



Diversity of wood-inhabiting Agaricomycotina on wood of different size classes in riparian forests of Uruguay



Sebastián Martínez ^{a,*}, Karen K. Nakasone ^b, Lina Bettucci ^c

^a Laboratorio de Patología Vegetal, INIA Treinta y Tres, Ruta 8 Km 281, CP 33000, Treinta y Tres, Uruguay

^b Center for Forest Mycology Research, Northern Research Station, U.S. Forest Service, Madison, WI, 53726-2398, USA

^c Laboratorio de Micología, Facultad de Ciencias, Universidad de la República, Iguá 4225, Montevideo, Uruguay

ARTICLE INFO

Article history:

Received 5 October 2018

Received in revised form

23 January 2019

Accepted 5 February 2019

Available online 6 February 2019

Keywords:

Agaricomycetes

Corticaceae

Fungal diversity

Polyporaceae

Warm temperate forest

ABSTRACT

Many Agaricomycotina species are saprobes, playing a fundamental role in nutrient cycling in forest ecosystems by decomposing wood. Little is known about factors affecting diversity of wood-inhabiting fungi in the neotropical, warm temperate native forests of Uruguay. Most of these native forests are riparian harboring about 300 tree species. In this study, we assessed the diversity of wood-inhabiting fungi on wood of different size classes in riparian forests of Uruguay. We recovered 186 species of Agaricomycotina, including 113 corticioid and 58 polyporoid taxa. Eleven taxa accounted for 38% of the all the samples. The highest number of species was found on fine woody debris (FWD, 2–10 cm diam) than coarse woody debris (CWD, >10 cm diam) and very fine woody debris (VFWD, <2 cm diam). Species-accumulation curves did not reach an asymptote for any of the groups or wood diameter classes studied. Polyporoids were more frequently recorded on CWD (61% of collections) and corticioids on VFWD (77%). Species richness estimated by non-parametric estimators indicates an Agaricomycotina species richness between 450 and 700 taxa. Our results show that Uruguayan riparian forests, despite its limited area and fragmentation, support a wood-inhabiting Agaricomycotina diversity comparable to less fragmented forests with more plant diversity.

© 2019 The Mycological Society of Japan. Published by Elsevier B.V. All rights reserved.

1. Introduction

In the biogeographical classification of Morrone (2006, 2014), Uruguay is in the Neotropical region, Chacoan sub-region, and Pampean province. The Pampean province is characterized by savanna vegetation with flooded lands and xeric and gallery forests (Morrone, 2006). This savanna is known as 'Campos' and is dominated by graminoids or herbaceous vegetation of the extensive grasslands located in Uruguay and southern Brazil (León, 1991). The Uruguayan Campos is a land area of 181 000 km² that sits between the temperate grasslands and neotropical forests (Olson et al., 2001).

The native forests of Uruguay cover approximately 8500 km² along riversides and isolated hillside patches, representing about 5.2% of the total area of the country (DIEA, 2016). In the north, nearly 13.8% of the area is forested (Traversa-Tejero and Alejano-

Monje, 2013). These forest ecosystems support more than 300 species of trees and shrubs of mostly of Chacoan or Paranaense origin (Brussa & Grela, 2007; Haretche, Mai, & Brazeiro, 2012; Legrand, 1968; Lombardo, 1964). Although some tree species can reach large dimensions, most Uruguayan species exist as small trees or shrubs that do not exceed 10 m high and 20 cm diam. These trees and shrubs are characterized as highly branched with tortuous stems (Carrere, 2010).

Riparian forests are composed of numerous and diverse microhabitats created by river dynamics that directly influence in the diversity, structure, and composition of the plant communities at small spatial scales (Naiman & Décamps, 1997). The riparian vegetation regulates light and temperature, acts as a source of woody debris that supports wood-rotting fungal diversity (Naiman & Décamps, 1997), and are critical for the filtering of agricultural contaminants (Sabo et al., 2005). Consequently, riparian forests have received increasing attention (Komonen et al. 2008). Woody debris are produced by multiple disturbances suffered by the living trees in the riparian forests (Naiman & Décamps, 1997). The volume of deadwood from very fine to coarse pieces provide crucial resources and habitats for a variety of deadwood-dependent

* Corresponding author.

E-mail addresses: smartinez@inia.org.uy (S. Martínez), knakasone@fs.fed.us (K.K. Nakasone), bettucci@fing.edu.uy (L. Bettucci).

organisms that comprise a substantial proportion of the forest biota (Lonsdale, Pautasso, & Holdenrieder, 2008). An important group of deadwood-dependent organisms are the wood-decomposing Basidiomycota (Lonsdale et al., 2008). Decomposition of woody debris is essential for nutrient cycling and humus formation in forest soils (Berg & McClaugherty, 2008) and is carried out mainly by saprobic fungi (Kjoller & Struwe, 1992; Schneider et al. 2012; Van der Wal et al., 2013).

The phylum Basidiomycota, with three subphyla, contains about 32% of described fungi, and the subphylum Agaricomycotina contains most of the macromycetes known today with agaricoid to gelatinous fruitbody forms (Kirk, Cannon, Minter, & Stalpers, 2008). The Agaricomycetes is a major class in the Agaricomycotina with about 21000 described species of saprotrophs, pathogens, and mutualists in a variety of fruitbody forms (Hibbett et al., 2014). The diversity in morphological and ecological roles presented by the Agaricomycetes is unmatched in the kingdom Fungi. Taxonomically, many groups of Agaricomycetes are poorly known and understudied, such as the corticioid and polyporoid species, albeit these are very conspicuous (Hibbett et al., 2014). Wood decay fungi are primarily responsible for decomposition of lignocellulose, the most recalcitrant molecules in wood, thus critical in nutrient cycling and carbon sequestration processes in forest ecosystems (Hibbett et al., 2014). Wood-decomposing Agaricomycetes produce three basic types of decay based on complex enzymatic systems, namely, white, brown, and soft rots (Schwarze et al., 2000).

The Agaricomycotina of the Uruguayan Campos is one of the understudied region of the world because its natural forest is greatly diminished. Nevertheless, around 200 species of wood-inhabiting Agaricomycotina with corticioid or polyporoid fruitbodies from Uruguay are known (Gazzano, 1998; Martínez, 2006; Martínez & Nakasone, 2005, 2010, 2014). In addition, about 150 species of Agaricomycotina with agaricoid fruitbodies are known, but only a small number of these are wood-rotters (Felippone, 1928; Herter, 1933; Rosa-Mato 1939). To date, almost no quantitative sampling of polyporoid or corticioid fungi has occurred in Uruguay; only check-lists have been published (Gazzano, 1998; Martínez & Nakasone, 2010, 2014). Although the number of recorded wood-inhabiting Agaricomycotina in riparian forests in Uruguay is modest, the continuous disturbances from flooding, wind, storms and pests and ecological conditions that limit the establishment of extensive forested areas could have an influence on the diversity of these fungi.

We undertook this study to contribute to the knowledge of wood-inhabiting Agaricomycetes in Uruguay by sampling 20 riparian forests sites to: 1) obtain a preliminary estimate of the total diversity of the corticioid and polyporoid fungi in the main forests of Uruguay; 2) discover what wood size classes support the fungal groups of interest, taking in to consideration the tree morphological diversity present in a small area; and 3) identify the taxa present in the riparian forests of the region.

2. Materials and methods

2.1. Study area

The present study took place in Uruguay between 2009 and 2012. The study area was identified and selected by employing satellite photographs from Google Earth[®]. Twenty sites were located in the southern region of Uruguay in the Departments of Cerro Largo, Durazno, Florida, Lavalleja, Rocha, Soriano and Treinta y Tres. The climate in the study areas is warm temperate with precipitation more or less evenly distributed throughout the year and classified as Cfa according to Köppen-Geiger scheme (Kottek, Grieser, Beck, Rudolf, & Rubel, 2006; Peel et al., 2007). Annual mean temperature is 17.7 °C (16.6–19.8 °C, SE to NW) and annual rainfall ranges from 1200 to 1600 mm from SW to NE (Castaño, Giménez, Ceroni, Furest, & Aunchayna, 2011).

2.2. Sample collection and fruitbody identification

Fungal collection and resource or substrate characterization were undertaken during different seasons. For each of the 20 sites, a trail approximately perpendicular to 11 river flows was established, taking into account the accessibility from a path (Table 1; Fig. 1). Plots of 10 m wide (5 m along each side of the pathway line) and 100–150 m long were established and inspected for collection in each location. According with the accessibility and size of the riparian forest, 2–3 of these plots were sampled at each location. Samplings were done in approximately the same area and at same time at each site. In these plots all standing or fallen wood pieces were sampled destructively as wood pieces were turned for examination and fungal specimens collected. Living trees inside the limit of these plots were superficially inspected for the presence of basidiomycete fruitbodies. One or several fresh or recently dead fruitbodies present on a wood piece were treated as one individual

Table 1
Sampling sites by Department, date of collection and number of specimens and species collected.

Site	Department	Date	Code	Samples	Species
Tapes River, Barriga Negra	Lavalleja	Oct 8, 2010	TAPE	33	23
Olimar River, Treinta y Tres	Treinta y Tres	Apr 30, 2011	OLIM	18	15
Sta. Lucía Chico River, Paso de la Arena	Florida	Sep 21, 2009	PAR1	25	15
Sta. Lucía Chico River, Florida	Florida	Sep 20, 2010	PROB	35	25
Yerbal River, Route 19	Treinta y Tres	Jun 11, 2011	YER1	41	22
Olimar Chico River, Route 14	Treinta y Tres	Jun 18, 2011	OCH1	40	24
Yerbal River, Treinta y Tres	Treinta y Tres	Jul 2, 2011	PYE1	35	24
Sta. Lucía Chico River, Paso de la Arena	Florida	Apr 18, 2010	PAR2	8	8
Olimar River, Villa Passano	Treinta y Tres	Nov 20, 2011	PASS	25	15
Cebollatí River, Charqueada	Rocha	Nov 20, 2011	CEBO	27	16
Olimar Chico River, Route 14	Treinta y Tres	Nov 19, 2011	OCH2	20	16
Valizas River, Valizas	Rocha	Jan 16, 2010	VAL1	38	29
Valizas River, Valizas	Rocha	Jan 20, 2012	VAL2	38	24
Cebollatí River, Averías	Lavalleja	Feb 12, 2012	AVER	20	13
Tacuarí River, Arachania	Cerro Largo	Apr 22, 2012	ARAC	18	16
Parao River, Route 8	Treinta y Tres	Apr 22, 2012	PARA	16	14
Yí River, Durazno	Durazno	Apr 30, 2012	YI	32	21
Yerbal River, Treinta y Tres	Treinta y Tres	May 20, 2012	PYE2	25	18
Olimar River, Paso de la Laguna	Treinta y Tres	Nov 22, 2012	UEPL	20	10
Monzón River, Route 57	Soriano	Dec 27, 2012	MON	22	16

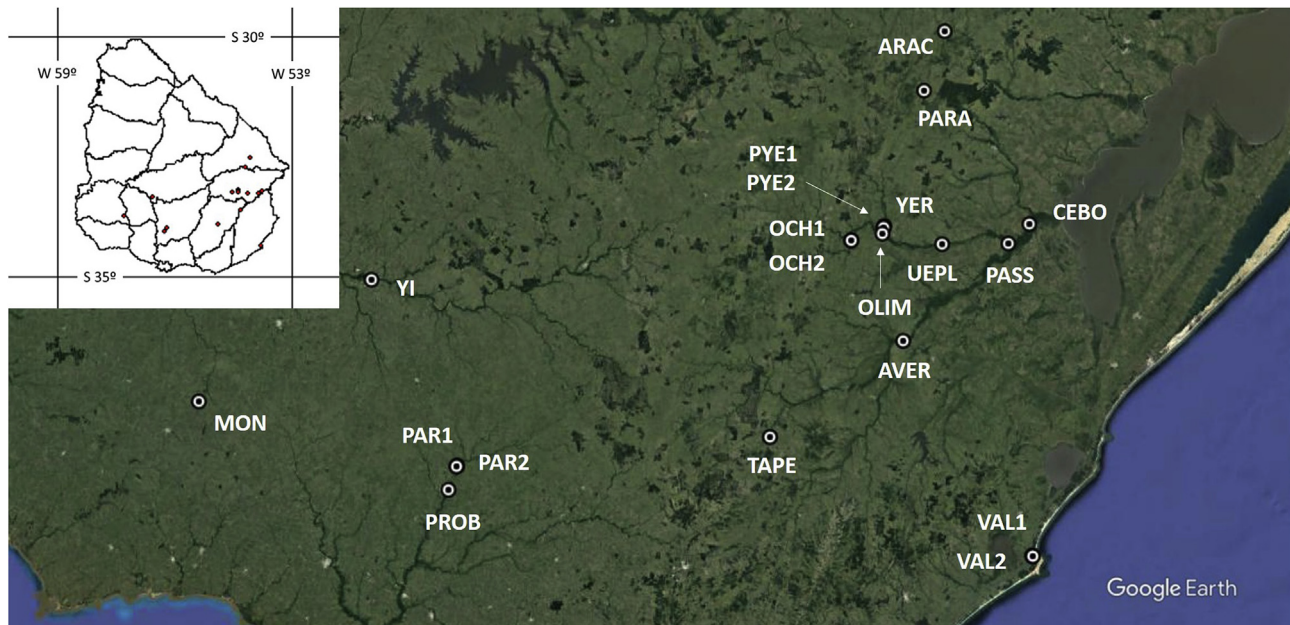


Fig. 1. Geographic location of the 20 study sites in Uruguay. For location abbreviations, see Table 1.

or record following Penttila et al. (2004). Only fruitbodies of the Agaricomycotina as defined by Hibbett et al. (2014) were sampled. These included all resupinate, pileate or stipitate fruitbodies with smooth, hydroid, lamellate to poroid hymenia as well as those with gelatinous fruitbodies (Hibbett, 2006).

Fungal samples were classified by fruitbody and hymenial configuration in four general basidiocarp morphologic groups: corticioid (COR) with resupinate to effused-reflexed fruitbodies and non-poroid hymenia; polyporoid (POL) with resupinate to stipitate fruitbodies and poroid hymenia; agaricoid (AGA) with pileate to stipitate fruitbodies and lamellate hymenia, and gelatinous fruitbodies (GEL) with varied basidiocarp construction (Hibbett, 2006). Agaricomycotina taxa with agaricoid and gelatinous fruitbodies are poorly known in Uruguay (Martínez & Nakasone, 2014). Fungi with phragmobasidia (e.g. *Heterochaete* Pat.) were classified as COR because of their resupinate, non-poroid hymenial configuration. Some species, especially polyporoid, were identified *in situ* by macromorphology, however, a number were collected and their identity confirmed using standard microscopic methods. Selected taxa were studied also with molecular methods and will be featured in a future taxonomic paper. Fungal samples were placed in paper bags, numbered, and dried thoroughly. Freehand sections were mounted in 5% (w/v) aqueous KOH and 1% (w/v) aqueous phloxine, 5% (w/v) cotton blue in 25% (w/v) lactophenol, and Melzer's reagent (Kirk et al., 2008). Literature consulted for species identification included Gilbertson and Ryvarden (1986, 1987), Jülich and Stalpers (1980), Larsen and Cobb-Poulsen (1990), Nuñez and Ryvarden (2000, 2001), Ryvarden (1991, 2004, 2005, 2010), and Ryvarden and Johansen (1980). Voucher specimens were deposited at the Mycological Herbarium of the Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay (MVHC) and are available upon request. Names of species follow Index Fungorum (www.indexfungorum.org, accessed 12 Dec 2017).

Resource size independently of the plant organ or structure (root, stump, standing tree, fallen trunk, and branch), whether it was dead or alive, were classified as very fine, fine, or coarse woody debris according to their diameter (VFWD < 2 cm, FWD 2–10 cm, CWD > 10 cm) (Abrego & Salcedo, 2013; Juutilainen, Monkkonen,

Kotiranta, & Halme, 2014, 2011; Küffer & Senn-Irlet, 2005; Lindner, Burdsall, & Stanosz, 2006).

2.3. Data analyses

Species accumulation curves integrating rarefaction and extrapolation were obtained from 100 randomizations runs for all tests with EstimateS 9.1.0 following Colwell (2013). Distribution of poroid or corticioid specimens was performed separately. Samples of agaricoid (12 samples) or gelatinous fruitbodies (3 samples) and those from soil (9 samples), presumably from roots or woody debris of unknown diameter, were not analyzed separately because of small sample size.

Non-parametric richness estimators Chao1 (Chao, 1984), Chao2 (Chao, 1987), Jackknife1 (Heltshel & Forrester, 1983), Jackknife2 (Burnham & Overton, 1978), ACE, ICE (Chao & Lee, 1992), and Bootstrap (Smith and van Belle 1984) were calculated and tested with EstimateS 9.1.0 (Colwell, 2013) to determine a predicted value for maximum species richness.

Diversity was estimated using Shannon's diversity index (H') and Simpson's (inverse) index of diversity ($1/D$) as calculated in EstimateS 9.1.0 (Colwell, 2013). Pielou's evenness index (J') was calculated as $J' = H'/H'_{max}$, where H' is the value obtained from Shannon-Wiener Diversity Index and H'_{max} represents the maximum diversity possible for the number of species (S) in the sample (Rollins and Stephenson 2013).

The relationship of specimen occurrence and species richness according with resource characteristics (diameter class) and season of sampling and collection was estimated using the statistical package JMP version 8 (SAS Institute Inc., Cary, NC, 1989–2007). The chi-square test (χ^2), with the significant level (α) set to 5%, was used to test differences in frequency of fungal specimens, warmer versus colder season, and abundance, species richness and life form groups according with wood size classes. Calculations were carried out using three datasets: Agaricomycotina (complete), corticioid fruitbody only, and polyporoid fruitbody only. Data from gelatinous forms (3 records) and agaricoids were ignored due to the low number of records. Resupinate forms without gelatinous hymenia

Table 2

Species richness and species diversity estimations of all Agaricomycotina, of corticioids and polyporoids separately and of those of each wood diameter classes. Numbers in brackets are percentages of each group or wood size diameter (column).

Categories	Agaricomycotina	Corticioid	Polyporoid	CWD	FWD	VFWD
Estimator ^a						
S	186	113	58	82	93	61
H'	4.58	4.15	3.39	3.89	4.05	3.89
J'	0.88	0.88	0.83	0.88	0.89	0.94
1/D	53.7	30.5	19.2	28.5	31.5	37.8
Singletons ^b	117 (62.9%)	76 (67.3%)	32 (55.2%)	46 (56.1%)	58 (63.4%)	42 (68.9%)
Doubletons	22 (11.8%)	15 (13.3%)	6 (10.3%)	13 (15.9%)	16 (17.2%)	9 (14.8%)
Uniques ^c	134 (72.0%)	89 (78.8%)	34 (58.6%)	55 (67.1%)	67 (72%)	47 (77%)
Duplicates	16 (8.6%)	9 (7.9%)	7 (12.1%)	14 (17.1%)	17 (18.3%)	8 (13.1%)

^a S, species number; H', Shannon's diversity index; J', Pielou's evenness index; 1/D, Simpson's (inverse) d index of diversity.

^b Singletons and doubletons are the number of species represented by one or two individuals, respectively.

^c Uniques and duplicates are the species that occur in only one or two samples, respectively.

and phragmobasidia (e.g. *Heterochaete* spp.) were included in the corticioid dataset due to character coincidence. Although related to polyporoid species, *Lentinus* spp. were treated here as agaricoid due to its lamellate hymenia.

3. Results

3.1. Species richness

A total of 536 fungal samples were collected and 186 species of wood-inhabiting Agaricomycotina taxa were identified. The 238 polyporoid morphotypes were assigned to 58 species, 254 corticioid morphotypes to 113 species (including four taxa with phragmobasidia), 41 agaricoid morphotypes to 12 species, and 3 gelatinous morphotypes to 3 species (see list in [Supplementary Table S1](#)). The mean number of recorded species for the 20 sites was 18; total species richness ranged from 8 in Paso de la Arena to 29 in Valizas 1 ([Table 1](#)).

Morphotypes that could not be identified, particularly those collected once or twice, were assigned to a genus or given a tentative name. Twenty-eight morphotypes were collected 5 or more times, accounting for 311 specimens; 47 morphotypes were collected 3 or more times for 375 specimens; 22 collected were twice (doubletons) and 117 morphotypes collected only once (singletons) ([Table 2](#); [Supplementary Table S1](#)).

The following 11 taxa (7 polyporoid, 3 corticioid and 1 agaricoid) were most frequently collected (>10 times): *Phlebia argentina* (30 collections), *Fomitiporia punctata* complex (28), *Ganoderma applanatum* complex (22), *Xylodon raduloides* (20), *Fuscoporia gilva* (20), *Phellinotus* sp. nov. (20), *Heterochaete shearii* (17), *Trametes villosa* (13), *Lentinus tigrinus* (12), *G. lucidum* complex (12), and *Hydnopolyporus fimbriatus* (12). These 11 species account for 206 collections or 38.4% of the total samples collected.

The abundance of Agaricomycotina fruit bodies collected during the warmer six months (47% from Oct–Mar) compared to the cooler months (53% from Apr–Sep) was not statistically different (χ^2 (1, $N = 536$) = 2.1582, $P = 0.142$). The abundance of wood-inhabiting fungi with different basidiocarp morphology was equally distributed over the warmer and colder six months (χ^2 (1, $N = 533$) = 4.25, $P = 0.119$).

Species accumulation curves for the three fungal fruitbody classes, which lack an asymptotic behavior at the reference samples sizes ([Fig. 2](#)), show that sampling is not complete. Similarly, species accumulation curves for the three wood diameter classes also lack an asymptotic behavior indicating incomplete sampling at all substrate sizes sampled ([Fig. 2](#)).

The frequency of samples collected from woody debris classes were – CWD, 41.8%, FWD 38.7%, and VFWD 19.5% ([Fig. 3](#)). These

differences were statistically significant (χ^2 (2, $N = 527$) = 50.05, $P < 0.0001$). The species richness was 49% in FWD, 43% in CWD, and 32% in VFWD and the differences are statistically significant (χ^2 (2, $N = 239$) = 7.68, $P = 0.022$) ([Fig. 3](#); [Table 2](#)). The number of singletons (58) and doubletons (16) was higher in FWD than in CWD ([Table 2](#)). Corticioid specimens were the most common both in VFWD and FWD classes whereas polyporoids were most common in CWD ([Fig. 3](#); [Table 2](#)). Fifty-five unique species were found on resources with diameter class FWD, 52 in CWD and 39 in VFWD. The percentages of these unique species were similar (59–64%) within each decay class. Only 12 species were shared between the three diameter classes ([Fig. 4](#)).

3.2. Species occurrence and diversity

The rank-abundance curve for polyporoid species declined most rapidly compared to the corticioids ([Fig. 5](#)). Relative abundance for polyporoid species declined more quickly than corticioids indicating that polyporoids were more unevenly represented ([Fig. 5](#)). The seven most frequently collected polyporoid species composed 53.4% of the total specimens collected, and 38 species were collected only once or twice ([Table 2](#)). In contrast, three corticioid species, *Phlebia argentina*, *Xylodon raduloides*, and *Heterochaete shearii*, accounted for 26.4% of all corticioid specimens collected whereas 91 species (80.5%) were represented by only 1 or 2 specimens ([Supplementary Table S1](#); [Table 2](#)).

Shannon's diversity index values show that corticioid species displayed greater taxonomic diversity than polyporoid species and a more homogeneous distribution as determined by the Pielou's evenness index. Also, Simpson's reciprocal index show a higher diversity for corticioids than polyporoids with a high value for the complete set of Agaricomycotina ([Table 2](#)).

The rank-abundance curve for the resource classes shows that CWD and FWD had similar slopes and declined more rapidly than VFWD which had the most uneven distribution of species for the three wood-diameter classes ([Fig. 5](#)). Shannon's diversity index indicated that FWD was characterized by higher taxonomic diversity than the CWD and VFWD fractions ([Table 2](#)). Pielou's evenness index showed that CWD and FWD have a more heterogeneous distribution of species compared to VFWD that displayed a mostly homogenous distribution. According to Simpson's reciprocal index, the highest diversity of species? was found in VFWD compared to CWD and FWD fractions which had similar values ([Table 2](#)).

Singletons represent 62.9% of the total number of species, corresponding to 67.3% of all corticioid species and 55.2% of all polyporoids. Depending on wood diameter classes, singletons ranged from 68.9% of species on VFWD to 56.1% on CWD ([Table 2](#)).

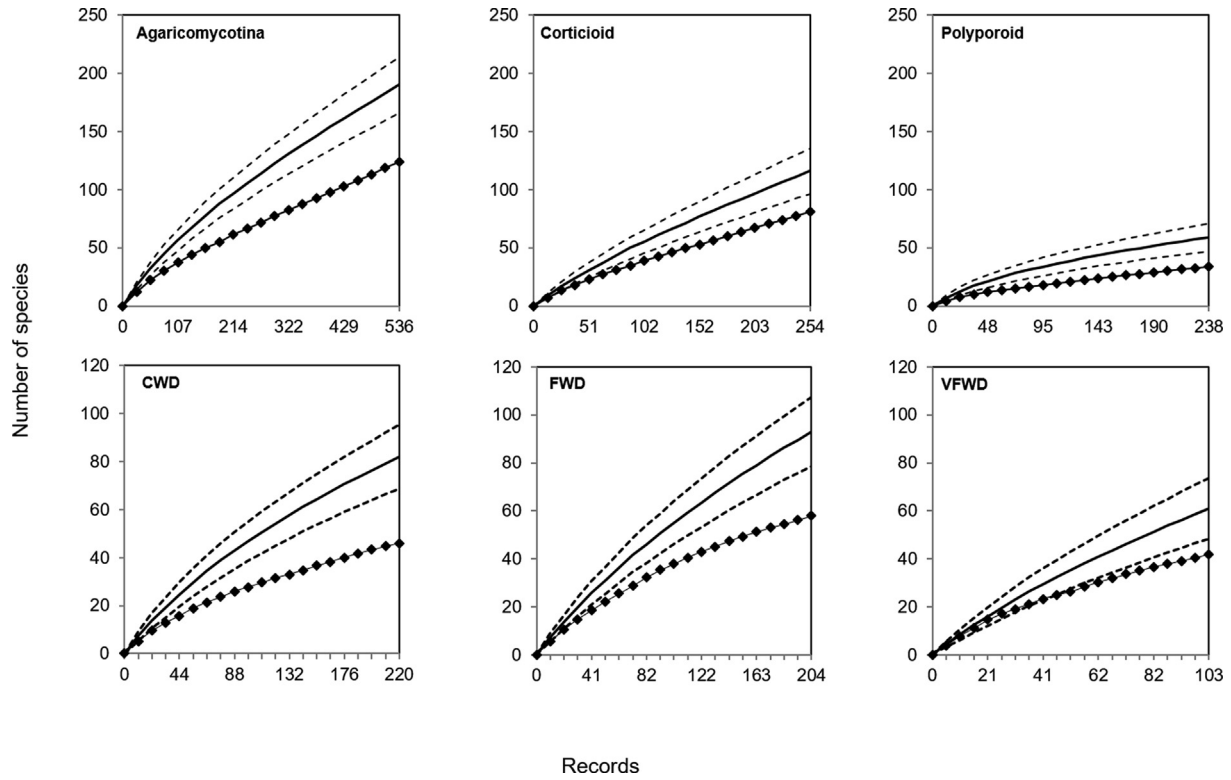


Fig. 2. Species accumulation curves, upper and lower 95% bound and number of singletons accumulated for Agaricomycotina, corticioid, and polyporoid species (top row) and species accumulation curves, upper and lower 95% bound and number of singletons accumulated for wood diameter classes CWD, FWD and VFWD (bottom row). Upper and lower 95% bound were calculated from the variance of the number of species drawn in 100 randomizations at each sample. Actual number of species observed (S) in samples (—); S 95% Confidence Interval Upper and Lower Bound (---); Singletons = number of species represented by a single individual (-◆-).

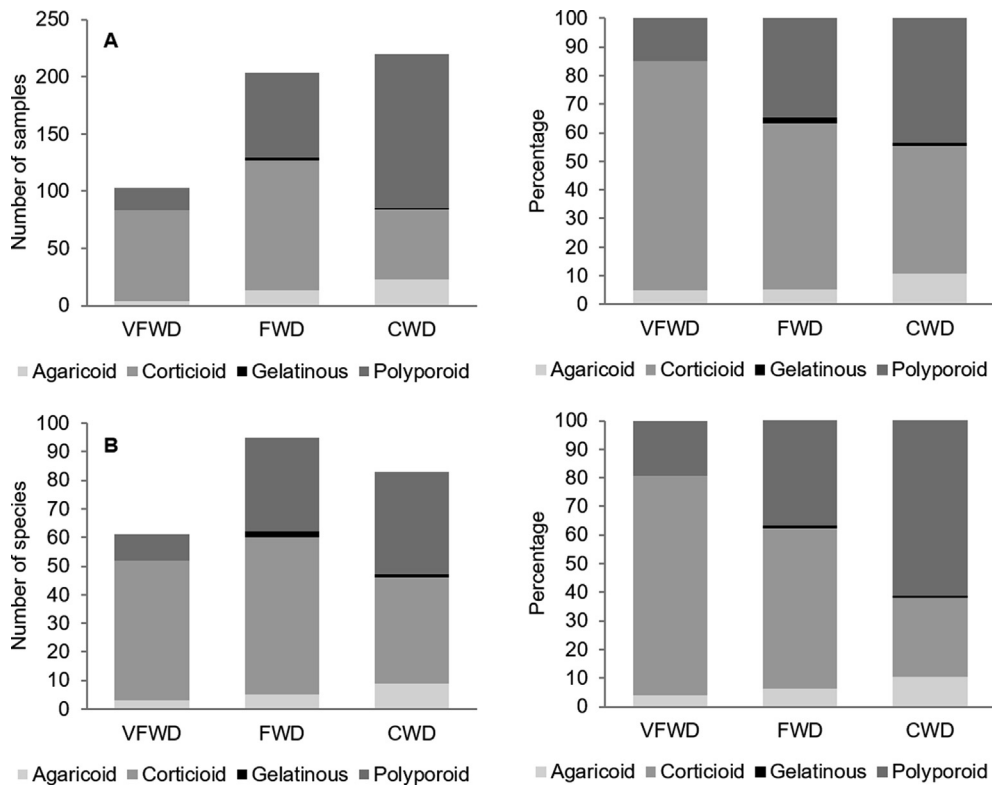


Fig. 3. Number of samples and species of Agaricomycotina collected according with basidiocarp configuration and by wood diameter class. A, total number (left) and percentage (right) of samples collected in the different wood diameter classes; B, total number (left) and percentage (right) of species collected in the different wood diameter classes. Abbreviations: VFWD <2 cm diam, FWD = 2–10 cm diam, CWS >10 cm diam.

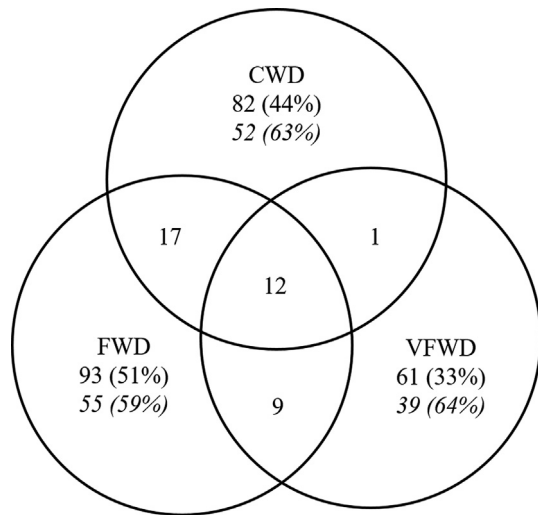


Fig. 4. Venn diagram showing each wood diameter class with number and percentage of the total and exclusive species (in *course*). Number of species shared between each pair and among the three wood diameter classes are also shown in the intersecting circles. Nine collections (4 species) are excluded because were from buried wood and of unknown wood diameter class.

3.3. Species richness estimation

Total species richness values were estimated using different estimators on six datasets. Three datasets were based on fungal fruitbody type, total Agaricomycotina, polyporoids alone, and corticioids alone and on the three different wood size classes, CWD, FWD, and VFWD (Table 3). Highest values for species richness were obtained using the Chao 2 estimator for the total Agaricomycotina, ICE for corticioid species, and Chao 1 for polyporoid species. Total species richness estimation ranged from 237 with Bootstrap to 719 using Chao 2 estimator with an observed diversity of 186 species of which 117 were collected only once (Table 2). This means that 63% of the species are singletons. These estimations represent a coverage of 26–78% for all Agaricomycotina, 21–77% for corticioid

species, and 41–82% for polyporoid species according with the number of species collected.

When the species richness on wood of different diameter class was estimated, the highest species richness values was obtained with the ICE estimator (305) and the lowest with Bootstrap (79) (Table 3). Estimations represent a coverage of 36–79% for CWD species, 30–78% for FWD species and 30–77% for VFWD species.

4. Discussion

In this study, samplings from 20 sites in riparian forests in Uruguay yielded 186 species of xylophilous Agaricomycotina. Because individuals were identified by fruitbody characteristics, taxa present as vegetative mycelia only could not be identified, therefore, diversity was probably underestimated.

According with Martínez and Nakasone (2014), a conservative estimate of 500–600 macromycete species are predicted to occur in Uruguay. Although sampling was limited in this study, the estimation of wood-inhabiting Agaricomycotina species richness should be considered an initial attempt to quantify Agaricomycotina richness and species diversity in Uruguay. Interestingly, the most common taxon was *Phlebia argentina*, a rare corticioid species that was described more than a century ago and rediscovered only recently in Uruguay (Gazzano, 1996). Also, seven of the 11 species collected more than 10 times were polyporoid taxa, including a probable new species in the genus *Phellinotus* of the Hymenochaetales, and three species complexes with multiple cryptic taxa (*Fomitiporia punctata*, *Ganoderma applanatum* and *G. lucidum*). *Fomitiporia cf. punctata* is a common species in Uruguay, and the morphotype recognized here probably corresponds to one of the species recently recognized in the Neotropics (Decock, Herrera Figueroa, Robledo, & Castillo, 2007). Thus, the number of recorded species herein is conservative, and molecular studies undoubtedly will uncover additional taxa.

The number of wood-inhabiting Agaricomycotina, corticioid, and polyporoid species estimation is high but variable depending on the non-parametric estimator used for calculations. Calculated estimates of diversity obtained herein ranged from 450 to 700 species of Agaricomycotina (Table 3), similar to the 500–600

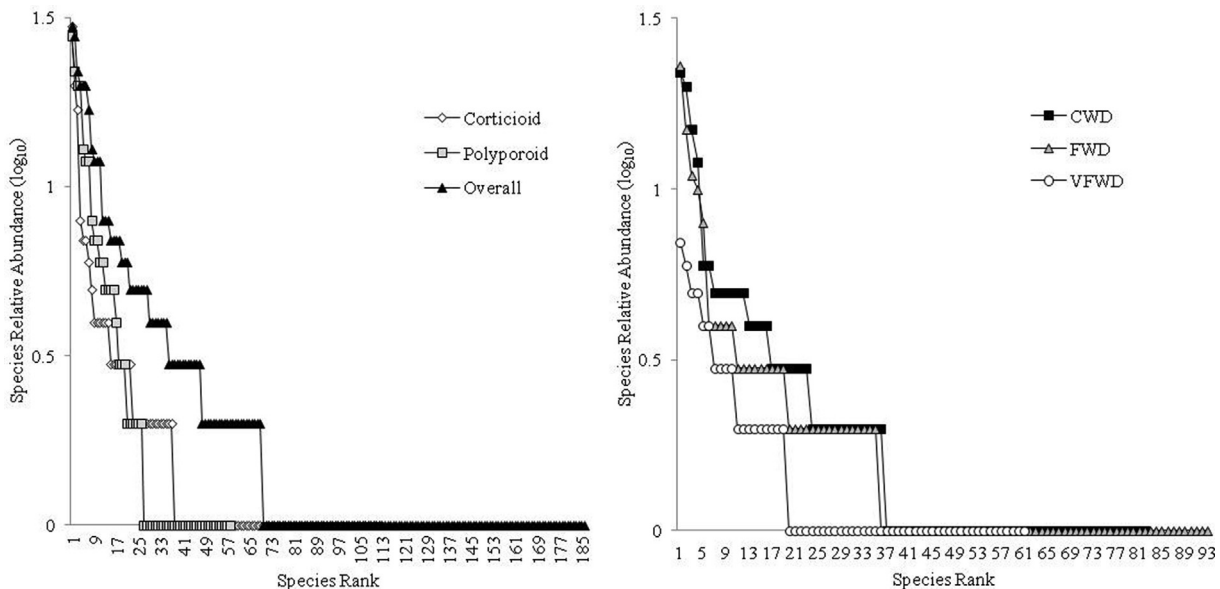


Fig. 5. Species rank curves based on species relative abundance plotted against rank abundance according with corticioid, polyporoid and overall (Agaricomycotina) species (left) and according with wood-diameter class (right).

Table 3

Species richness according with ACE, Chao1, and incidence estimators for the whole Agaricomycotina, corticioid and polyporoid species and wood-diameter classes.

	S ^a	ACE ^b	ICE	Chao 1	Chao 2	Jack1	Jack2	Bootstrap
Agaricomycotina	186	448	632	497	719	313	420	237
Corticioid	113	292	545	305	531	198	270	146
Polyporoid	58	119	125	143	136	90	115	71
CWD	82	147	228	163	185	134	172	104
FWD	93	217	305	198	218	157	202	119
VFWD	61	156	205	158	192	106	141	79

^a S, Number of species.^b ACE and Chao1 are abundance-based richness estimators. All others are incidence-based estimators.

macrofungal species proposed by Martínez and Nakasone (2014) who extrapolated from the plant:macrofungal ratio for the region.

Polyporoids is the only group where observed richness may accurately measure the number of species in the country, for about 40% of the estimated species were collected. For corticioids, observed richness clearly underestimated species richness for sampling saturation was not achieved as the increasing singleton curve and wide divergence between estimated and observed richness values indicated. Estimated species richness of tropical plants is correlated with sampling effort (Magurran, 2017), and differences in abundance may reflect differences in conditions for collection or observation (Gotelli & Colwell, 2001). If these observations are applied to Agaricomycotina and corticioid from published reports in South America, a range of potential species richness can be estimated. Gibertoni et al. (2016) from 124 samplings found 153 polyporoid species and results in an estimated 184 in total species richness (Jackknife 1) from the Brazilian Amazonian forest. For the Atlantic Rain forest of northeastern Brazil, Gibertoni, Nogueira-Melo, de Lira, Baltazar, and Santos (2015) collected 138 polyporoid species in 110 samplings, resulting in species richness estimates between 154 (Bootstrap) and 185 (Jackknife 2). Comparing results obtained herein with those from tropical forest are difficult since the Uruguayan riparian forests occupy an area that represents just 0.1% of the Amazonian forest. However, 58 polyporoid species recorded with an estimated richness calculated between 71 (Bootstrap) and 143 (Chao 1) suggests that the riparian forests of Uruguay supports a diverse and extensive polypore community (Table 3). But assessing biodiversity is more difficult for corticioids since there are few studies in tropical regions. Greslebin and Rajchenberg (2003) recorded 168 species of corticioids from Patagonia with an estimated richness between 250 and 290 species. Actual number of recorded corticioid species in Uruguay is about 140 (Martínez & Nakasone, 2005, 2010, 2014; Gazzano, 2010). It is probable that new records could be added to the already known species, since nearly half of the corticioid species collected in this study were not reported from Uruguay before. Furthermore, in the present study, 63% of the corticioids were encountered as singletons (Table 2), a number very similar to the 62% singletons found in the hyperdiverse North American pine forests (Rosenthal et al., 2017).

The diversity, ecological role, and importance of CWD (>10 cm) wood-inhabiting fungi in forests ecosystems are well established (Küffer, Gillet, Senn-Irlet, Aragno, & Job, 2008). Smaller wood fractions, however, received less attention in biodiversity studies, and few studies focused on the importance of FWD or VFWD for wood-inhabiting fungi (Juutilainen et al., 2014, 2017, 2011; Abrego & Salcedo, 2013; Küffer et al., 2008; Küffer & Senn-Irlet, 2005; Lindner et al., 2006). Fungal communities that inhabit fine woody debris must be able to withstand unstable climatic conditions, high decomposition rates, and high wood surface/volume ratio.

Differences were found in the species richness on woody debris of different size classes with the highest species richness was found

on FWD (Fig. 4; Table 2). However, no significant differences were found in species richness among size classes of woody debris compared at the same sampling effort (Fig. 2).

In contrast, Juutilainen, Halme, Kotiranta, and Monkkonen (2011) found that the largest size classes have the highest species richness with the smallest size classes supporting only 10% of the species found in boreal forests. Similarly, Nordén, Ryberg, Goetmark, and Olausson (2004) found more records on CWD than FWD in temperate broadleaf forests in the Northern Hemisphere. Generally, larger diameter wood pieces are more durable providing more resources, microhabitats, and supporting higher diversity than smaller diameter wood (Lonsdale et al., 2008). Küffer and Senn-Irlet (2005), however, found highest richness and exclusive species in VFWD. These small wood diameter fractions are important in managed forest because this is what remained after removal of larger wood pieces (Küffer & Senn-Irlet, 2005; Lindner et al., 2006; Abrego & Salcedo, 2013). The situation in unmanaged riparian forest of Uruguay is different for large wood fractions generally remain in the understory. Juutilainen et al. (2011) found that setting lower limit of wood diameter to 1 cm resulted in an underestimation of species richness by 10% and of occurrences by 46%. Our smallest size class (<2 cm diam, VFWD) is comparable to that of Juutilainen et al. (2011) and supported 33% of the total number of species. Debris of 2–10 cm supported half of the total number of species in our study (Fig. 4), but this diameter classes were ignored in most studies which dealt mostly with wood >10 cm diam (e.g., Juutilainen et al., 2011).

In our study, different fungal morphological groups preferred different wood diameter classes for fructification (Fig. 3). Corticioids are more frequently associated with the smaller wood fractions (VFWD to FWD) and polyporoids with larger wood fractions (FWD to CWD). These findings are similar to those of Nordén et al. (2004) who reported more corticioid and stereoid forms on FWD (1–10 cm), corresponding to the smaller wood fractions. Agaricoid and polyporoid fungi preferred CWD but were present with almost equal frequency in FWD and VFWD fractions. Specialist taxa are more sensitive to habitat fragmentation than generalists that can colonize many plant species and different wood fragmentation sizes (Nordén et al., 2004). Furthermore, accurate assessment of total species richness using fruitbody inventories is hampered by the reproductive effort and the durability of fruitbodies.

Biodiversity of wood-decay fungi is an important factor in the health of forest ecosystems. In this initial study, we attempted to quantify species richness and estimate the diversity of wood-inhabiting Agaricomycotina in the natural riparian forests of Uruguay. Because this ecosystem supports a high diversity of trees and shrubs by unit area, we expected a corresponding diversity of wood-inhabiting fungi. By studying the wood rotting fungi, mainly Agaricomycotina, present on dead wood material, we can begin to understand one of the factors essential for the functioning of riparian forests. This is particularly relevant in understudied geographic regions such as Uruguay (Hawksworth, 1991).

Disclosure

The authors declare no potential conflict of interest for this study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.myc.2019.02.001>.

References

- Abrego, N., & Salcedo, I. (2013). Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages: is it a question of quantity or quality? *Forest Ecology and Management*, 291, 377–385. <https://doi.org/10.1016/j.foreco.2012.11.025>.
- Berg, B., & McLaugherty, C. (2008). *Plant litter: Decomposition, humus formation, carbon sequestration* (2nd. Ed). Berlin Heidelberg, Germany: Springer-Verlag.
- Brussa, C. A., & Grell, I. A. (2007). *Flora arbórea del Uruguay. Con énfasis en las especies de Rivera y Tacuarembó*. Montevideo: Empresa Gráfica Mosca.
- Burnham, K. P., & Overton, W. S. (1978). Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika*, 65, 625–633. <https://doi.org/10.2307/2335915>.
- Carrere, R. (2010). *Monte indígena: mucho más que un conjunto de árboles*. Reedición Montevideo: Nordan, Guayubira, Ciedur, EGP. Montevideo (Uruguay).
- Castaña, J. P., Giménez, A., Ceroni, M., Furest, J., & Aunchayna, R. (2011). *Caracterización agroclimática del Uruguay 1980-2009*. INIA Serie Técnica N° 193. Montevideo: Editorial Hemisferio Sur.
- Chao, A. (1984). Nonparametric-estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, 11, 265–270.
- Chao, A. (1987). Estimating the population size for capture-recapture data with unequal catchability. *Biometrics*, 43, 783–791.
- Chao, A., & Lee, S. M. (1992). Estimating the number of classes via sample coverage. *Journal of the American Statistical Association*, 87, 210–217.
- Colwell, R. K. (2013). EstimateS: statistical estimation of species richness and shared species from samples. Version 9: user's guide and application. <http://purl.oclc.org/estimates>.
- Decock, C., Herrera Figueroa, S., Robledo, G., & Castillo, G. (2007). *Fomitiporia punctata* (Basidiomycota, Hymenochaetales) and its presumed taxonomic synonyms in America: taxonomy and phylogeny of some species from tropical/subtropical area. *Mycologia*, 99, 733–752. <https://doi.org/10.1080/15572536.2007.11832537>.
- DIEA. (2016). *Anuario Estadístico Agropecuario 2016*. MGAP. <http://www.mgap.gub.uy/unidad-ejecutora/oficina-de-programacion-y-politicas-agropecuarias/publicaciones-diea/anuario2016>.
- Felippone, F. (1928). Contribution à la flore mycologique de l'Uruguay. *Annals du Cryptogamie Exotique*, 1, 338–348.
- Gazzano, S. (1996). Notas sobre Basidiomycetes xilófilos del Uruguay. VII. Nuevos registros de Aphylophorales resupinados (Corticaceae y Polyporaceae). *Comunicaciones Botánicas del Museo de Historia Natural de Montevideo*, 6(106), 1–8.
- Gazzano, S. (1998). Notas sobre Basidiomycetes xilófilos del Uruguay. VIII. Registro de Aphylophorales y sus sustratos arbóreos. *Comunicaciones Botánicas del Museo de Historia Natural de Montevideo*, 6(109), 1–12.
- Gazzano, S. (2010). Notas sobre Basidiomycetes xilófilos del Uruguay. XIII. Aphylophorales (Basidiomycota, Opisthokonta) de la Región Litoral Oeste y Noroeste de Uruguay. *Comunicaciones Botánicas del Museo de Historia Natural de Montevideo*, 6(138), 1–16.
- Gibertoni, T. B., Medeiros, P. S., Soares, A. M. S., Gomes-Silva, A. C., Santos, P. J. P., Sotão, H. M. P., et al. (2016). The distribution of polypore fungi in endemism centres in Brazilian Amazonia. *Fungal Ecology*, 20, 1–6. <https://doi.org/10.1016/j.funeco.2015.09.012>.
- Gibertoni, T. B., Nogueira-Melo, G. S., de Lira, C. R. S., Baltazar, J. M., & Santos, P. J. P. (2015). Distribution of poroid fungi (Basidiomycota) in the Atlantic Rain Forest in Northeast Brazil: implications for conservation. *Biodiversity & Conservation*, 24, 2227–2237. <https://doi.org/10.1007/s10531-015-0991-8>.
- Gilbertson, R. L., & Ryvarden, L. (1986). *North American polypores* (Vol. 1). Oslo: Fungiflora.
- Gilbertson, R. L., & Ryvarden, L. (1987). *North American polypores* (Vol. 2). Oslo: Fungiflora.
- Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>.
- Greslebain, A. G., & Rajchenberg, M. (2003). Diversity of Corticiaceae sens. lat. in Patagonia, Southern Argentina. *New Zealand Journal of Botany*, 41, 437–446. <https://doi.org/10.1080/0028825X.2003.9512861>.
- Haretche, F., Mai, P., & Brazeiro, A. (2012). Woody flora of Uruguay: inventory and implication within the Pampean region. *Acta Botanica Brasílica*, 26, 537–552. <https://doi.org/10.1590/S0102-33062012000300004>.
- Hawksworth, D. L. (1991). The fungal dimension of biodiversity: magnitude, significance, and conservation. *Mycological Research*, 95, 641–655.
- Heltsh, J. F., & Forrester, N. E. (1983). Estimating species richness using the jack-knife procedure. *Biometrics*, 39, 1–11.
- Herter, G. (1933). *Plantae Uruguayenses novae vel criticae IV*. *Revista Sudamericana de Botánica*, 7, 171–260.
- Hibbett, D. S. (2006). A phylogenetic overview of the Agaricomycotina. *Mycologia*, 98, 917–925. <https://doi.org/10.3852/mycologia.98.6.917>.
- Hibbett, D. S., Bauer, R., Binder, M., Giachini, A. J., Hosaka, K., Justo, A., et al. (2014). Agaricomycetes. In D. J. McLaughlin, & J. W. Spatafora (Eds.), *Systematics and Evolution. The Mycota: A Comprehensive Treatise on Fungi as Experimental Systems for Basic and Applied Research*. 7A (pp. 373–429). Berlin, Heidelberg: Springer-Verlag.
- Jülich, W., & Stalpers, J. A. (1980). The resupinate non-poroid Aphylophorales of the temperate northern hemisphere. *Verhandelingen Koninklijke Nederlandse Akademie van Wetenschappen Afdeling Natuurkunde*, 74, 1–335.
- Juutilainen, K., Halme, P., Kotiranta, H., & Monkkonen, M. (2011). Size matters in studies of dead wood and wood-inhabiting fungi. *Fungal Ecology*, 4, 342–349. <https://doi.org/10.1016/j.funeco.2011.05.004>.
- Juutilainen, K., Monkkonen, M., Kotiranta, H., & Halme, P. (2014). The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions. *Forest Ecology and Management*, 313, 283–291. <https://doi.org/10.1016/j.foreco.2013.11.019>.
- Juutilainen, K., Monkkonen, M., Kotiranta, H., & Halme, P. (2017). Resource use of wood-inhabiting fungi in different boreal forest types. *Fungal Ecology*, 27, 96–106. <https://doi.org/10.1016/j.funeco.2017.03.003>.
- Kirk, P. M., Cannon, P. F., Minter, D. W., & Stalpers, J. A. (2008). *Ainsworth & Bisby's Dictionary of the fungi* (10th ed.). Wallingford: CAB International.
- Kjoller, A., & Struwe, S. (1992). Functional groups of microfungi in decomposition. In G. C. Carroll, & D. T. Wicklow (Eds.), *The fungal community: its organization and role in the ecosystem* (2nd ed., pp. 619–630). New York: Marcel Dekker Inc.
- Komonen, A., Niemi, M. E., & Junninen, K. (2008). Lakeside riparian forests support diversity of wood fungi in managed boreal forests. *Canadian Journal of Forest Research*, 38, 2650–2659. <https://doi.org/10.1139/X08-105>.
- Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, 15, 259–263. <https://doi.org/10.1127/0941-2948/2006/0130>.
- Küffer, N., Gillet, F., Senn-Irlet, B., Aragno, M., & Job, D. (2008). Ecological determinants of fungal diversity on dead wood in European forests. *Fungal Diversity*, 30, 83–95.
- Küffer, N., & Senn-Irlet, B. (2005). Influence of forest management on the species richness and composition of wood-inhabiting Basidiomycetes in Swiss forests. *Biodiversity & Conservation*, 14, 2419–2435. <https://doi.org/10.1007/s10531-004-0151-z>.
- Larsen, M. J., & Cobb-Poulsen, L. A. (1990). *Phellinus (Hymenochaetales): a survey of the world taxa*. Oslo: Fungiflora.
- Legrand, D. (1968). *Las Mirtáceas del Uruguay III*. *Boletín Facultad de Agronomía N°* (Vol. 101). Montevideo: Universidad de la República.
- León, R. J. C. (1991). Geographic limits of the region, geomorphology and geology, regional subdivisions, floristic aspects, description of the vegetation. In R. T. Coupland (Ed.), *Natural Grasslands: Introduction and Western Hemisphere*. Amsterdam: Elsevier, 367–347.
- Lindner, D. L., Burdsall, H. H., & Stanosz, G. R. (2006). Species diversity of polyporoid and corticioid fungi in northern hardwood forests with differing management histories. *Mycologia*, 98, 195–217. <https://doi.org/10.1080/15572536.2006.11832692>.
- Lombardo, A. (1964). *Flora arbórea y arborescente del Uruguay* (2 nd ed). Montevideo: Concejo Departamental de Montevideo, Dirección de Paseos Públicos.
- Lonsdale, D., Pautasso, M., & Holdenrieder, O. (2008). Wood-decaying fungi in the forest: conservation needs and management options. *European Journal of Forest Research*, 127, 1–22. <https://doi.org/10.1007/s10342-007-0182-6>.
- Magurran, A. E. (2017). The important challenge of quantifying tropical diversity. *BMC Biology*, 15, 14. <https://doi.org/10.1186/s12915-017-0358-6>.
- Martínez, S. (2006). The genera *Inocutis* and *Inonotus* (Hymenochaetales) in Uruguay. *Mycotaxon*, 96, 1–8.
- Martínez, S., & Nakasone, K. K. (2005). The genus *Phanerochaete* (Corticaceae, Basidiomycotina) sensu lato in Uruguay. *Sydowia*, 57, 94–101.
- Martínez, S., & Nakasone, K. K. (2010). New records and checklist of corticioid Basidiomycota from Uruguay. *Mycotaxon*, 114, 481–484. <https://doi.org/10.5248/114.481>.
- Martínez, S., & Nakasone, K. K. (2014). New records of interesting corticioid Basidiomycota from Uruguay. *Check List*, 10, 1237–1242. <https://doi.org/10.15560/10.5.1237>.
- Morrone, J. J. (2006). Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. *Annual Review of Entomology*, 51, 467–494. <https://doi.org/10.1146/annurev.ento.50.071803.130447>.
- Morrone, J. J. (2014). Biogeographical regionalization of the Neotropical region. *Zootaxa*, 3782, 1–110. <https://doi.org/10.11646/zootaxa.3782.1.1>.
- Naiman, R. J., & Décamps, H. (1997). The ecology of interfaces: Riparian Zones. *Annual Review of Ecology and Systematics*, 28, 621–658.
- Nordén, B., Ryberg, M., Goetmark, F., & Olausson, B. (2004). Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. *Biological Conservation*, 117, 1–10. [https://doi.org/10.1016/S0006-3207\(03\)00235-0](https://doi.org/10.1016/S0006-3207(03)00235-0).
- Núñez, M., & Ryvarden, L. (2000). *East Asian Polypores* (Vol. 1). Oslo: Fungiflora.
- Núñez, M., & Ryvarden, L. (2001). *East Asian Polypores* (Vol. 2). Oslo: Fungiflora.

- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V., Underwood, E. C., et al. (2001). Terrestrial ecoregions of the world: a new map of life on earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, 51, 933–938. CO:2 [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0).
- Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen–Geiger climate classification. *Hydrology and Earth System Sciences*, 11, 1633–1644. <https://doi.org/10.5194/hess-11-1633-2007>.
- Penttilä, R., Siitonen, J., & Kuusinen, M. (2004). Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. *Biological Conservation*, 117, 271–283. <https://doi.org/10.1016/j.biocon.2003.12.007>.
- Rollins, A. W., & Stephenson, S. (2013). Myxomycetes associated with grasslands of the western central United States. *Fungal Diversity*, 59, 147–158. <https://doi.org/10.1007/s13225-012-0204-7>.
- Rosa-Mato, F. (1939). Agaricales del Uruguay. *Physis*, 15, 123–127.
- Rosenthal, L. M., Larsson, K. H., Branco, S., Chung, J. A., Glassman, S. I., Liao, H. L., et al. (2017). Survey of corticioid fungi in North American pinaceous forests reveals hyperdiversity, underpopulated sequence databases, and species that are potentially ectomycorrhizal. *Mycologia*, 109, 115–127. <https://doi.org/10.1080/00275514.2017.1281677>.
- Ryvarden, L. (1991). *Genera of polypores—nomenclature and taxonomy*. Oslo: Fungiflora.
- Ryvarden, L. (2004). *Neotropical Polypores. Part 1. Introduction, Hymenochaetaceae and Ganodermataceae*. Oslo: Fungiflora.
- Ryvarden, L. (2005). *The genus Inonotus—a synopsis*. Oslo: Fungiflora.
- Ryvarden, L. (2010). *Stereoid fungi of America*. Oslo: Fungiflora.
- Ryvarden, L., & Johansen, I. (1980). *A preliminary polypore flora of East Africa*.
- Sabo, J. L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Heffernan, J., et al. (2005). Riparian zones increase regional species richness by harboring different, not more, species. *Ecology*, 86, 56–62. <https://doi.org/10.1890/04-0668>.
- Schneider, T., Keiblinger, K. M., Schmid, E., Sterflinger-Gleixner, K., Ellersdorfer, G., Roschitzki, B., et al. (2012). Who is who in litter decomposition? Meta-proteomics reveals major microbial players and their biogeochemical functions. *The ISME Journal*, 6, 1749–1762. <https://doi.org/10.1038/ismej.2012.11>.
- Schwarze, F. W. M. R., Engels, J., & Mattheck, C. (2000). *Fungal Strategies of Wood Decay in Trees*. Berlin-Heidelberg: Springer-Verlag. <https://doi.org/10.1007/978-3-642-57302-6>.
- Smith, E. P., & van Belle, G. (1984). Non-parametric estimation of species richness. *Biometrics*, 40, 119–129.
- Traversa-Tejero, I. P., & Alejano-Monge, M. R. (2013). Caracterización, distribución y manejo de los bosques nativos en el norte de Uruguay. *Revista Mexicana de Biodiversidad*, 84, 249–262. <https://doi.org/10.7550/rmb.23314>.
- Van der Wal, A., Geydan, T. D., Kuyper, T. W., & de Boer, W. (2013). A thready affair: linking fungal diversity and community dynamics to terrestrial decomposition processes. *FEMS Microbiology Reviews*, 37, 477–494. <https://doi.org/10.1111/1574-6976.12001>.