

## MINIREVIEW

# Learning from 80 years of studies: a comprehensive catalogue of non-*Saccharomyces* yeasts associated with viticulture and winemaking

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**One sentence summary:** The present manuscript systematizes 80 years of literature describing 293 non-*Saccharomyces* yeast species isolated from grapes and/or grape musts.

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## ABSTRACT

Non-*Saccharomyces* yeast species are nowadays recognized for their impact on wine's chemical composition and sensorial properties. In addition, new interest has been given to the commercial exploitation of non-*Saccharomyces* starter cultures in the wine sector. However, over many years, these yeast species were considered sources of contamination in wine production and conservation, mainly due to the high levels of volatile acidity obtained. The present manuscript systematizes 80 years of literature describing non-*Saccharomyces* yeast species isolated from grapes and/or grape musts. A link between each reference, the accepted taxonomic name of each species and their geographical occurrence is presented, compiling information for 293 species, in a total of 231 citations. One major focus of this work relates to the isolation of non-*Saccharomyces* yeasts from grapevines usually ignored in most sampling studies, also as isolation from damaged grapes. These particular niches are sources of specific yeast species, which are not identified in most other explored environments. These yeasts have high potential to be explored for important and diversified biotechnological applications.

**Keywords:** yeast species; non-*Saccharomyces* yeasts; grapes; vineyards; *Vitis vinifera*; *Vitis non-vinifera*; damaged grapes

## THE IMPORTANCE OF NON-SACCHAROMYCES YEASTS IN WINE: A HISTORICAL OVERVIEW

Non-*Saccharomyces* yeasts, defined as the yeast species found in wine production, excluding *Saccharomyces cerevisiae* (Jolly, Varela and Pretorius 2014), were originally considered as sources of microbial contamination in wine production and conservation,

mainly due to the high levels of volatile acidity detected. Although wines resulting from spontaneous fermentations, through ecological succession of these yeasts, culminate with the dominance of *Saccharomyces cerevisiae*, they are often described as more complex and revealing terroir-associated characteristics. More recently, the number of studies analyzing non-*Saccharomyces* yeast diversity in several locations worldwide

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has increased, revealing that a great number of those species considerably enhance the sensory profile of wines. In particular, some selected non-*Saccharomyces* yeasts are nowadays associated with a higher wine aromatic complexity, contributing with several positive organoleptic key characteristics: (i) increase of specific compounds such as glycerol content and total acidity; (ii) reduction of acetic acid content; (iii) enhancement of the aromatic profile, namely, of esters, higher alcohols and volatile thiols; (iv) secretion of enzymes that enrich wine aroma, specifically esterases,  $\beta$ -glucosidases, lipases, proteases and others; (v) reduction of ethanol content; (vi) control of the spoilage microflora; and (vii) improvements to the overall wine quality and complexity (Andorrà et al. 2008, 2010; Jolly, Varela and Pretorius 2014; Ciani and Comitini 2015; Liu et al. 2016; Aranda 2019; Ivit, Longo and Kemp 2020; Mateus et al. 2020). A large diversity of non-*Saccharomyces* species can be detected even before the fermentation process starts, e.g. during ripening and harvest processes (reviewed by Benito, Calderón and Benito 2019). After processing, three groups of non-*Saccharomyces* yeasts can then be found in the first stages of grape must fermentation (reviewed by Mateo et al. 2020), in which they proliferate due to their lower tolerance to ethanol: aerobic yeasts (e.g. yeasts of genera *Pichia*, *Rhodotorula* and *Cryptococcus*), yeasts with low fermentation ability (e.g. genus *Kloeckera*) and yeasts with typical fermentative metabolism (*Metschnikowia*, *Kluyveromyces*, *Zygosaccharomyces*, *Torulaspota*). These yeasts are then gradually replaced by *Saccharomyces cerevisiae*, which has a much higher tolerance to ethanol and a capacity to produce high amounts of volatile compounds and metabolites that are relevant in yeast selection programs (Pretorius and Høj 2005; Franco-Duarte et al. 2016; Lambrechts and Pretorius 2000). The importance of non-*Saccharomyces* yeasts is nowadays recognized by the use of non-*Saccharomyces* consortia in the early stages of fermentation (Steensels and Verstrepen 2014; Albertin et al. 2017; Kosel et al. 2017; Padilla et al. 2017; Escribano-Viana et al. 2018; Binati et al. 2019). In fact, at least 26 starter cultures, using 10 species of non-*Saccharomyces* species/strains, are currently commercially available (reviewed by Roudil et al. 2020). By benefiting from the use of these starter yeasts, winemakers can, in this way, produce stable, sustainable and diverse products.

Non-*Saccharomyces* yeasts are known to be present in a variety of environmental habitats, being in vineyards, isolated mainly from the grape surfaces and from their musts (Morrison-Whittle and Goddard 2018). Other places are also associated as niches for non-*Saccharomyces* species, such as the soil, the wine cellar equipment, the air and the cellar floor and walls (Barata, Malfeito-Ferreira and Loureiro 2012a; Bokulich et al. 2014; Pinto et al. 2014; Drumonde-Neves et al. 2016, 2017; Padilla, Gil and Manzanares 2016; Varela and Borneman 2017). Yeast diversity and presence are affected by external factors, such as grape variety, grape maturity, geographical location, climatic conditions, annual temperature, average rainfall, pesticide/fungicide treatments and agronomic practices (such as trellising and canopy management), among others (Barata, Malfeito-Ferreira and Loureiro 2012a; Bokulich et al. 2014; Pinto et al. 2014; Drumonde-Neves et al. 2016, 2017; Padilla, Gil and Manzanares 2016; Varela and Borneman 2017).

### Species diversity found on grapes and grape must

Even though there is a wide recognition about the potential of non-*Saccharomyces* yeast species to improve wine complexity, the great majority of studies only analyze and characterize the most well-represented species on grapes and/or musts.

One major concern about this is the fact that, despite the latest taxonomic revision performed by Kurtzman et al. (2011) (<https://theyeasts.org>), who recognized an overall total of nearly 1500 yeast species belonging to 149 genera, only about 40 species were documented on grapes or in grape must in 2014 (Jolly, Varela and Pretorius 2014) and around 150 in 2020 (Xu et al. 2020). The wide diversity associated with these environments has been emphasized in several publications, and many have highlighted the necessity to isolate, identify and characterize the native strains, even the ones less represented. In this way and for the first time, a comprehensive assessment of the literature describing non-*Saccharomyces* yeast species isolated from grape and/or grape musts is collected in Supplementary data S1. In this analysis we gathered information from 231 scientific papers, published from 1940 to 2020. A direct link between each species and the bibliographic citation in which its isolation was described is available. In total, 293 non-*Saccharomyces* species were catalogued, being isolated from grapes and/or grape musts, belonging to two phyla—Ascomycota and Basidiomycota—in a total of 9 orders, 18 classes and 37 families. This number of species corresponds to a much higher diversity than the one commonly associated with wine environments, and to the 150 documented as representing non-*Saccharomyces* species present on grapes in the year 2020 (Xu et al. 2020). In this catalogue, both culture-dependent and culture-independent isolation methods were considered, although only procedures that identified yeasts taxonomically to the species level were included. Metabarcoding studies identifying yeasts only to the genus level were excluded from the analysis. One interesting observation is related to the finding of 16 yeast species that were only detected by direct identification (without plating) methods: *Auriculibuller fuscus*, *Candida maltosa*, *Candida metapsilosis*, *Filobasidium chernovii*, *Hanseniaspora meyeri*, *Kluyveromyces hubeiensis*, *Kuraishia cidri*, *Lipomyces tetrasporus*, *Naganishia friedmanii*, *Papiliotrema nemorosa*, *Rhodospordiobolus colostri*, *Rhodospordium lusitanae*, *Sakaguchia lamellibrachiae*, *Sporobolomyces carnicolor*, *Sporobolomyces longiusculus* and *Tausonia pullulans*. These species were isolated using culture-independent methods such as PCR-DGGE, in which DNA is extracted directly from must and grapes, meta-amplification of barcodes using metagenomic approaches that allowed identification of some yeasts to species level, or Fourier Transform-Infrared Spectroscopy, identifying yeast species directly using infrared light. These methods are highlighted in Supplementary Table S1 using the superscript letters 'DI'. This fact points to the importance of the method used to analyze yeast diversity and also to the method considered when performing isolation. These 16 species would be overlooked if only methods contemplating plating cultivation were assessed. In addition, we achieved yeast species identification using molecular methods. When this was not the case, it is noted in the assembled table that the identification of the species was performed using non-molecular methods, so that the reader can be aware of this. Special attention should be given to the fact that different identification methods may result in a different identification accuracy. As discussed before, many molecular methods, or even DNA sequencing methods using a small region of the genome, might not be reliable enough to describe fungal communities. However, this fact is beyond the scope of this work, which focuses only on assessing the biological diversity associated with the presence of non-*Saccharomyces* species on grapes and grape musts, considering the best methods available to authors at the time.

The compiled table also combines information for the synonyms used in literature to describe the same species isolated

from grapes (identifying also the teleomorphic and anamorphic forms), which means that if all the described names in the literature were to be considered, more than 450 yeast species would be acknowledged. Especially in older references, it is not uncommon to find lists of identified yeast species containing synonyms treated as different taxonomic units. The work of Kurtzman *et al.* (2011) was used as the basis to define the accepted name of each species, but if changes to the nomenclature occurred since 2011, the particular research paper describing the change was cited in the table, next to the species' current name. In detail, 78 name changes/new names were reported. In this way, the present work constitutes an important data systematization for researchers working with non-*Saccharomyces* yeasts, to improve their understanding about its diversity and to analyze patterns of distribution and microbial ecology.

A total of eight species are reported in Supplementary Data S2 as being isolated in more than 50 isolation campaigns, with *Hanseniaspora uvarum* being the most cited one, in a total of 129 studies (Supplementary Data S2). The following species with higher occurrences were *Metschnikowia pulcherrima* (100 publications), *Starmerella bacillaris* (72), *Pichia terricola* (65), *Torulaspora delbrueckii* (61), *Pichia kudriavzevii* (56), *Hanseniaspora guilliermondii* (51) and *Lachancea thermotolerans* (50). Each of a total of 120 yeast species were reported only in one study (Supplementary Data S2). The attention given to these non-conventional yeasts constitutes an important landmark of this study, especially because species with low occurrences are ignored many times in this type of study. These yeasts should be the focus of particular attention in the future, to understand if they are exclusively associated to a particular wine region or grape type, or, on the contrary, if the isolation methods are not robust enough to be able to detect more than the most representative species.

### Yeast diversity and geographical distribution

In our previous work (Drumonde-Neves *et al.* 2016, 2017, 2018), several yeast species were isolated from a group of remote islands—Azores Archipelago, Portugal—and comparisons were made regarding the yeast community composition between islands, sampling years and cultivation schemes. In the light of our results, we understood that the most representative yeast genera occurring on grapes from vineyards of the Azores Archipelago were comparable with those identified in hundreds of other reports dealing with grape microbial communities in continental Europe, Africa, Asia and South America. However, we found occasional occurrences of several species that were not previously reported in any other grape- or wine-associated environments and that were described as new yeast species (Čadež *et al.* 2020; Drumonde-Neves *et al.* 2020).

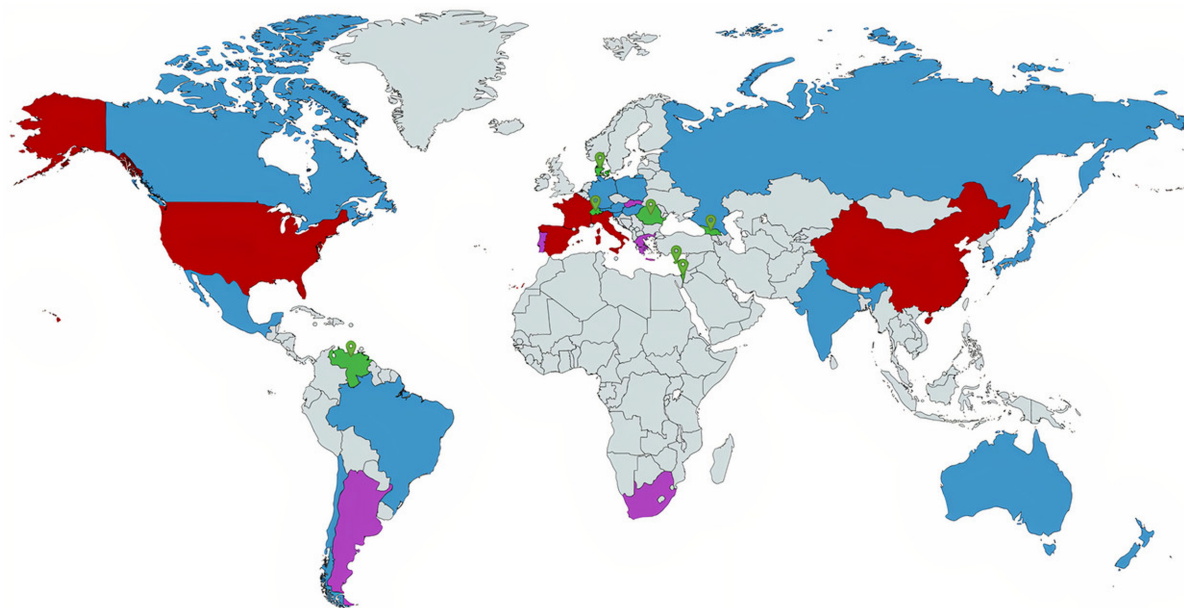
In the present work, geographical locations where the 293 non-*Saccharomyces* yeast species were reported were also considered. Fig. 1 represents the 33 countries (encompassing 4 continents) considered in this study, where non-*Saccharomyces* species have been isolated from grapes or grape must. Colors represent the number of different sampling campaigns reported in each country. Europe has the highest number of species isolated per country, albeit similar to the values found in the USA and China, with very few occurrences reported in Africa. The majority of samplings detecting only one species were associated with European countries. A detailed list combining each one of the 293 yeast species and the countries in which they were identified in grapes or grape musts are available in Supplementary Data S3. Although no clear and direct association could

be established between any particular genus and a geographical location, some patterns could be confirmed as being associated with the climates where the grapes were collected. However, when analyzing these patterns, attention should be given to the fact that many times, different sampling efforts can lead to different results. Some yeasts seem to be overrepresented in cooler climates, like the ones found in central Europe, as shown before (Cioch-Skoneczny *et al.* 2020). In this study we found some patterns for genera *Filobasidium*, *Saccharomycopsis* and *Dioszegia* showing some preference for grapes from these cold areas. On the contrary, some genera had a higher number of occurrences in grapes from warmer areas like Spain, Portugal and South Africa: *Barnettozyma*, *Hanseniaspora*, *Metschnikowia* and *Naganishia*. In particular, South Africa, probably due to its latitude and its peculiar climate, shows a very specific species pattern, with 12 species found only in this geographical location. The particular conditions found in this region were assessed in the past, because South Africa combines the cooler coastal region with the warmer inland area, which constitutes an unusual and irregular ecosystem for winemaking (Jolly, Augustyn and Pretorius 2003; Pretorius, van der Westhuizen and Augustyn 2017), leading to high biodiversity in terms of wine yeasts. Gayevskiy and Goddard (2012) published one of the first studies objectively demonstrating variation in non-*Saccharomyces* yeast species and communities associated with geographic location. Since then, a large number of research articles have discussed the association between geographical patterns and yeast distribution, mainly due to the fact that the concept of 'terroir' in oenology refers to a particular geographical area that is characterized by the particularities of that region, such as the climate, the human factors, the type of soil and the microbiome composition (Sicard and Legras 2011; Franco-Duarte *et al.* 2015; Mendes *et al.* 2017; Legras *et al.* 2018; Pretorius 2020). Increased importance has been attributed to the latter, claiming that the yeast species diversity found in a certain area, in combination with its microbiome, could be important to define the regional wine typicity. However, more studies are needed to expand this knowledge.

### Ascomycota versus Basidiomycota diversity on grapes

A comparative analysis was also performed for higher taxonomic levels considering the 293 species analyzed in this study, in particular the evaluation of diversity at the phylum level. Many ascomycetous yeasts are well known for their role in biotechnology and have been used for centuries in several biotechnological processes, such as in food production (reviewed in Johnson 2013a). By contrast, the importance of basidiomycetous yeasts for biotechnology is less well known (Johnson 2013b). This fact is also noticeable when analyzing yeast diversity in grapes, which led many times to the conclusion that the diversity and distribution of basidiomycetes in different countries is limited. The main reason for this, in the light of our analysis, is the lesser importance attributed to basidiomycetes, which leads to the majority of sampling campaigns ignoring basidiomycetes yeasts by not employing adequate identification methods. It is common to read in some scientific articles sentences such as 'Because basidiomycetous yeasts are not regarded as relevant to winemaking, no further identification analysis was done for these strains' (Barata *et al.* 2008a). This leads, inevitably, to a smaller registered number of basidiomycetes per study and per country. Nowadays the scenario is changing and increasing importance is being attributed to basidiomycetes (Liu *et al.* 2020). In the present manuscript, we analyzed the number of





**Figure 1.** Geographical locations where isolation of non-*Saccharomyces* species has been reported. Countries are colored in accordance with the number of sampling campaigns reporting yeast species isolated from grapes: **green**– 1 isolation campaign reported (a total of 7 countries); **blue**– from 2 to 5 campaigns (16 countries); **purple**– 6 to 10 campaigns (5 countries); **red**– more than 10 isolation campaigns (5 countries). Data were collected from the 231 scientific papers cited in Supplementary Table S1.

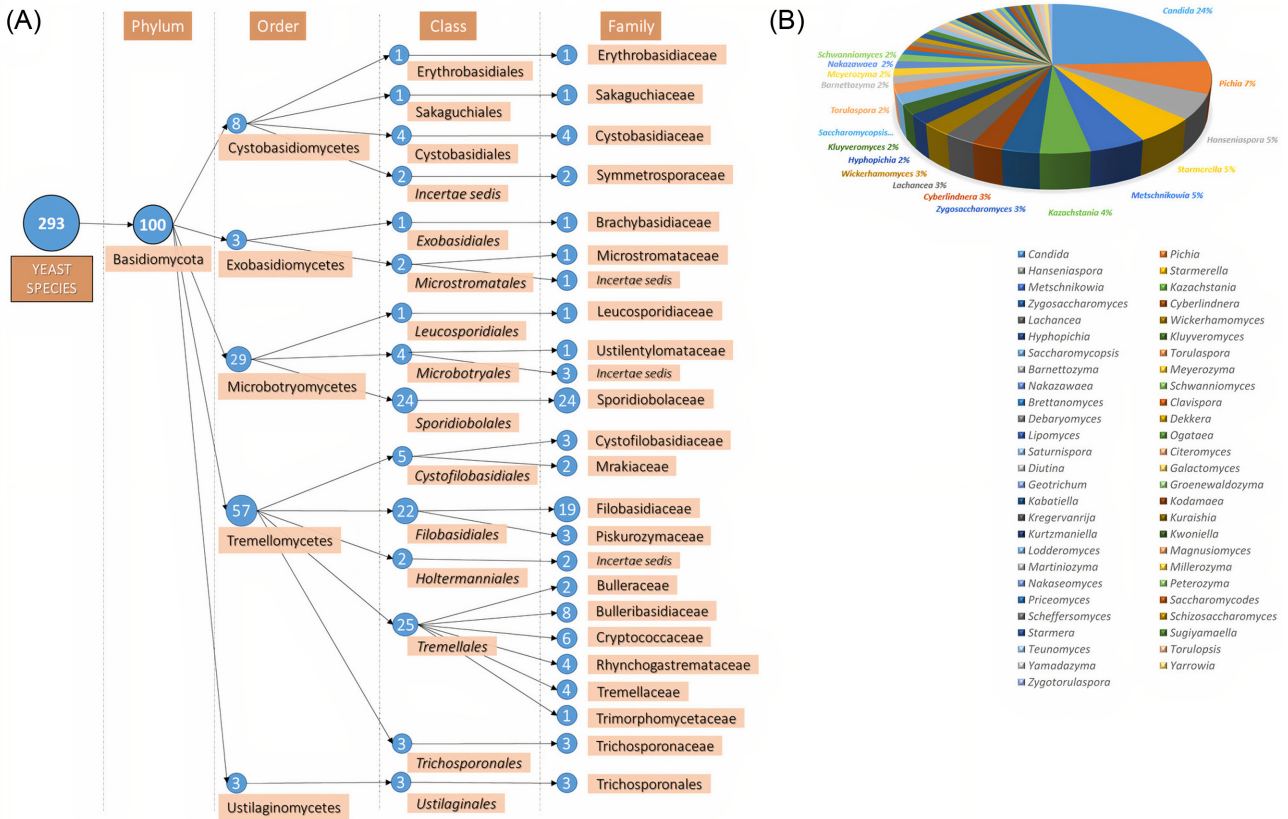
taxonomic units isolated from grapes belonging to Ascomycota (Fig. 2) or Basidiomycota (Fig. 3) phyla, even though it is our understanding that differences can be attributed in a large proportion to different sampling efforts, as already discussed, and also to the fact that fewer species of basidiomycetes are single celled and may have different growth requirements to ascomycetes yeasts.

From the 293 non-*Saccharomyces* yeast species analyzed in this study, 65.6% (191) belong to the phylum Ascomycota. The Basidiomycota diversity (101 species; 34.5%), although smaller, represents a number relevant enough to go against the lower importance attributed to this phylum in the past. Even in terms of taxonomic diversity, a higher number of taxonomic divisions (order, class and families) were found when analyzing Basidiomycetes (Fig. 3) than for Ascomycetes (Fig. 2). The five orders represented in Fig. 3 for the phylum Basidiomycota encompassed 15 classes and 24 families. Ascomycetes, although having a smaller diversity of orders, classes and families, had the majority of species identified as belonging to the family Saccharomycetaceae (class Saccharomycetes, order Saccharomycetales). One fact to highlight is that only one class/family was found under the classes Dothideomycetes, Lecanoromycetes and Schizosaccharomycetes, showing that almost all the diversity associated with this phylum can be encompassed under the Saccharomycetes class. When observed at genus level, the scenario is slightly different. Basidiomycetes encompassed 36 different genera (Fig. 3), while this number was more than double that for the Ascomycota phylum (Fig. 2).

## NON-SACCHAROMYCES YEAST DIVERSITY IN VITIS NON-VINIFERA CULTIVARS

The assembly of data from 231 scientific papers also considered the grape cultivar from which the 293 non-*Saccharomyces* species were isolated. In Supplementary Table S1, a superscript note is added to species not isolated from *Vitis vinifera*, identifying the

cultivar reported during the isolation campaign: *Vitis labrusca*, *Vitis rotundifolia*, *Vitis amurensis* and *Vitis davidii*. To the extent of our knowledge, this is the first study considering yeast isolation from five different *Vitis* cultivars. In the last few years, important differences were identified when comparing the diversity of non-*Saccharomyces* yeasts isolated from *V. vinifera* and *V. non-vinifera* grape varieties, which led to the conclusion that the yeast diversity might be a characteristic of the grape variety (This, Lacombe and Thomas 2006; Grimplet et al. 2009; Baffi et al. 2011; Bezerra-Bussoli et al. 2013; Raymond Eder et al. 2017, 2019; Eder, Conti and Rosa 2018; Raymond Eder and Rosa 2019). As expected, the majority of yeast species considered in this work were detected in *V. vinifera* grape variety: 99% (288 out of 291 species). However, the number of sampling campaigns is highly discrepant when assessing yeast diversity in the *V. vinifera* and *V. non-vinifera* cultivars, which make comparisons between habitats impossible. In this way, comparisons will only be made in terms of the research articles considered, without overanalyzing these differences, due to different sampling efforts, as already discussed. Differences between the sampling campaigns assessing yeast diversity in *V. vinifera* and *V. non-vinifera* relate mainly to law regulations in several countries that only allow cultivation of grape varieties of *V. vinifera*, which has led to a higher number of research articles isolating species from this grape variety in the last few years. In the present work, only three species were isolated from *V. vinifera* in any campaign: *Cryptococcus humicola*, *Saturnispora diversa* and *Sugiyamaella smithiae* (Supplementary data S1). In addition to the presence/absence of the different species in each of the *V. non-vinifera* grape cultivar, we also collected data for the relative abundance of each of the species present. Fig. 4A summarizes the relative frequencies calculated for each species gathered from the seven scientific papers reporting isolation from *V. labrusca* cultivars. This type of comparison was already performed by another research group (Raymond Eder and Rosa 2019), although only comparing data from the Azorean, Portugal (Drumonde-Neves et al. 2016) and

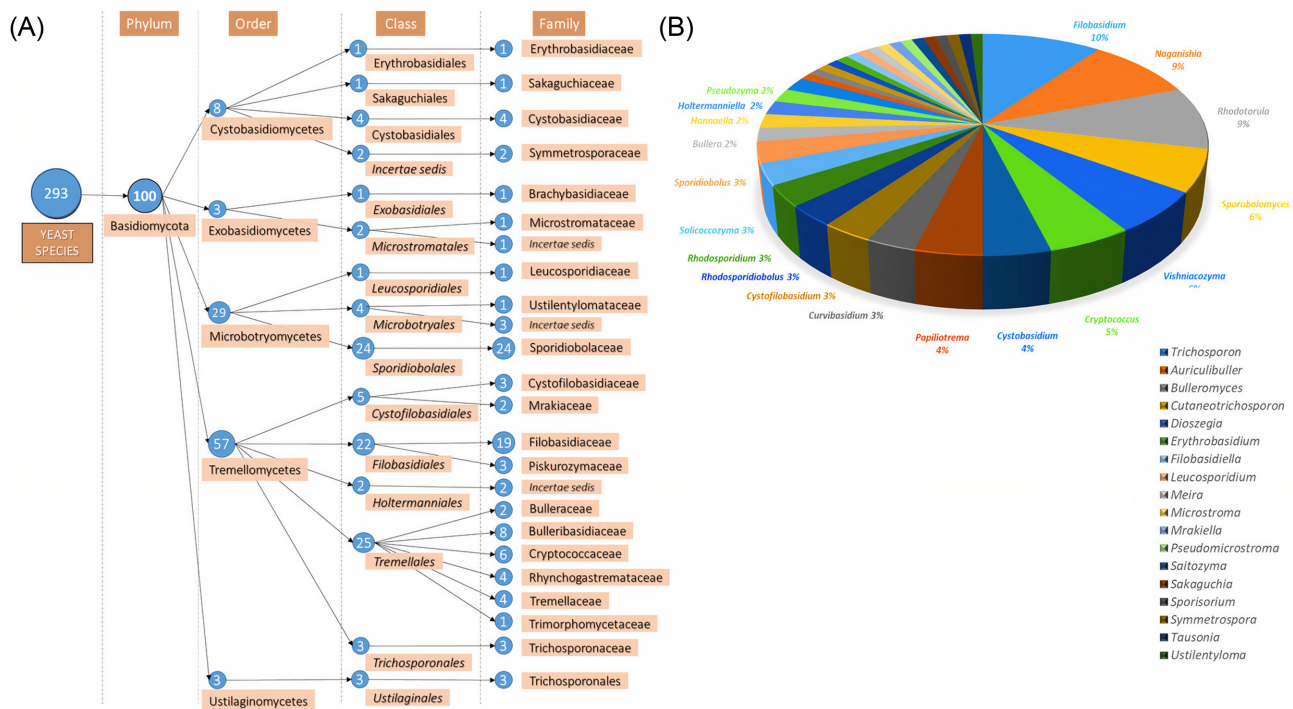


**Figure 2.** Ascomycota diversity distributed by order, class and families (A) and by genera (B). Node sizes in panel A are proportional to the number of studies (values inside the circles) in which each taxon was detected on grapes. In panel B, percentages of detection of each genus are indicated after its name, with the exception of the genera detected in less than 2% of the studies, which are detailed below the graph. Data were collected from the 231 scientific articles detailed in Supplementary Table S1.

Carola, Argentina (Raymond Eder et al. 2017) campaigns. In this work we extended this comparative analysis to other geographical areas, considering four additional works (Baffi et al. 2011; Bezerra-Bussoli et al. 2013; Hong and Park 2013; Gaensly et al. 2015).

The present analysis shows that *H. uvarum* is the dominant yeast species in the great majority of the campaigns whose data are summarized in Fig. 4A, a result in accordance with isolations from *V. vinifera*. Although identified in all the campaigns, and being the dominant species in almost all of them, *H. uvarum* was not the dominant species in one of the geographical areas. In the study performed in Carola, Argentina, in 2007 (Raymond Eder et al. 2017), *Starmerella bacillaris* was the main yeast species identified (59.7%), with a value five times higher than the relative frequency calculated for *H. uvarum* (11.1%) in that campaign. Besides *H. uvarum*, 15 other yeast species were detected in more than one isolation campaign considering *V. labrusca* grapes. *Starmerella bacillaris* and *Zygoascus meyeriae* were identified in four of the six mentioned research papers, and *Pichia kudriavzevii* and *Candida azymoides* were reported in three of the six campaigns. Twelve species were associated with this cultivar exclusively in the work of Drumonde-Neves et al. (2016): *Saccharomycopsis vini*, *Saturnispora diversa*, *Metschnikowia pulcherrima*, *Meyeromyces carpophila*, *Pichia membranaefaciens*, *Candida raillenensis*, *Saccharomycopsis crataegensis*, *Candida azyma*, *Pichia fermentans*, *Barnettomyces californica*, *Candida incommunis* and *Saturnispora zaruensis*. This is the most detailed examination of yeast diversity associated with the *V. labrusca* cultivar.

A similar analysis is shown in Fig. 4B, but this time describing the diversity associated with *V. rotundifolia*, *V. amurensis* and *V. davidii* grape cultivars. Although less known and less used, these grapevine varieties are popular, especially in geographical areas in which *V. vinifera* is particularly sensitive to pests, heavy rainfalls and other environmental stresses (Parish and Carroll 1985; Lee et al. 2006; Camargo and Ritschel 2008; Hong and Park 2013; Wang, Wu and Qiu 2019; Ye et al. 2019; Wei et al. 2020). Some of these studies already reported the use of grapes from these alternative varieties to produce wine, with interesting results in terms of sensorial and aromatic profiles. Our analysis (Fig. 4B) shows a high heterogeneity and different yeast profiles associated with each cultivar when considering non-*Saccharomyces* species. In particular, grapes from the *V. rotundifolia* variety revealed a high diversity of associated species and an exclusive species profile. With the exception of *Saccharomyces cerevisiae*, no other species detected in *V. amurensis* or in *V. davidii* were isolated from *V. rotundifolia* grapes, and the nine species identified in the *V. rotundifolia* grapevine were absent from the other two: *Pichia membranaefaciens*, *Candida humicola* (current name *Cryptococcus humicola*), *Hanseniaspora osmophila*, *Lodderomyces elongisporus*, *Candida sake*, *Rhodotorula glutinis*, *Rhodotorula minuta* (current name *Cystobasidium minutum*), *Candida albicans* and *Candida edax* (current name *Sugiyamaella smithiae*). In addition, and to highlight the exclusive yeast profile associated with this cultivar, from these nine yeast species, eight of them were also absent from *V. labrusca* cultivar and two were not detected in any *V. vinifera* analysis: *Candida humicola* (*Cryptococcus humicola*) and



**Figure 3.** Basidiomycota diversity distributed by order, class and families (A) and by genera (B). Node sizes in panel A are proportional to the number of studies (values inside the circles) in which each taxon was detected on grapes. In panel B, percentages of detection of each genus are indicated after its name, with the exception of the genera detected in less than 2% of the studies, which are detailed below the graph. Data were collected from the 231 scientific articles detailed in Supplementary Table S1.

*Candida edax* (*Sugiyamaella smithiae*), which points to the possibility that the presence of these species is exclusive to *V. rotundifolia* grapes. However, we cannot exclude the hypothesis that these absences are due to different sampling efforts between studies. The profile of yeast diversity isolated from *V. amurensis* and *V. davidii*, on the contrary, was similar, with the exception of two species exclusively from *V. amurensis*: *Kazachstania hellenica* and *Issatchenkia terricola*. The data assembled in this work could be of great importance to confirm the association between yeast consortia and grape cultivars, which would allow recognition of yeasts with oenological importance.

## INFLUENCE OF GRAPE DAMAGE ON YEAST DIVERSITY

The last point of focus in this work relates to yeasts isolated from damaged berries. Increased attention has been given in the last decade to the impact of damaged grapes on yeast ecology, after the health status of grapes was largely disregarded in the past. This fact is associated mainly with inaccurate grape sampling, because it was thought that the state of grapes was not relevant to explain the acquired microbial biodiversity. However, it was reported that damaged berries, which are hidden many times in apparently sound bunches, are associated with a higher number of species in comparison with samplings containing only sound grapes. Of relevance in this matter is the work of Barata et al. (Barata et al. 2008a,c; Barata, Malfeito-Ferreira and Loureiro 2012a,b) analyzing the microbiota of sour rotten wine grapes and its impact on fermentations. These authors concluded, during several years of samplings, that yeast diversity was much higher in rotten grape samples, and that particular yeast species were associated with sour rotten grapes, such as *Issatchenkia*

*occidentalis* (current name *Pichia occidentalis*), *Zygoascus hellenicus* and *Zygosaccharomyces bailii*. In order to expand this analysis, and using data assembled in Supplementary Data S1, we analyzed all the collected literature to compare yeast communities found in healthy and damaged grapes. Results should be analyzed with caution, since, as already discussed, different sampling efforts between campaigns could lead to different results in terms of species diversity. Table 1 summarizes the data collected in terms of yeast species isolated from damaged/rotten grapes in a total of 13 scientific papers (le Roux, Eschenbruch and de Bruin 1973; Guerzoni and Marchetti 1987; Nisiotou and Nychas 2007; Nisiotou, Spiropoulos and Nychas 2007; Rao et al. 2007; Barata et al. 2008a,b; Combina et al. 2008; Francesca et al. 2010; Barata, Malfeito-Ferreira and Loureiro 2012b; Nemcová et al. 2015; Sipiczki 2016; Lleixà et al. 2018). It is our belief that other works, especially older ones, possibly report yeast isolation, also from unhealthy grapes. However, little attention was given in the past to this fact when designing/performing grape collection campaigns. Results show that a total of 81 yeast species were detected in damaged/rotten grapes. When detailing these results (data in Supplementary Data S1), one can observe that nine yeast species were exclusively found in damaged grapes (marked in bold in Table 1), being absent in all the other studies considering healthy ones: *Candida ethanolica*, *Candida hyderabadensis*, *Candida pini*, *Candida robusta*, *Kabatiella microsticta*, *Kazachstania africana*, *Kluyveromyces dobzhanskii*, *Solicocozyma keelungensis* and *Torulopsis holmii*. *Hanseniaspora uvarum* was once again the most represented species, identified in 11 of the 13 research studies. *Pichia kudriavzevii* and *Zygosaccharomyces bailii* also showed a higher association with damaged grapes, being identified in six and seven studies, respectively. All three species also showed a high dominance in campaigns



**Table 1.** Yeast species isolated from damaged/rotten grapes. Data were collected from original research articles, as indicated by the plus signs. Numbers after references indicate the publication number used in Supplementary Table S1. Species isolated only from damaged grapes (no occurrences were reported for healthy grapes) are highlighted in bold.

Yeast species	Isolation from healthy grapes (number of studies)	Isolation from damaged/rotten grapes												
		Sipiczki et al. 2016 [15]	Nemcová et al. 2015 [40]	Lleixà et al. 2018 [44]	Barata et al. 2008 [48]	Nisiotou et al. 2007 [50]	Le Roux et al. 1973 [53]	Rao et al. 2007 [54]	Barata et al. 2008 [65]	Barata et al. 2012 [98]	Guertzoni and Marchetti 1987 [135]	Nisiotou and Nychas 2007 [142]	Francesca et al. 2010 [183]	Combina et al. 2008 [205]
<i>Bulleromyces albus</i>	6	+												
<i>Candida californica</i>	14			+										
<i>Candida ethanolica</i>	NO				+									
<i>Candida glabrata</i>	9	+												
<i>Candida</i>	NO							+						
<b><i>hyderabadensis</i></b>														
<i>Candida inconspicua</i>	3													
<i>Candida melinii</i>	1													
<i>Candida oleophila</i>	14													
<i>Candida parapsilosis</i>	14													
<i>Candida pini</i>	NO													
<b><i>Candida robusta</i></b>	NO													
<i>Candida tropicalis</i>	4													
<i>Candida vanderwaltii</i>	3													
<i>Clavispora fructus</i>	1													
<i>Clavispora lusitanae</i>	8													
<i>Curvibasidium</i>	3	+												
<i>cygneicollum</i>														
<i>Curvibasidium</i>	4	+												
<i>pallidicorallinum</i>														
<i>Cystobasidium</i>	7													
<i>minutum</i>														
<i>Debaryomyces</i>	33													
<i>hanseni</i>														
<i>Dioszegia hungarica</i>	3													
<i>Filobasidium elegans</i>	1													
<i>Filobasidium magnum</i>	25	+												
<i>Filobasidium</i>	1	+												
<i>stepposum</i>														
<i>Filobasidium</i>	3													
<i>wieringae</i>														
<i>Hanseni</i>	47													
<i>guilliermondii</i>														
<i>Hanseni</i>	8													
<i>Hanseni</i>	18													
<i>occidentalis</i>														
<i>Hanseni</i>	20													
<i>opuntiae</i>														
<i>Hanseni</i>														
<i>osmophila</i>														

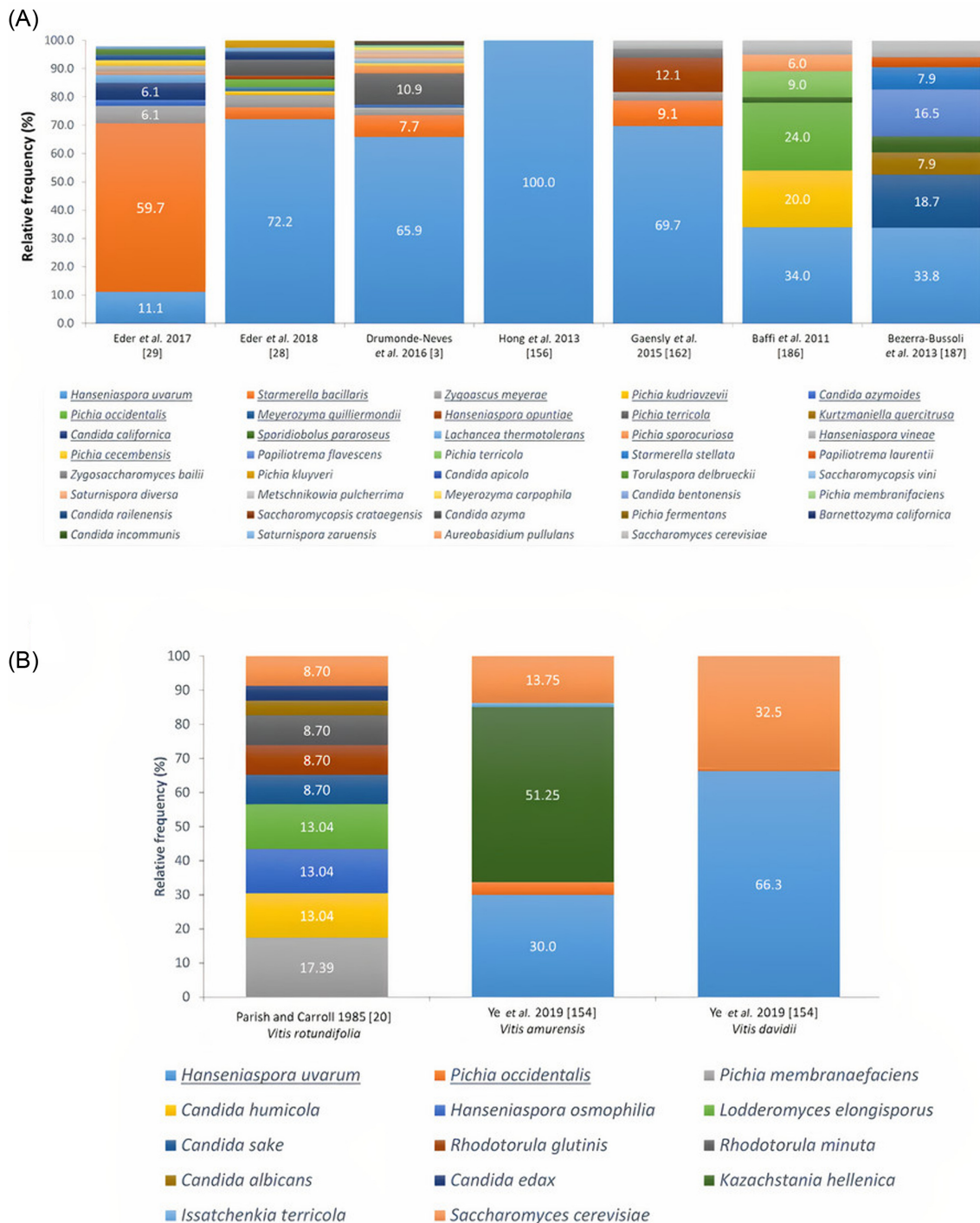
Table 1. Continued

Yeast species	Isolation from healthy grapes (number of studies)	Isolation from damaged/rotten grapes												
		Sipiczki 2016 [15]	Nemcová et al. 2015 [40]	Lleixà et al. 2018 [44]	Barata et al. 2008 [48]	Nisiotou et al. 2007 [50]	Le Roux et al. 1973 [53]	Rao et al. 2007 [54]	Barata et al. 2008 [65]	Barata et al. 2012 [98]	Guerzoni and Marchetti 1987 [135]	Nisiotou and Nychas 2007 [142]	Francesca et al. 2010 [183]	Combina et al. 2008 [205]
<i>Hanseniaspora uvarum</i>	118	+	+	+	+	+	+	+	+	+	+	+	+	
<i>Hanseniaspora vineae</i>	22	+												
<i>Holtermanniella festucosa</i>	1	+												
<i>Kabatiella microsticta</i>	NO	+												
<i>Kazachstania africana</i>	NO			+										
<i>Kluyveromyces dobzhanskii</i>	NO	+			+									
<i>Kregervanrija fluxuum</i>	8	+				+								
<i>Lachancea thermotolerans</i>	45	+			+	+		+						
<i>Metschnikowia fructicola</i>	11													+
<i>Metschnikowia pulcherrima</i>	94		+			+					+		+	
<i>Meyerozyma caribbica</i>	8													
<i>Meyerozyma guilliermondii</i>	29												+	
<i>Microstroma bacarum</i>	5		+											
<i>Naganishia diffluens</i>	4										+			
<i>Papiliotrema flavescens</i>	16	+												
<i>Papiliotrema laurentii</i>	23													
<i>Pichia deserticola</i>	1													
<i>Pichia fermentans</i>	26	+												
<i>Pichia kluyveri</i>	37	+				+								+
<i>Pichia kudriavzevii</i>	49	+	+			+							+	
<i>Pichia manshurica</i>	15													
<i>Pichia membranifaciens</i>	39	+											+	
<i>Pichia occidentalis</i>	28													
<i>Pichi sporocuriosa</i>	12													
<i>Pichia terricola</i>	60			+										
<i>Rhodotorula glutinis</i>	37					+								+
<i>Rhodotorula graminis</i>	5	+												+
<i>Rhodotorula mucilaginosa</i>	36													+



Table 1. Continued

Yeast species	Isolation from healthy grapes (number of studies)	Isolation from damaged/rotten grapes												
		Sipiczki 2016 [15]	Nemcová et al. 2015 [40]	Lleixà et al. 2018 [44]	Barata et al. 2008 [48]	Nisiotou et al. 2007 [50]	Le Roux et al. 1973 [53]	Rao et al. 2007 [54]	Barata et al. 2008 [65]	Barata et al. 2012 [98]	Guerzoni and Marchetti 1987 [135]	Nisiotou and Nychas 2007 [142]	Francesca et al. 2010 [183]	Combina et al. 2008 [205]
<i>Rhodotorula nothofagi</i>	11	+												
<i>Saccharomyces amapae</i>	3							+						
<i>Saccharomyces crataegensis</i>	7		+					+		+				
<i>Saccharomyces vini</i>	7									+				
<i>Saturnispora diversa</i>	16				+					+				
<i>Schizosaccharomyces pombe</i>	4													
<i>Solicozyma keelungensis</i>	NO	+												
<i>Sporidiobolus pararoseus</i>	14		+											
<i>Starmera stellimalicola</i>	2								+					
<i>Starmerella bacillaris</i>	68													
<i>Starmerella stellata</i>	33					+			+					
<i>Symmetospora coprosmae</i>	2	+												
<i>Symmetospora oryzicola</i>	2	+												
<i>Torulaspora delbrueckii</i>	59	+												
<i>Torulaspora microellipsoides</i>	3													
<i>Torulopsis holmii</i>	NO													
<i>Vishniacozyma carnescens</i>	12	+												
<i>Vishniacozyma victoriae</i>	11	+												
<i>Wickerhamomyces anomalus</i>	43	+												
<i>Zygoascus hellenicus</i>	16													
<i>Zygoascus meyeriae</i>	15	+												
<i>Zygosaccharomyces bailii</i>	28	+												
<i>Zygosaccharomyces bisporus</i>	6													
<i>Zygosaccharomyces rouxii</i>	6													
<i>Zygotulasporea florentina</i>	9	+												



**Figure 4.** Relative frequency (%) of non-Saccharomyces yeast species isolated from (A) *Vitis labrusca* and (B) *V. rotundifolia*, *V. amurensis* and *V. davidii* cultivars. Underlined species' names indicate the ones isolated from more than one study/campaign. Numbers after references indicate the publication number used in Supplementary Table S1.

contemplating healthy grapes, which led to the conclusion that their abundance was not related to the health status of the grapes. In conclusion, results indicate that grape damage is a highly important factor to be accounted for in yeast ecology studies. It was demonstrated that several yeast species were only associated with these particular environments, which can, if associated with negative effects, compromise the winemaking process.

In conclusion, our work presents, for the first time, an in-depth, broad and comprehensive assessment of 231 scientific papers published during the last 80 years reporting identification of non-Saccharomyces yeasts from grapes and/or grape must. A total of 293 yeast species were catalogued and linked to each bibliographic reference, together with their isolation environment, grapevine and health status of the grapes. Although the majority of species reported in this work belong to the

phylum Ascomycota, a high diversity of Basidiomycota yeasts was also described, going against the lower importance attributed to this phylum in the past. In addition, information from the grape cultivar considered in each campaign was assessed, showing a high diversity of yeasts collected from *Vitis non-vinifera* cultivars. For the first time, yeasts isolated from *V. labrusca*, *V. rotundifolia*, *V. amurensis* and *V. davidii* were categorized. Our study also showed the importance of grape health status and its influence in yeast diversity, with the disclosure of nine species detected exclusively in damaged grapes. Data assembled in this work could be of great importance to researchers working with yeasts in winemaking or in other areas of biotechnological relevance. The diversity systematized here, especially regarding the less explored yeast species, will open doors to study new patterns of microbial distribution and ecology in vineyard environments.

## SUPPLEMENTARY DATA

Supplementary data are available at [FEMSYR](https://femsyr.com) online.

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**Conflict of interest.** None declared.

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