020). Mineral Composition of Three Popular Wild Mushrooms from Poland. *Molecules*, *25*(16), 3588. https://doi.org/10.3390/molecules25163588.

Garrido-Ruiz, C., Sandoval, M., Stolpe, N., & Sanchez-Hernandez, J. C. (2022). Fire impacts on soil and post fire emergency stabilization treatments in Mediterranean-climate regions. *Chilean Journal of Agricultural Research*, *82*(2), 335–350. http://dx.doi.org/10.4067/S0718-58392022000200335.

Gerke, J. (2022). The Central Role of Soil Organic Matter in Soil Fertility and Carbon Storage. *Soil Systems*, *6*(2), 33. https://doi.org/10.3390/soilsystems6020033.

Gómez-Rey, M. X., & González-Prieto, S. J. (2014). Short and medium-term effects of a wildfire and two emergency stabilization treatments on the availability of macronutrients and trace elements in topsoil. *Science of the Total Environment*, *493*, 251–261. https://doi.org/10.1016/j.scitotenv.2014.05.119.

Gursoy, N., Sarikurkcu, C., Cengiz, M., & Solak, M. (2009). Antioxidant activities, metal contens, total phenolics and flavonoids of seven Morchella species. *Food and Chemical Toxicology*, *47*(9), 2381-2388. https://doi.org/10.1016/j.fct.2009.06.032.

Hatano, T., Kagawa, H., Yasuhara, T. & Okuda, T. (1998). 2 new flavonoids and other constituents in licorice root – their relative astringency and radical scavenging effects. *Chemical and Pharmacological Bulletin*, *36*(6), 2090-2097. https://doi.org/ 10.1248/cpb.36.2090.

Heleno, S. A., Barros, L., Martins, A., Morales, O., Fernández-Ruiz, V., Glamoclija, J., Sokovic, M., & Ferreira, I. (2015). Nutritional value, bioactive compounds, antimicrobial activity and bioaccessibility studies with wild edible mushrooms. *LWT - Food Science and Technology*, *63*(2), 799-806. https://doi.org/10.1016/j.lwt.2015.04.028.

Hussain, S., & Sher, H. (2021). Ecological characterization of Morel (*Morchella* spp.) habitats: A multivariate comparison from three forest types of district Swat, Pakistan. *Acta Ecologica Sinica*, *41*(1), 1–9. https://doi.org/10.1016/j.chnaes.2020.10.007.

Instituto Forestal. (2024). Boletín de exportaciones de productos forestales no madereros (N.º 43). Ministerio de Agricultura.

Isildak, Ö., Turkekul, İ., Elmastaş, M., & Tuzen, M. (2004). Analysis of heavy metals in some wild-grown edible mushrooms from the middle Black Sea region, Turkey. *Food Chemistry*, *86*(4), 547–552. https://doi.org/10.1016/j.foodchem.2003.09.007.

Jacinto-Azevedo, B. Valderrama, N., Henríquez, K., Aranda, M., & Aqueveque, P. (2021). Nutritional value and biological properties of Chilean wild and commercial edible mushrooms. *Food Chemistry*, *356*, Article 129651. https://doi.org/10.1016/j.foodchem.2021.129651.

Kalač, P. (2016). *Edible mushrooms: Chemical composition and nutritional value*. Academic Press.

Kalač, P., & Svoboda, L. (2000). A review of trace element concentrations in edible mushrooms. *Food Chemistry*, *69*(3), 273–281. https://doi.org/10.1016/S0308-8146(99)00264-2.

Khan, A., Lu, L-X., Yao, F-J., Fang, M., Wang, P., Zhang, Y-M., Meng, J-J., Ma, X-X., He, Q., Shao, K-S, Wei, Y-H, & Xu, B. (2023). Characterization, antioxidant activity, and mineral profiling of Auricularia Cornea mushroom strains. *Frontiers in Nutrition*, 10,1167805. https://doi.org/10.3389/fnut.2023.1167805.

Kumar, S., Stecher, G., Li, M., Knyaz, C., & Tamura, K. (2018). MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. *Molecular Biology and Evolution*, *35*(6), 1547-1549. https://doi.org/10.1093/molbev/msy096.

Li, S., Gao, A., Dong, S., Chen, Y., Sun, S., Lei, Z., & Zhang, Z. (2017). Purification, antitumor and immunomodulatory activity of polysaccharides from soybean residue fermented with Morchella esculenta. *International Journal of Biological Macromolecules*, *96*, 26–34. https://doi.org/10.1016/j.ijbiomac.2016.12.007.

Li, X., Fu, T., Li, H., Zhang, B., Li, W., Zhang, B., Wang, X., Wang, J., Chen, Q., He, X., Chen, H., Zhang, Q., Zhang, Y., Yang, R., & Peng, Y. (2023a). Safe Production Strategies for Soil-Covered Cultivation of Morel in Heavy Metal-Contaminated Soils. *Journal of Fungi, 9*(7), Article 765. https://doi.org/10.3390/jof9070765.

Li, Y., Chen, H., & Zhang, H. (2023b). Cultivation, nutritional value, bioactive compounds of morels, and their health benefits: A systematic review. *Frontiers in Nutrition, 17*(10), Article 1159029. https://doi.org/10.3389/fnut.2023.1159029.

Liu, P.-H., Huang, Z.-X., Luo, X.-H., Chen, H., Weng, B.-Q., Wang, Y.-X., & Chen, L.-S. (2020). Comparative transcriptome analysis reveals candidate genes related to cadmium accumulation and tolerance in two almond mushroom (*Agaricus brasiliensis*) strains with contrasting cadmium tolerance. *PLoS ONE*, *15*(9), e0239617. https://doi.org/10.1371/journal.pone.0239617.

Liu, Q. Y., Liu, H. M., Chen, C. Q., Wang, J., Han, Y., & Long, Z. F. (2017). Effects of element complexes containing Fe, Zn and Mn on artificial morel’s biological characteristics and soil bacterial community structures. *PLoS ONE*, *12*(3), e0174618. https://doi.org/10.1371/journal.pone.0174618.

Liu, Q., Ma, H., Zhang, Y., & Dong, C. (2018). Artificial cultivation of true morels: current state, issues and perspectives. *Critical Reviews in Biotechnology*, *38*(2), 259–271. https://doi.org/10.1080/07388551.2017.1333082.

Liu, W., He, P., Shi, X., Zhang, Y., Perez-Moreno, J., & Yu, F. (2023). Large-Scale Field Cultivation of Morchella and Relevance of Basic Knowledge for Its Steady Production. *Journal of Fungi*, *9*(8), Article 855. https://doi.org/10.3390/jof9080855.

Loizides, M. (2017). Morels: The story so far. *Field Mycology*, *18*(2), 42–53. https://doi.org/10.1016/j.fldmyc.2017.04.004.

Machuca, A., Córdova, C., Gómez, C., Gerding, M., & Silva, F. (2014). *Manual de recolección sustentable de Morchella spp. de la Patagonia Chilena* (Project CONAF FIBN 077/2013). Corporación Nacional Forestal.

Machuca, A., Gerding, M., Chávez, D., Palfner, G., Oyarzúa, P., Guillén, Y., & Córdova, C. (2021). Two New Species of Morchella from Nothofagus Forests in Northwestern Patagonia (Chile). *Mycological Progress*, *20*(6), 781–795. https://doi.org/10.1007/s11557-021-01703-x.

Malik, N. A., Kumar, J., Wani, M. S., Tantray, Y. R., & Ahmad, T. (2021). Role of mushrooms in the bioremediation of soil. In M. Kumar, V. Kumar, R. Prasad, & D. K. Choudhary (Eds.), *Microbiota and biofertilizers* (Vol. 2, pp. 77–102). Springer International Publishing. https://doi.org/10.1007/978-3-030-48771-3_5.

Meng, X., Che, C., Zhang, J., Gong, Z., Si, M., Yang, G., Cao, L. & Liu J. (2019). Structural characterization and immunomodulating activities of polysaccharides from a newly collected wild *Morchella sextelata*. International *Journal of Biological Macromolecules*, *129*, 608–614. http://doi.org/10.1016/j.ijbiomac.2019.01.226.

Miles, P. G., & Chang, S.T. (2004). *Mushrooms: Cultivation, nutritional value, medicinal effect, and environmental impact* (2nd ed.). CRC Press. https://doi.org/10.1201/9780203492086.

Mohammad, J., Khan, S., Shah, M., Din, I. & Ahmed, A. (2015). Essential and nonessential metal concentrations in morel mushroom (*Morchella esculenta*) in Dir-Kohistan, Pakistan. *Pakistan Journal of Botany*, *47*, 133-138.

Muñoz-Espinoza, C., Di Genova, A., Correa, K., Silva, R., Maass, A., González-Agüero, M., Orellana, A. & Hinrichsen, P. (2016). Transcriptome profiling of grapevine seedless segregants during berry development reveals candidate genes associated with berry weight. *BMC Plant Biology*, *16*, Article 104. http://dx.doi.org/10.1186/s12870-016-0789-1.

Murtić, S., Karić, L., Zahirović Sinanović, Ć., Hasanbegović, A., Avdić, J., Šerbo, A., & Hadžić, A. (2024). Heavy metals accumulation in the oyster mushroom basidiomes cultivated on different substrates. *Acta Mycologica*, 59, 1-7. https://doi.org/10.5586/am/191601.

National Institutes of Health, Office of Dietary Supplements. (2022a). *Potassium: Fact sheet for health professionals*. U.S. Department of Health and Human Services.

National Institutes of Health, Office of Dietary Supplements. (2022b). *Phosphorus: Fact sheet for health professionals*. U.S. Department of Health and Human Services.

National Institutes of Health, Office of Dietary Supplements. (2022c). *Sodium: Fact sheet for health professionals*. U.S. Department of Health and Human Services.

Nitha, B., Meera, C. R., & Janardhanan, K. K. (2007). Anti-inflammatory and antitumour activities of cultured mycelium of morel mushroom, *Morchella esculenta*. *Current Science*, *92*(2), 235–239.

Olowoyo, J. O., Van Heerden, E., Fischer, J. L., & Baker, C. (2010). Trace metals in soil and leaves of Jacaranda mimosifolia in the Tshwane area, South Africa. *Atmospheric Environment*, *44*(14), 1826–1830. https://doi.org/10.1016/j.atmosenv.2010.01.048.

Palfner, G., & Casanova-Katny, A. (2019). Comparison of the mycobiota in remnants of native forests and forest plantations in the Arauco Peninsula of the Biobío Region, highlighting functional and conservation aspects. In C. Smith-Ramírez & F. A. Squeo (Eds.), *Biodiversidad y ecología de los bosques costeros de Chile* (pp. 175–210). Editorial Universidad de Los Lagos.

Papadaki, A., Diamantopoulou, P., Papanikolaou, S., & Philippoussis, A. (2019). Evaluation of biomass and chitin production of Morchella mushrooms grown on starch-based substrates. *Foods*, *8*(7), 239. https://doi.org/10.3390/foods8070239.

Pfister, D. H., Healy, R., LoBuglio, K. F., Furci, G., Mitchell, J., & Smith, M. E. (2022). South American morels in the Elata group: mitosporic states, distributions, and commentary. *Mycological Progress*, *21*, 97. https://doi.org/10.1007/s11557-022-01846-5.

Pildain, M. B., Visnovsky, S. B., & Barroetaveña, C. (2014). Phylogenetic diversity of true morels (Morchella), the main edible non-timber product from native Patagonian forests of Argentina. *Fungal Biology*, *118*(9-10), 755–763. https://doi.org/10.1016/j.funbio.2014.03.008.

Qin, G., Liu, J., Zou, K., He, F., Li, Y., Liu, R., Zhang, P., Zhao, G., Wang, T., & Chen, B. (2024). Analysis of heavy metal characteristics and health risks of edible mushrooms in the mid-western region of China. *Scientific Reports*, *14*, 26960. https://doi.org/10.1038/s41598-024-78091-1.

Qiu, Z., Ren, S., Zhao, J., Cui, L., Li, H., Jiang, B., Zhang, M., Shu, L. & Li, T. (2024). Comparative analysis of the nutritional and biological properties between the pileus and stipe of *Morchella* sextelata. *Frontiers in Nutrition*, *10*, 1326461. https://doi.org/10.3389/fnut.2023.1326461.

Reis, F. S., Barros, L., Martins, A., & Ferreira, I. C. F. R. (2012). Chemical composition and nutritional value of the most widely appreciated cultivated mushrooms: An inter-species comparative study. *Food and Chemical Toxicology*, *50*(2), 191–197. https://doi.org/10.1016/j.fct.2011.10.056.

Robinson, J. R., Isikhuemhen, O. S., & Anike, F. N. (2021). Fungal–Metal Interactions: A Review of Toxicity and Homeostasis. *Journal of Fungi*, *7*(3), 225. https://doi.org/10.3390/jof7030225.

Sadzawka, R. (1990). *Métodos de análisis de suelos*. Instituto de Investigaciones Agropecuarias.

Sadzawka, A., Carrasco, M., Grez, R., Mora, M., Flores, H., & Neaman, A. (2006). *Métodos de análisis recomendados para los suelos de Chile*. Instituto de Investigaciones Agropecuarias.

Salihovic, M., Pazalja, M., Spirtovic-Halilovic, S., Veljovic, E., Huremovic, M., & Srabovic, M. (2022). Micro and macroelements content and health risk assessment of *Morchella esculenta* and *Lactarius piperatus* from Bosnia and Herzegovina. *Journal of Chemists and Chemical Engineering*, *71*(7-8), 457-464. https://doi.org/10.15255/KUI.2021.082.

Sambyal, K., & Singh, R. V. (2021). A comprehensive review on *Morchella importuna*: cultivation aspects, phytochemistry, and other significant applications. *Folia Microbiologica*, *66*, 147–157. https://doi.org/10.1007/s12223-020-00849-7.

Sandoval, M., Dörner, J., Seguel, O., Cuevas, J., & Rivera, D. (2012). *Métodos de análisis físicos de suelos*. Publicaciones Departamento de Suelo y Recursos Naturales, Universidad de Concepción.

Sanz-Rocha, M., Gerding, M, Quezada, T, Vargas, M, Chávez, D., & Machuca, A. (2023). Molecular and cultural characterization of *Morchella* spp. from disturbed environments of central-southern Chile. *Fungal Biology, 127*(3), 938-948. https://doi.org/10.1016/j.funbio.2023.01.009.

Slinkard, K., & Singleton, V. L. (1977). Total phenol analysis: automation and comparison with manual methods. *American Journal of Enology and Viticulture*, *28*, 49-55. https://doi.org/ 10.5344/ajev.1977.28.1.49.

Tamjidi, S., Ameri, A., & Esmaeili, H. (2023). A review of the application of fungi as an effective and attractive bio-adsorbent for biosorption of heavy metals from wastewater. *Environmental Monitoring and Assessment*, *195*, 91. https://doi.org/10.1007/s10661-022-10687-4.

Taşkın, H., Süfer, Ö., Attar, Ş. H., Bozok, F., Baktemur, G., Büyükalaca, S., & Kafkas, N. E. (2020). Total phenolics, antioxidant activities and fatty acid profiles of six Morchella species. *Journal of Food Science and Technology*, *58*(2), 692–700. https://doi.org/10.1007/s13197-020-04583-3.

Tian, Y., Ou, Z., Xiong, W., Fan, W., Yang, W., Zhang, B., Pan, L., & Ren, H. (2025). Extraction and optimization of polyphenols from *Morchella* spp. using ultrasound-assisted deep eutectic solvents: Potential intervention for type 2 diabetes mellitus. *Journal of Food Science*, *90*(3), Article e70145. https://doi.org/10.1111/1750-3841.70145.

Tietel, Z., & Masaphy, S. (2018). True morels (Morchella)—nutritional and phytochemical composition, health benefits and flavor: A review. *Critical Reviews in Food Science and Nutrition*, *58*(11), 1888–1901. https://doi.org/10.1080/10408398.2017.1285269.

Turkekul, İ., Elmastaş, M., & Tuzen, M. (2004). Determination of iron, copper, manganese, zinc, lead, and cadmium in mushroom samples from Tokat, Turkey. *Food Chemistry*, *84*(3), 389–392. https://doi.org/10.1016/S0308-8146(03)00245-0.

Ulery, A. L., Graham, R. C., & Amrhein, C. (2017). *The effects of fire on soil properties*. In R. Lal (Ed.), *Fire effects on soils and restoration strategies* (pp. 95–118). CRC Press. https://doi.org/10.1201/9781315154689-5.

Valverde, M. E., Hernández-Pérez, T., & Paredes-López, O. (2015). Edible mushrooms: Improving human health and promoting quality life. *International Journal of Microbiology*, *2015*(1), 376387. https://doi.org/10.1155/2015/376387.

Vieira, V., Fernandes, A., Barros, L., Glamoclija, J., Ciric, A., Stojkovic, D., Martins, A., Sokovic, M. & Ferreira, I. (2016). Wild *Morchella conica* Pers. from different origins: a comparative study of nutritional and bioactive properties. *Journal of the Science of Food and Agriculture*, *96*(1), 90–98. https://doi.org/10.1002/jsfa.7063.

Voltr, V., Menšík, L., Hlisnikovský, L., Hruška, M., Pokorný, E., & Pospíšilová, L. (2021). The Soil Organic Matter in Connection with Soil Properties and Soil Inputs. *Agronomy*, *11*(4), 779. https://doi.org/10.3390/agronomy11040779.

White, T. J., Bruns, T., Lee, S., & Taylor, J. (1990). *Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics*. In M. A. Innis, D. H. Gelfand, J. J. Sninsky, & T. J. White (Eds.), *PCR protocols* (pp. 315–322). Academic Press. https://doi.org/10.1016/B978-0-12-372180-8.50042-1.

Whitney, EN., & Rolfes, SR. (2016). *Comprendiendo la nutrición* (14.ª ed.). Cengage Learning.

Wu, H., Chen, J., Liu, Y., Cheng, H., Nan, J., Park, H.J., Yang, L., & Li, J. (2023), Digestion profile, antioxidant, and antidiabetic capacity of *Morchella esculenta* exopolysaccharide: in vitro, in vivo and microbiota analysis.

Journal of the Science of Food and Agriculture, *103*(9), 4401-4412. https://doi.org/10.1002/jsfa.12513.

Xu, Ch., Qian, L., Meng, O., & Sun, Y. (2025). State-of-the-art review of morel: From chemistry to nutrition and health benefits. *Journal of Food Composition and Analysis*, *141*, 107351. https://doi.org/10.1016/j.jfca.2025.107351.

Xu, H., Xie, Z., Guo, J., & Men, Q. (2021). Morphological changes and bioaccumulation in response to cadmium exposure in *Morchella spongiola*, a fungus with potencial for detoxification. *Canadian Journal Microbiology*, *67*(11), 789-798. https://doi.org/10.1139/cjm-2020-057.

Xu, Y., Tang, J., Wang, Y., He, X., Tan, H., Yu, Y., Chen, Y., & Peng, W. (2022). Large-scale commercial cultivation of morels: Current state and perspectives. *Applied Microbiology and Biotechnology, 106*(12), 4401-4412. https://doi.org/10.1007/s00253-022-12012-y.

Zhang, F., Long, L., Hu, Z., Yu, X., Liu, Q., Bao, J., & Long, Z. (2019). Analyses of artificial morel soil bacterial community structure and mineral element contents in ascocarp and the cultivated soil. *Canadian Journal of Microbiology*, *65*(10), 738–749. https://doi.org/10.1139/cjm-2018-0600.

Zhang, S., Liu, T., He, M., Zhang, S., Liao, J., Lei, T., Wu, X., Yu, Y., Wang, T. & Tan, H. (2024). A nationwide study of heavy metal (loid) s in agricultural soils and the soil-grown black morel *Morchella sextelata* in China. *Journal of Environmental Management*, *369*, 122243. https://doi.org/10.1016/j.jenvman.2024.122243.

FUNDING SOURCES

This research was supported by the Universidad de Concepción through the Research and Development Vice-Rectory (VRID) (Projects 2021000363MUL and 2024001183INV).

ACKNOWLEDGMENTS

The authors would like to thank the Electroanalysis Laboratory team at the Universidad de Santiago, especially F. Liendo, J. Penagos and B. Pichun. The authors would also like to thank J. Venegas and S. Suescun from the Animal Nutrition Laboratory at the Universidad de Concepción for their assistance with the laboratory analyses.

AUTHOR CONTRIBUTIONS

AM and TE-H designed the study and conducted the field sampling. TE-H, RS, YG, MS-R, and ME performed the laboratory analyses. TE-H and CM-E performed the statistical analyses and interpreted the data. AM and TE-H wrote the original manuscript draft. VV, RS, CM-E, EZ, DCh, and MG contributed to the review and editing of the manuscript. AM supervised the study, providing project administration and funding acquisition.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

SUPPLEMENTARY MATERIAL

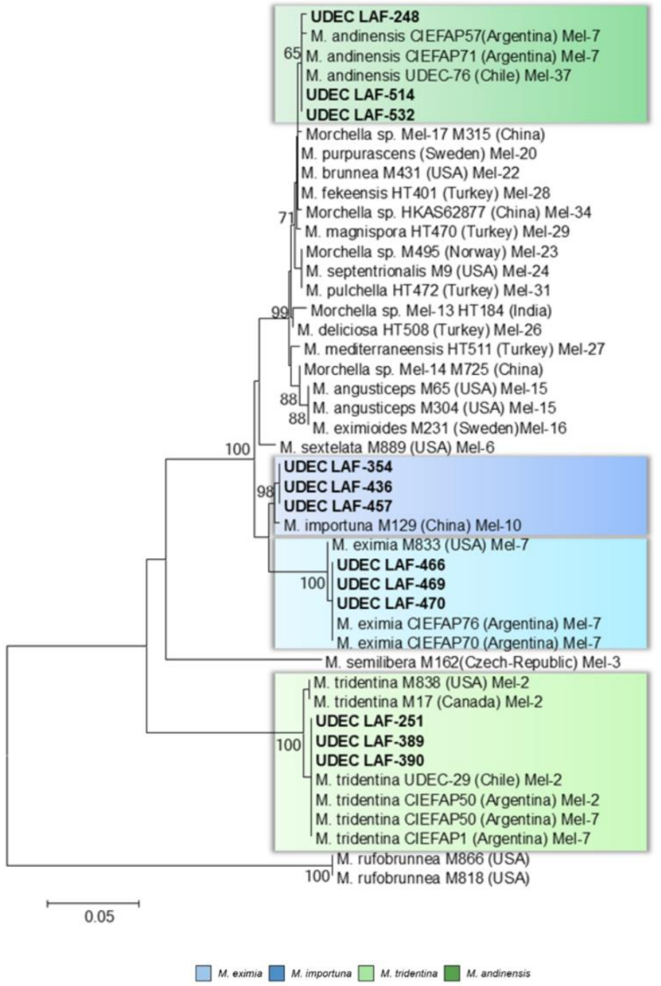

Figure S4. Phylogenetic relationships of *Morchella* spp. from south-central Chile based on ITS sequences.

Phylogenetic tree of *Morchella* spp. from south-central Chile, based on ITS region sequences. The analysis included *M. eximia* (Cerro Cayumanqui), *M. importuna* (Huaqui), *M. tridentina* (Peralillo), and *M. andinensis* (Cerro Pelado), along with reference sequences from GenBank. The tree was constructed using the maximum likelihood method with the Kimura 2 + I evolutionary model and 1000 bootstrap replicates. The sequences generated in this study are highlighted in blue tones for strains originating in forest plantations (*M. eximia* and *M. importuna*) and in green tones for those originating in native forests (*M. tridentina* and *M. andinensis*).

Figure S5. Morchella ascocarps from distinct forest environments in south-central Chile.

Ascocarps representative of *Morchella* species from different study sites in south-central Chile, identified as *M. eximia* (A), *M. importuna* (B), *M. tridentina* (C), and *M. andinensis* (D). Photographs were taken during the fruiting period in a burned forest plantation (A), a logged forest plantation (B), and a native forest (C and D).

Table S4. Characteristics of the study sites where *Morchella* spp. fruits naturally in south-central Chile.

Site	Administrative region	Geographical coordinates	Altitude (m a.s.l)	Predominant vegetation	Type of disturbance
Forest plantation (Cerro Cayumanqui)	Ñuble	36°44'41.11"S 72°34'16.17"O	512	*Pinus radiata* (burned tree debris)	Forest fire
Forest plantation (Huaqui)	Biobío	37°22'9.32"S 72°38'15.43"O	137	*Pinus radiata* (logged tree debris)	Logging
Relic of Native Forest (Peralillo)	Biobío	37°23'39.30"S 71°48'32.72"O	621	*Nothofagus* spp.	Relict of native forest with forestry and livestock influence
Relic of Native Forest (Cerro Pelado)	La Araucanía	37°50'52.58"S 72°53'6.98"O	955	*Nothofagus* spp.	Human and domestic animal traffic influence

Table S5. Molecular identification of *Morchella* spp. collected from different study sites in south-central Chile.

Site	Specie identified	Closest reference (GenBank access)	BLAST identity (%)
Burned forest plantation (CCa)	*M. eximia*	MT952472.1	100.00
	M. eximia	PV874418.1	99.70
	M. eximia	KM587970.1	99.85

Logged forest plantation (Hu)	*M. importuna*	PV501037.1	100.00
	M. importuna	MH982689.1	100.00
	M. importuna	PV501037.1	100.00
Native forest (Pe)	*M. tridentina*	MN355532.1	100.00
	M. tridentina	KJ439679.1	100.00
	M. tridentina	KJ439679.1	100.00
Native forest (CPe)	*M. andinensis*	MT952467.1	99.84
	M. andinensis	MT952467.1	100.00
	M. andinensis	MT952470.1	100.00

Species identification was based on sequence comparison of the ITS region with reference sequences available in GenBank using BLAST. CCa: Cerro Cayumanqui, Hu: Huaqui, Pe: Peralillo, CPe: Cerro Pelado.