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The fungal community associated with the ambrosia beetle *Xylosandrus compactus* invading the mediterranean maquis in central Italy reveals high biodiversity and suggests environmental acquisitions

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ABSTRACT

In summer 2016 a severe infestation of the alien ambrosia beetle *Xylosandrus compactus* was recorded from the Mediterranean maquis in the Circeo National Park in Central Italy. Trees and shrubs were infested and displayed wilting and necrosis of terminal branches caused by the combined impact of the insect and associated pathogenic fungi. A preliminary screening carried out on captured adults resulted in the isolation of a discrete number of fungal taxa with different life strategies, ranging from true mutualist (e.g. *Ambrosiella xylebori*) to plant pathogens (*Fusarium* spp.). In the present study, high-throughput sequencing was applied to determine the total diversity and functionality of the fungal community associated with *X. compactus* adults collected in the galleries of three Mediterranean woody hosts, *Quercus ilex*, *Laurus nobilis*, and *Ceratonia siliqua*. The effect of season and host in determining the composition of the associated fungal community was investigated. A total of 206 OTUs composed the fungal community associated with *X. compactus*. Eighteen OTUs were shared among the three hosts, including *A. xylebori* and members of the *Fusarium solani* complex. All but two were previously associated with beetles.

Sixty-nine out of 206 OTUs were resolved to species level, identifying 60 different fungal species, 22 of which already reported in the literature as associated with beetles or other insects. Functional guild assigned most of the fungal species to saprotrophs and plant pathogens. Effects of seasonality and host on fungal community assemblage were highlighted suggesting the acquisition by the insect of new fungal taxa during the invasion process. The consequences of enriched fungal community on the risk of the insurgence of novel threatful insect–fungus association are discussed considering direct and indirect effects on the invaded habitat.

1. Introduction

The ambrosia beetle *Xylosandrus compactus* (Eichhoff) (Coleoptera: Curculionidae, Scolytinae; black twig borer) is an important pest of a wide range of woody hosts. It is widespread in Africa, the Americas, and Southeast Asia. It has recently invaded Europe and is spreading in natural ecosystems and parks and gardens in Italy and Southern France (Delgado and Couturier, 2010; Rabaglia et al., 2006; Vannini et al., 2017). The native range of *X. compactus* is probably East Asia (Chong et al., 2009; Wood, 1982). *X. compactus* is a primary pest of over 200 hosts worldwide with a high impact in cultivated and natural environments. Healthy twigs are attacked by females that bore into the living tissues (Ngoan et al., 1976). *X. compactus* is currently included in the European Plant Protection Organization (EPPO) alert list, in the A1 list of the Caribbean Agricultural Health and Food Safety Agency (CAHFSA), and the Organismo Internacional Regionale de Sanidad Agropecuaria and considered a quarantine pest in Israel (OIRSA – Central America); It is considered a quarantine pest in Israel and Morocco. Due to its

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capacity for inbreeding, *X. compactus* establishes active populations very rapidly especially in the presence of suitable environmental conditions, killing live shoots in a short period. Symptoms include small entrance holes (0.8 mm in diameter), shoots wilt, and wood necrosis often extending distally and proximally alongside the branches (Dixon et al., 2003; Vannini et al., 2017). *X. compactus* is commonly associated with fungi. Some of these fungi, such as *Ambrosiella xylebori*, are considered true mutualists and supply the diet for the larvae in the galleries (Bateman et al., 2016). True mutualists are typically carried in the mycangia, and provide the diet for larvae through so-called fungus-farming (Hulcr and Stelinski, 2017). Others may be pathogenic and contribute to symptom developments on host plants. Among these many *Fusarium* spp., often members of the *Fusarium solani* complex (FSSC), considered stable associates and that are involved in necrosis development on infested twigs/branches (Bateman et al., 2016; Bosso et al., 2012; Vannini et al., 2017). Beside establishing a stable association, *Fusarium* spp. are not harboured in *X. compactus* mycangia; Bateman et al. (2016) demonstrated their localization mostly in the abdomen and on external surfaces of the insect.

In summer 2016 a severe infestation of the alien ambrosia beetle *X. compactus* was recorded from the Mediterranean maquis in the Circeo National Park in Central Italy. Trees and shrubs were infested and displayed wilting and necrosis of terminal branches caused by the combined impact of the insect and associated pathogenic fungi. A multimember community of fungal species, many originating in the invaded environment, are found associated with *X. compactus* in Central Italy, with life strategies and functionality ranging from parasitism to saprotrophic. Vannini et al. (2017) isolated 18 different taxa from *X. compactus* bodies and galleries in Italy, including *A. xylebori*, FSSC members, and many other taxa; the native *Biscogniauxia mediterranea*, and the cosmopolitan *Botryosphaeria stevensii* were also present. Other fungi present included *Geosmithia pallida*, a recently described pathogen of live oak in the USA (Lynch et al., 2014), often associated with a range of wood–boring insects (Kolařík et al., 2004); *Epicoccum nigrum* reported associated with other species of *Xylosandrus* (Kostovcik et al., 2015); and *Pestalotiopsis* sp. previously recorded from *X. compactus* in Florida (Bateman et al., 2016).

The ongoing EU LIFE project SAMFIX was launched having among the objectives to monitor *X. compactus* invasion of the Mediterranean basin and to predict the risks for natural areas. The introduction and diffusion of plant pathogenic fungi associated with the insect are among the potential risks to monitor. As recently reported by Rassati et al. (2019), the mycobiome of ambrosia beetles is enriched with fungi found in the invaded areas that can establish new associations with the insect. The authors demonstrated such a process for *Xylosandrus germanus* invading forest areas in northern Italy. Thus, the present study aims to describe and analyze the total fungal community associated with the alien ambrosia beetle *X. compactus* invading the Mediterranean maquis; to determine their functional guild, ecology, and taxonomic position; to analyze 'new' and already recorded associations using taxonomy and life-style as references; finally to discuss of the possible risk for an insurgence of invasive insect–fungus interactions.

2. Materials and methods

2.1. Sampling area

The sampling area was in the National Park of Circeo in the 'Quarto freddo' of the Circeo Promontory (41°14,050″ N 13°02035 E) province of Latina in the Latium region (Italy). The area is characterized by a biodiverse Mediterranean maquis with *Quercus ilex, Laurus nobilis,* and *Ceratonia siliqua* composing the upper vegetation layer. *X. compactus* was first recorded in the area in summer of 2016 (Vannini et al., 2017). The sampling of adults of *X. compactus* from the galleries was carried out along three linear transects established within the Park, one for each of the three host tree species *Q. ilex*, *L. nobilis,* and *C. siliqua*.

2.2. Sampling of X. compactus adults

Four, 12, and 10 trees of *C. siliqua*, *Q. ilex,* and *L. nobilis*, respectively, with symptoms of *X. compactus* attack (wilting of shoots and presence of entrance hole) were sampled. Sampling took place in September 2016 and May 2017. For each tree, symptomatic terminal branches were excised (at least one per tree), each stored in a separate bag and taken to the laboratory. From each branch, adults of Scolytinae were carefully collected from tunnels found on branches and stored each in a sterile 2 mL test tubes at 5 °C for a maximum of 24 h before DNA extraction. The species was determined based on morphological characteristics and following published keys (Dole and Cognato, 2010). A total of 26 adults of *X. compactus* from *L. nobilis*, 48 from *Q. ilex*, and 50 from *C. siliqua* were collected from galleries in September 2016. The number of captured insects in May 2017 was 15, 36, and 28 from *L. nobilis*, *Q. ilex,* and *C. siliqua*, respectively. The number of adults collected from each branch ranged from 1 to 3. Adults collected were not dissected and not washed before DNA extraction. Six bulk of insects, one bulk per each tree species and season, were processed for HTS analysis.

2.3. DNA extraction and amplification

Total DNA was extracted from insect bodies using the DNeasy PowerSoil Kit (Qiagen, Germany), following the manufacturer's instructions. The ITS1 region was amplified with a dual indexing primer using the tagged primer pair ITS1F (5′-xxxCTYGGTCATTTAGAGGAAGTAA-3′) and ITS2 (5-xxxGCHRCGTTCTTCATCGDTGC-3′), where xx represents the barcoding key. The PCR reaction mixture comprised 12.5 μl of Maxima Hot Start PCR Master Mix (2X) (Thermo Fisher Scientific, USA) and 1 μM of each primer in a total volume of 25 μl containing 24 μl of the reaction mixture and 1 μl template. The thermal cycle was an initial denaturation at 94 °C for 10 min followed by 30 cycles of 95 °C for 40 s, 60 °C for 40 s and 72 °C for 1 min, and a final elongation step of 72 °C for 10 min. Eight PCRs were carried out and pooled per sample. Amplicons were purified using the MagJET NGS Cleanup (Thermo Scientific, USA), quantified with the Qubit Quantitation kit (Invitrogen, USA), and pooled at equal concentrations for sequencing. Paired-end sequencing (2 × 300 bp) was carried out on an Illumina MiSeq sequencer by Eurofins Genomics GmbH (Germany). Two mock communities ('even' and 'staggered') were used as an internal control to evaluate HTS results. Both were constituted by a DNA mix from the same fungal taxa (7 Ascomycota and 1 Mortierellales). In the 'even' mock community DNA concentration was equal among isolates, while in the 'staggered' the DNA concentration differed by 5 folds among members. The composition and characteristics of the Mock community are reported in Table S1.

2.4. Bioinformatics analysis

Data sets were analyzed following the pipeline described by Gómez et al. (2019). To reduce the phenomenon of cross-contamination and false assignments, only the reads containing the combination of 5'barcode and forward primer as well as the expected 3'barcode and reverse primer were paired and used in the analyses. For the identification of barcode and primer sequences, no

mismatches were allowed. Raw read pairs were quality filtered (limit = 0.05) and trimmed using CLC Genomic Workbench Version 8.5.1 (QIAGEN bioinformatics, Aarhus, Denmark) filtering out all sequences containing "N"s and sequences with a minimum length of 100 nucleotides or a maximum length of 400 nucleotides. After this process, the paired-end reads were assembled. If there were mismatches between the overlapping fragments of the forward and reverse reads, these were corrected according to the base call with the higher sequencer-assigned quality score.

After quality filtering, paired-end assembly, and demultiplexing, the sequences were processed, and similarity clustering performed based on the UPARSE pipeline of USEARCH v8 (Edgar, 2010) using a 97 % clustering threshold (Lindahl et al., 2013). Sequences failing alignment or identified as chimeric were removed before downstream analysis.

Consensus OTUs were identified using the BLAST tool in the Genbank database with the algorithm parameters: word size = 11, match/mismatch scores = 2,-3, gap cost existence = 5, and gap cost extension = 2. The xml file from the BLAST and the blasted fasta file were imported into MEGAN (Huson et al., 2007) to compute and explore the taxonomic content of the data set, employing the NCBI taxonomy to summarize and order the results. The lowest common ancestor parameters were: Min score = 170; Max. expected = 0.01; Top percent = 2.0, Min support percent = 0.3; Min support = 1 and LCA percent = 40), and with the following minimum requirements of similarity to accept the proposed taxonomy: Species 99 %, Genus 97 %, Family 95 %, Order 90 %, Class 85 %, and Phylum 80 %.

Finally, an OTU abundance table was generated with USEARCH v8 (Bálint et al., 2014; Edgar, 2010). Any OTU representing less than 0.001 % of the total filtered sequences was removed to avoid the inclusion of erroneous reads, which could lead to inflated estimates of diversity (Parks et al., 2013). The Venn diagram was calculated using the online application available on http://bioinformatics.psb.ugent.be/webtools/Venn.

The reads generated in this work are available in the NCBI Sequence Read Archive (SRA) https://submit.ncbi.nlm.nih.gov/subs/sra/SUB5662116/overview under the project name PRJNA544630:*X. compactus* associated fungi.

Each OTU was classified into an ecological guild using FUNGuild (Nguyen et al., 2016). A downstream check was carried out on the output table by extending the identification to species level where applicable and choosing the appropriate guild, when more than one option was provided, with the support of the USDA Fungal Database (Farr and Rossman, 2020). OTUs ranked as 'possible' and not passing the downstream check were considered 'unclassified' in the final output.

The OTU abundance and taxonomy tables, and representative-sequences Fasta files, were transformed in qza format for use in QIIME2 2018.2, https://qiime2.org (Caporaso et al., 2010) for diversity, taxonomy, distance matrices calculation, Kruskal–Wallis (alpha diversity) and PERMANOVA (beta diversity). Faith's Phylogenetic Diversity (PD) (Faith, 1992) was used for the calculation of alpha-diversity. PD is the phylogenetic analog of taxon richness and is expressed as the number of tree units that are found in a sample. Weighted UniFrac distance was used for beta-diversity assessment. UniFrac is a distance metric used for comparing biological communities. The software incorporates information on the relative relatedness of community members by incorporating phylogenetic distances between observed organisms in the computation. Weighted UniFrac distance accounts for the abundance of observed organisms (Lozupone and Knight, 2005). Principal coordinates (PcoA) analysis of Weighted UniFrac distance matrix was performed with the software PAST version 3.24 (Hammer et al., 2001).

3. Results

From the 6-insect bulk analyzed, 1.512.473 reads were clustering with a 97 % similarity in 206 OTUs with a minimum frequency of 207.990 reads per sample and a median frequency of 253.402.5 reads. All the members of the 'even' and staggered' mock communities were identified although *Fusarium oxysporum*, *Fusarium aveacenarum*, *Verticillium dahliae,* and *Verticillium tricorpus* were resolved at the genus level. The number of reads did not correlate with the DNA concentration (Table S1). No false positives were generated from the mock communities.

Alpha rarefaction curves constructed for each of the 6 bulks showed saturation for the fungal community, suggesting that most of the biodiversity of the samples was detected (data not shown).

No significant differences in richness, calculated with the Faith-PD index (alpha diversity), were found among the 6 samples, while the September 2016 sample was significantly richer in diversity than the May 2017 sample (Kruskal–Wallis, H = 3.86; P = 0.04).

Principal Coordinates Analysis (PCoA) of weighted UniFrac distances (beta diversity) between the six fungal communities is shown in Fig. 1; clustering according to plant hosts was evident; coordinate 1 accounted for 55.4 % of the variance. However, no significant differences were found with PERMANOVA among the 6 samples and between periods.

Over the total of 206 OTUs, Ascomycota and Basidiomycota were represented by 173 (83.9 %) and 23 (11.1 %) OTUs respectively, while 10 OTU's did not cluster in any fungal phylum. Among Ascomycota, Dothideomycetes was the most represented class (67 OTUs), followed by Sordariomycetes (48); Eurotiomycetes (27), and Saccharomycetes (7) (Fig. 2). Among Basidiomycota, Tremellomycetes accounted for 18 OTUs (78,3 % of the total OTUs of the phylum) (Fig. 2).

The Venn diagram of the number of OTUs per host species combination is shown in Fig. 3.

Eighteen OTUs were shared among the insect samples from the three plant hosts. These OTUs clustered the 65,54 % (991.231 reads) of the reads with a median frequency of 155.535.5 reads per sample and identified fifteen fungal taxa. These fifteen taxa assumed as the most stable species associates with the insect adults formed the core-biome of the whole fungal community (Fig. 4). The order of Capnodiales contributed with 2 families, Capnodiaceae (6 OTUs), and Tetrasphaeriaceae (2 OTUs). OTUs 10, 32, and 99 were identified as *Cladosporium* sp., while OTU26 as *Cladosporium austrohemisphaericum*, and OTUs 31 and 56 as *Cladosporium domenicanum.* OTUs 50 and 101 were identified as *Recurvomyces* sp. and *Devriesia* sp. respectively. The order of Hypcreales was represented by 2 families, Nectriaceae (OTU1 and 132 referring to *F. solani* s.c. and *Fusarium* sp., respectively), and Bionectriaceae (OTU2, *G. pallida*). Furthermore, OTU14 referred to the Hypocreales incertae sedis *Sarocladium strictum*. The mutualist ambrosia fungus *A. xylebori* (Microascales, Ceratocystidaceae, OTU47) was also a member of the core-biome. Additional taxa were represented by *Candida germanica* (Saccharomycetales, incertae-sedis, OTU5); *Penicillium brevicompactum* (Eurotiales, Aspergillaceae, OTU7); *Aureobasidion* sp. (Dothideales, Aureobasidiaceae, OTU54); the Basidiomycota *Vishniacozyma carnescens* (Tremellales, Bullaribasidiaceae, OTU28); finally a OTU62, identified as a member of Chaetotyriales.

Sixty-nine OTUs out of 206 were resolved at species level (including species complexes) identifying 60 different fungal species (Table 1).

The functional guilds of the 60 species are summarized in Fig. 5. Saprotrophs were the most represented group (23 species, 11 of which were yeasts), followed by plant pathogens (16 species), and endophytes (9 species). Symbionts included two lichenicolous

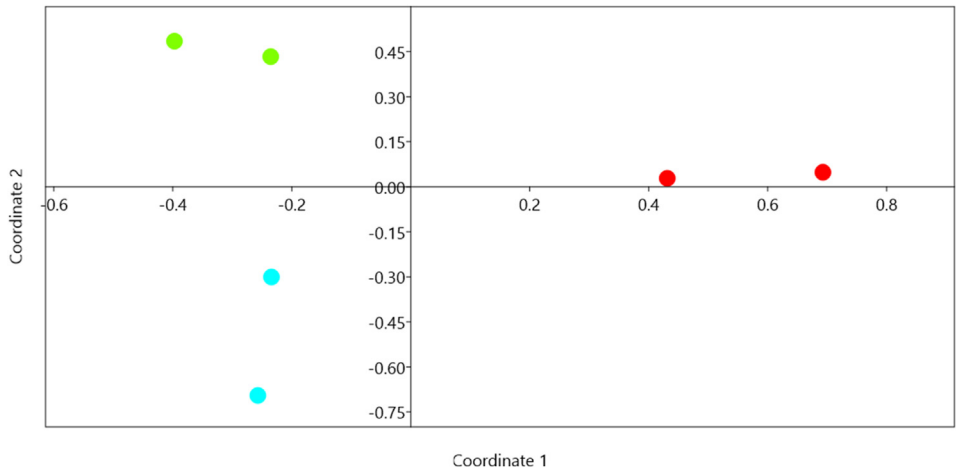

Fig. 1. Principal Coordinates Analysis (PCoA) of weighted UniFrac distances (beta diversity) between the six fungal communities detected from adults of *Xylosandrus compactus* sampled in galleries on *Quercus ilex*, *Laurus nobilis,* and *Ceratonia siliqua* in the National Park of Circeo (Latina, Italy). Different colours indicate different hosts: *Q. ilex* (light blue); *L. nobilis* (green); *C. siliqua* (red).

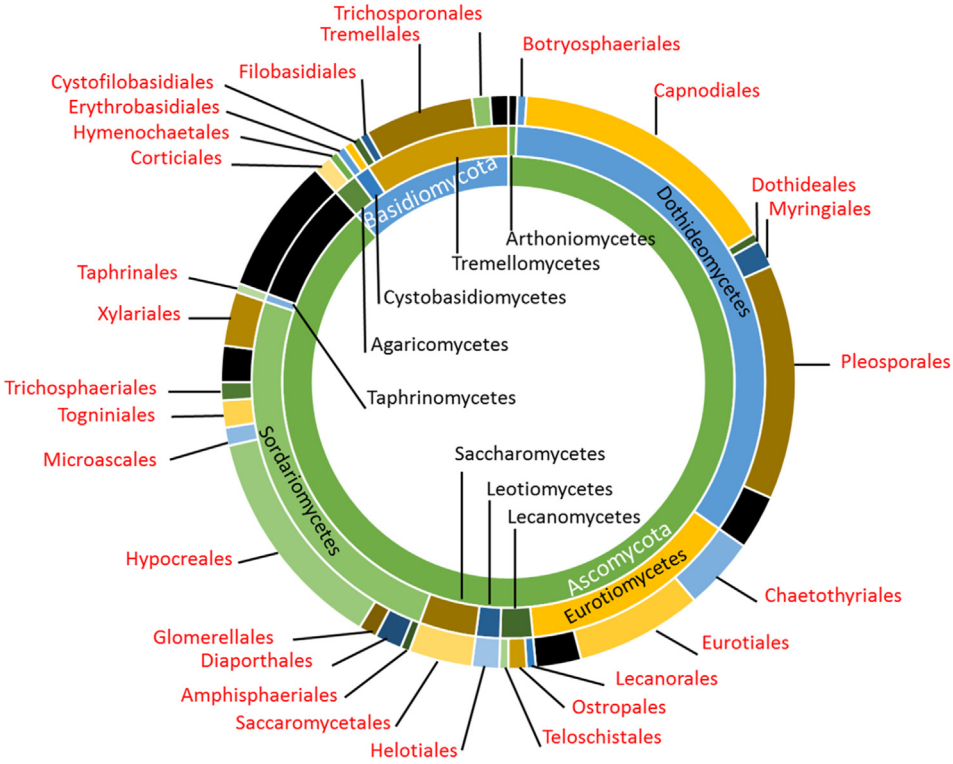

Fig. 2. Taxonomic complexity of the overall fungal community (206 OTUs) associated with *X. compactus* adults captured from galleries of three woody hosts, *Quercus ilex*, *Laurus nobilis,* and *Ceratonia siliqua* in the Circeo National Park.

fungi, and two insect's symbionts, *A. xylebori*, and *Geosmithia lavendula*. Among these species, most were distributed worldwide or present in Europe. For six species this was the first record from Europe (Table 1).

Moreover, twenty-two fungal species out of sixty were previously recorded in association with insect bodies and/or galleries. As described in Table 1 and summarized in Fig. 6, twelve of these species were already reported in the literature as associated with ambrosia beetles; nine were reported as associated with beetles other than ambrosia beetles; one species was associated with other insects.

4. Discussion

In the present study, the Illumina MiSeq mass sequencing resulted highly informative to investigate at once the fungal community associated with adults of *X. compactus*. The results of the sequencing of the 'even' and a 'staggered' mock communities confirmed the accuracy of the identification of the OTUs and

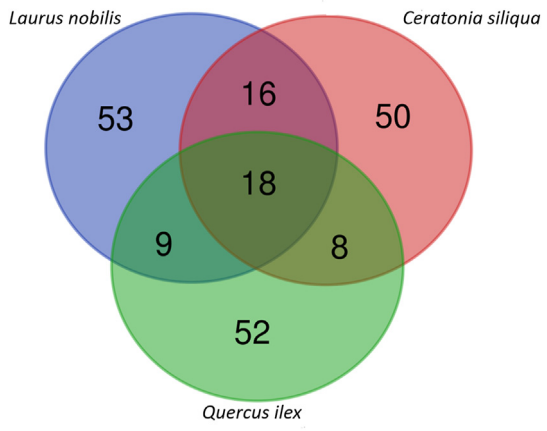

Fig. 3. Venn diagram of the number of OTUs per host species combination. Eighteen OTUs out of 206 were common between the three hosts (core-biome).

evidenced that the method is not quantitative, in the sense that the number of reads does not correlate with the abundance of the organisms in the environmental sample (i.e. the insect body). Furthermore, besides the single marker choice, the number of taxa identified at species level was over 29 %.

The fungal community associated with adults of *X. compactus* was very diverse based on the number of OTUs (206) obtained. In a similar study carried out with the invasive ambrosia beetle *X. germanus* from the northeast of Italy Rassati et al. (2019) found 121 OTUs associated with the adult of the pest. The core-biome in the present study was defined as 'a priori' as the group of OTUs detected from all the bulk samples in the 2 sample campaigns. A restricted number of fungal orders were represented in the core-biome (8 out of 28 identified overall), most of which included fungal genera or species known as associates of *X. compactus*, other ambrosia beetles, or bark beetles. Although some are classified as plant pathogens affecting bark and woody tissues, none of these taxa are the cause of serious plant diseases that can put at risk the sustainability of the habitat, except for the genus *Fusarium*.

The order Microascales was represented by *A. xylebori* that is considered a stable nutritional mutualist of *X. compactus* prevalent in mycangia (Bateman et al., 2016); it was recorded from *X. compactus* from the same area at the National Park of Circeo (Vannini et al., 2017), as well as from Florida (Bateman et al., 2016), Hawaii (Daehler and Dudley, 2002; Kuo, 2010) and Japan (Masuya, 2007). Another order of the Sordaryomycetes, the Hypocreales, was represented by genera and species all reported as associates of ambrosia beetles in the Circeo National Park or elsewhere, and with an evident ability in colonizing woody tissues. Together with *A. xylebori*, the genus *Fusarium*, including members of FSSC, is found as a stable associate of ambrosia beetles at a global scale (Bateman et al., 2016) and has been isolated from *X. compactus* at the Circeo National Park (Vannini et al., 2017), in Southern Italy (Bosso et al., 2012), from USA, and Japan (Bateman et al., 2016). The genus *Fusarium* includes serious tree pathogens causing bark and wood cankers, such as *Fusarium circinatum* on pine (Wingfield et al., 2008), and vascular wilt, such as *F. oxysporum* f. sp. *albedinis* on palms (Tantaoui et al., 1996). Moreover, members of FSSC isolated from *X. compactus* galleries and the adjacent black-stained woody tissues showed to be highly pathogenic on *Q. ilex* in Southern Italy (Bosso et al., 2012). The hypocrelean *S. strictum* was previously found associated with bark beetles (Hutchison, 1999; Jankowiak and Kolařík, 2010; Jankowiak et al., 2007), and the ambrosia beetle *Euwallacea fornicatus* in China (Li et al., 2016). This species belongs to the cohort of fungi involved in the grapevine trunk disease (Arzanlou et al., 2013). *G. pallida* was previously isolated from *X. compactus* at the National Park of Circeo (Vannini et al., 2017); this fungus is widely reported in association with several beetles in the Mediterranean region and temperate Europe (Kolařík et al. 2004, 2007, 2008). Although some *Geosmithia* spp. are considered true nutritional mutualist of ambrosia beetles (Hulcr and Stelinski, 2017), *G. pallida* appears to be more a no specific commensal. It was reported from other plant–insect interactions, such as *Castanea sativa* and the Cynipidae wasp *Dryocosmus kuriphilus*, by Morales-Rodríguez et al. (2019a) as a member of the fungal community associated with the adults of the insect. Moreover, *G. pallida* is not considered a plant pathogen in Europe, although, as cited in the introduction, is reported as the cause of Foamy Bark Canker of live oak in the USA (Lynch et al., 2014). Within the order of Capnodiales, two families, Capnodiaceae and Teratosphaeriaceae, contributed with the genera *Devriesia* and *Cladosporium* both previously reported associated, respectively, with the bark beetle *Orthotomicus*

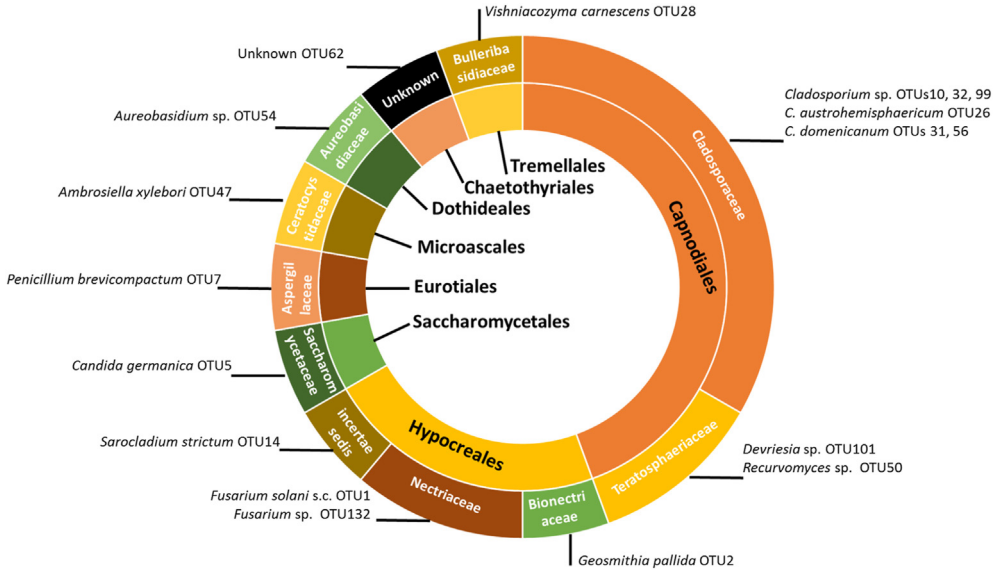

Fig. 4. Taxonomic complexity of the eighteen OTUs forming the core-biome (see Venn diagram in Fig. 3).

Table 1
Taxonomic position, life strategy, occurrence and recorded hosts/substrate for each of the sixty fungal species identified by HTS analysis. In bold, the alien fungal species recorded from native and invasion areas of *Xylosandrus compactus*.

	Fungus			Functional guild	Occurrence	Reported host/substrate	Reported plant host (this study)	Reference
OTU	Species	Phylum*	Order					
18	*Acremonium fusidioides*	A	Hypocreales	nd**	widespread including Europe	Woody and herbaceous hosts; marine environments; clinical material	*L. nobilis*	(Mułenko et al., 2008; Perdomo et al., 2011)
157	*Alternaria infectoria*	A	Pleosporales	plant pathogen	widespread in temperate regions including Europe	broad-host range; associated with the ambrosia beetle *Platypus cylindrus*	*C. siliqua*	(Belhoucine et al., 2011; Farr and Rossman, 2020)
47, 153	*Ambrosiella xylebori*	A	Microascales	Ambrosia fungus, insect symbiont	cosmopolitan	mycangial symbiont of *Xc***	Core-biome	Vannini et al. (2017)
129	*Arthrinium arundinis*	A	Xylariales	endophyte/weak plant pathogen	cosmopolitan	broad host/substrate range	*Q. ilex*	Farr and Rossman (2020)
208	*Athallia cerinella*	A	Teloschistales	lichenicolous fungus	New Zealand and Turkey	different hosts, common on *Quercus* spp.	*L. nobilis*	Vondrak et al. (2016)
191	*Botrytis cinerea*	A	Helotiales	plant pathogen	cosmopolitan	broad-host range; mutualistic with the Torticidrae *Lobesia botrana*; associated as genus with the bark beetle *Orthotomicus erosus*	*C. siliqua*	(Farr and Rossman, 2020; Malacrinò et al., 2017; Mondy and Corio-Costet, 2000)
189	*Buckleyzyma aurantiaca*	B	Incertae_sedis	yeast/saprotroph	widespread in temperate regions including Europe	different substrates	*C. siliqua*	Wang et al. (2015)
5	*Candida germanica*	A	Saccharomycetales	yeast/saprotroph	Europe; USA	different substrates; associated with ambrosia beetles	Core-biome	(Carrillo et al., 2016; Kurtzman et al., 2001)
33	*Candida quercitrusa*	A	Saccharomycetales	yeast/human pathogen	Europe, Asia	human tissues; associated with Lepidoptera gut	*C. siliqua*	(Stefanini, 2018; Xiao et al., 2014)
213	*Cladosporium aggregatocicatricatum*	A	Capnodiales	saprotroph	New Zealand, Europe, North America (USA)	On plant material, tempeh, fruits, and hypersaline water; the genus associated with ambrosia beetles (considered weed)	*C. siliqua*	(Bensch et al., 2015; Kinuura, 2002)
26	*Cladosporium austrohemisphaericum*	A	Capnodiales	saprotroph	New Zealand; Africa; China; Spain	On plant material and fruits of different hosts	Core-biome	Bensch et al. (2015)
31, 56	*Cladosporium dominicanum*	A	Capnodiales	saprotroph	Philippines (NA# of *Xc*) and Dominican Republic (AoI of *Xc*)	*Citrus* spp. and *Dracaena* spp.	Core-biome	Bensch et al. (2015)
64	*Clavispora lusitaniae*	A	Saccharomycetales	yeast/human pathogen	widespread including Europe	different substrates; associated with the bark beetle *Dendroctonus ponderosae*	*C. siliqua*	(Hadfield et al., 1987; Lee et al., 2006)
21	*Clonostachys rosea*	A	Hypocreales	antagonist	cosmopolitan	broad-host range; associated with bark beetle galleries	*L. nobilis*; *Q. ilex*	(Farr and Rossman, 2020; Kirschner, 2001)

(*continued on next page*)

Table 1 (*continued*)

	Fungus			Functional guild	Occurrence	Reported host/substrate	Reported plant host (this study)	Reference
133	*Cryptococcus amylolentus*	B	Tremellales	yeast/saprotroph	widespread including Europe	different substrates; associated with the bark beetle *Dendroctonus ponderosae*	*L. nobilis*	(Bloom et al., 2019; Lee et al., 2006)
41	*Devriesia sardiniae*	A	Capnodiales	saprotroph	Italy	rock substrates; genus associated with ambrosia beetles	*L. nobilis; C. siliqua*	(Isola et al., 2016; Malacrinò et al., 2017)
168	*Diaporthe foeniculina*	A	Diaporthales	plant pathogen	Africa, America, Europa, Oceania	Broad-host range	*C. siliqua*	Farr and Rossman (2020)
127	*Dicyma pulvinata*	A	Xylariales	antagonist	widespread including Europe	Broad-host range	*L. nobilis*	Farr and Rossman (2020)
118	*Erythrobasidium hasegawianum*	B	Erythrobasidiales	yeast/saprotroph	Nd	different substrates	*C. siliqua*	Sugiyama and Hamamoto (1998)
86	*Eutypa leptoplaca*	A	Xylariales	plant pathogen	scattered records including Europe	Woody hosts (common on *Quercus* spp.)	*Q. ilex*	Farr and Rossman (2020)
108	*Filobasidium wieringae*	B	Filobasidiales	yeast/saprotroph	Europe	Fruit and other plant material	*L. nobilis*	Glushakova and Kachalkin (2017)
4, 198, 182	*Fusarium lateritium s.c.*	A	Hypocreales	plant pathogen	cosmopolitan;	Broad-host range; associated with galleries of *X. germanus* and *X. crassiusculus* (ambrosia beetles)	*Q. ilex*; *C. siliqua*	(Farr and Rossman, 2020; Ranger et al., 2016)
1,	*Fusarium solani s.c.*	A	Hypocreales	plant pathogen	cosmopolitan;	broad-host-range; associated with ambrosia beetles	Core-biome	(Bateman et al., 2016; Farr and Rossman, 2020; Ranger et al., 2016)
24	*Fusicolla violacea*	A	Hypocreales	plant pathogen	Iran; Europe; Oceania	*Prunus* spp.; different substrates	*Q. ilex*	Farr and Rossman (2020)
63	*Geosmithia lavendula*	A	Hypocreales	putative insect symbiont	widespread including Europe	Associated with beetles on woody hosts (record on the ambrosia beetle *Cnestus mutilatus*); rare on other substrates	*C. siliqua*	(Kolařík et al., 2007; Six et al., 2009)
2, 27, 34	*Geosmithia pallida*	A	Hypocreales	plant pathogen	widespread including Europe	associated with the bark beetle *Pseudopityophthorus pubipennis* on *Quercus* spp., *Pinus* spp., *Malus* spp.	Core-biome	Farr and Rossman (2020)
70	*Hortaea thailandica*	A	Capnodiales	saprotroph	Thailand (NA of *Xc*), Spain	*Syzygium siamense*	*L. nobilis*; *C. siliqua*	(Crous et al., 2009) Ruibal
92	*Lecanora strobilina*	A	Lecanorales	lichenicolous fungus	Europe, North America	woody species	*Q. ilex*	LaGreca and Lumbsch (2013)
109	*Libertasomyces platani*	A	Pleosporales	saprotroph	New Zealand	*Platanus* sp.	*C. siliqua*	Crous et al. (2016)
152	*Lophiostoma cynaroidis*	A	Pleosporales	endophyte	widespread	Mangrove and fynbos ecosystems; hardwoods	*Q. ilex*	(Marincowitz et al., 2008; Xing et al., 2011) Floren
55	*Nakazawaea holstii*	A	Saccharomycetales	yeast/saprotroph	scattered records Canada, USA, Germany	different substrated including Scolytinae	*C. siliqua*	http://gcm.wfcc.info/speciesPage.jsp?strain_name=Nakazawaea%20holstii; (Stefanini, 2018)
96	*Neocucurbitaria cava*	A	Pleosporales	plant pathogen	widespread including Europe	woody hosts including *Q. ilex*; associated with galleries of the wood beetle *Coraebus florentinus*	*Q. ilex*	(Farr and Rossman, 2020; Pinna et al., 2019)
111	*Neodevriesia bulbillosa*	A	Capnodiales	saprotroph	widespread including Europe	different substrates	*L. nobilis*	(Crous et al., 2015; Egidi et al., 2014)
113	*Neofusicoccum luteum*	A	Botryosphaeriales	plant pathogen	widespread including Europe	broad-host range	*L. nobilis*	Farr and Rossman (2020)
130	*Nigrograna obliqua*	A	Pleosporales	saprotroph	Europe	hardwood	*C. siliqua*	Kolařík (2018)

122, 193	*Nigrospora sphaerica*	A	Trichosphaeriales	endophyte/weak pathogen	cosmopolitan	broad-host range; associated with galleries of the ambrosia beetle *Megaplatypus mutatus*	*L. nobilis*; *Q. ilex*	(Ceriani-Nakamurakare et al., 2016; Farr and Rossman, 2020)
39	*Papiliotrema terrestris*	B	Tremellales	yeast/saprotroph	nd	nd	*L. nobilis*; *C. siliqua*	Ke et al. (2018)
143	*Parastagonospora phoenicicola*	A	Pleosporales	endophyte	New Zealand; China, Taiwan (NA of *Xc*)	*Phoenix canariensis*; *Acanthus ilicifolius* (Mangrove plant)	*L. nobilis*	(Chi et al., 2019; Farr and Rossman, 2020)
23	*Penicillium adametzioides*	A	Eurotiales	saprotroph	Italy; Japan	*Vitis vinifera*	*C. siliqua*	Farr and Rossman (2020)
7	*Penicillium brevicompactum*	A	Eurotiales	plant pathogen	cosmopolitan	broad-host range	Core-biome	Farr and Rossman (2020)
11	*Penicillium brocae*	A	Eurotiales	endophyte	Mexico; Thailand (NA of *Xc*) China, India, Turkey, Brazil, USA, Colombia	*Hypothenemus hampei* coffee berry borer (ambrosia beetle) in Mexico; rice	*C. siliqua*	(Peterson et al., 2003; Shiratori et al., 2017)
43, 45	*Penicillium coffeae*	A	Eurotiales	endophyte	Hawaii (AoI of *Xc*); China (NA of *Xc*) Vietnam, Ivory Coast	*Coffea arabica* (main host of *Xc*); *Laguncularia racemosa* (Mangrove plant)	*L. nobilis*; *C. siliqua*	(Cao et al., 2019; Peterson et al., 2005)
66	*Penicillium fluviserpens*	A	Eurotiales	endophyte	Colombia; USA	*Coffea arabica* (main host of *Xc*)	*L. nobilis*	(Nguyen et al., 2020; Peterson et al., 2015)
53	*Penicillium phoenicum*	A	Eurotiales	saprotroph	Europe	different substrates	*C. siliqua*	(Refai and El-Yazid,)
9	*Penicillium spathulatum*	A	Eurotiales	saprotroph	Europe	different substrates	*Q. ilex*; *C. siliqua*	Frisvad et al. (2013)
51	*Pestalotiopsis biciliata*	A	Xylariales	plant pathogen	Europe	*Eucalyptus* spp. and other hardwoods	*L. nobilis*; *C. siliqua*	Morales-Rodríguez et al. (2019b)
77	*Phaeoacremonium fraxinopennsylvanicum*	A	Togniniales	endophyte/weak pathogen	widespread including Europe	hardwoods including *Quercus* spp.; associated with larval galleries	*Q. ilex*	Farr and Rossman (2020)
35	*Phaeoacremonium prunicola*	A	Togniniales	endophyte/weak pathogen	South Africa (AoI of *Xc*)	hardwoods	*C. siliqua*	Spies et al. (2018)
48	*Ramularia eucalypti*	A	Capnodiales	plant pathogen	Europe, Australia	*Eucalyptus* spp.; other woody and herbaceous hosts; associated with the gut of rove beetles	*L. nobilis*; *C. siliqua*	(Farr and Rossman, 2020; Stefani et al., 2016)
110	*Ramularia hydrangea-macrophyllae*	A	Capnodiales	plant pathogen	Iran, New Zealand; intercepted in Italy	*Vitis vinifera*, *Hydrangea macrophylla;* associated with the ambrosia beetle *Xyleborinus saxesenii*	*L. nobilis*	(Bakhshi, 2018; Braun and Hill, 2008; Malacrinò et al., 2017)
14	*Sarocladium strictum*	A	Hypocreales	plant pathogen	cosmopolitan	broad-host range; associated with the ambrosia beetle *Euwallacea fornicatus*	Core-biome	(Farr and Rossman, 2020; Li et al., 2016)
194	*Taphrina sadebeckii*	A	Taphrinales	plant pathogen	Europe; Canada	Alnus spp.	*C. siliqua*	Farr and Rossman (2020)
180	*Tausonia pullulans*	B	Cystofilobasidiales	yeast/saprotroph	USA, Europe, Antarctica	different substrates	*C. siliqua*	http://www.mycobank.org/MB/812190
106	*Trimmatostroma cordae*	A	Capnodiales	nd	Europe, India	Nd	*L. nobilis*	http://www.mycobank.org/BioloMICS.aspx?TableKey=14682616000000067&Rec=423987
126	*Vermiconia calcicola*	A	Capnodiales	saprotroph	Italy	rock inhabitant fungus	*L. nobilis*	Isola et al. (2016)
28	*Vishniacozyma carnescens*	B	Tremellales	yeast/saprotroph	New Zealand; Antartica	water; plant material	Core-biome	http://www.mycobank.org/MB/813274
49, 131	*Vishniacozyma heimaeyensis*	B	Tremellales	yeast/saprotroph	Europe	different substrates	*L. nobilis, C. siliqua*	http://www.mycobank.org/MB/813278
38	*Vishniacozyma victoriae*	B	Tremellales	yeast/saprotroph	Europe; South America	broad-host-range	*L. nobilis*	Gramisci et al. (2018)
22	*Vuilleminia comedens*	B	Corticiales	wood decaying	Europe; Asia	*Quercus* spp. and other hardwoods	*Q. ilex*	Farr and Rossman (2020)
8	*Xenoacremonium falcatus*	A	Hypocreales	nd	Europe, Asia	*Castanea sativa*; other substrates	*Q. ilex; C. siliqua*	Aghayeva et al. (2017)

* A = Ascomycota; B= Basidiomycota ** nd = not determined *** *Xc* = *Xylosandrus compactus* ¥ AoI = Area of Introduction # NA= Native Area according to CABI.

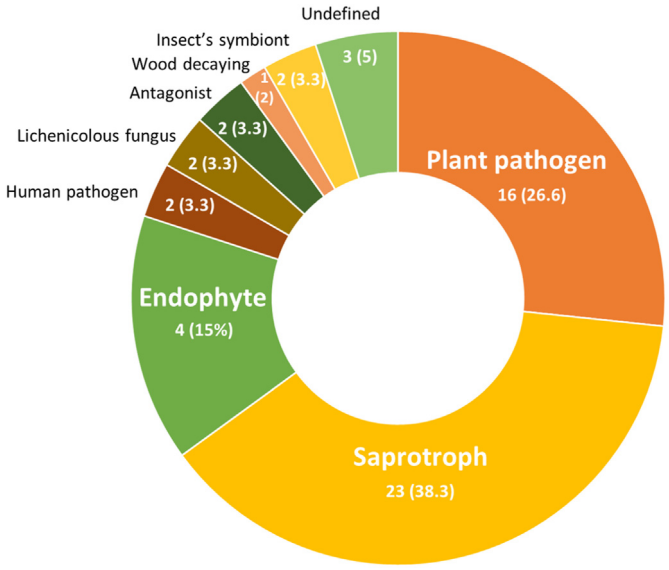

Fig. 5. Assignment of the functional guilds to the 60 fungal taxa resolved at species level, following downstream checks. Numbers refer to the number of taxa and percentage (in brackets).

erosus and the ambrosia beetle *Xyleborinus saxesenii* that were intercepted at Italian harbors by Malacrinò et al. (2017). *Cladosporium* sp. was also isolated from *X. compactus* in Florida (Bateman et al., 2016). The two species *C. austrohemisphaericum* and *C. dominicanum* were not reported as associates of ambrosia beetles before; furthermore, this study represents the first record from Europe of *C. dominicanum* whose presence was recorded from limited geographic range, native or introduction areas of *X. compactus* (Table 1). Within the order Eurotiales, the species

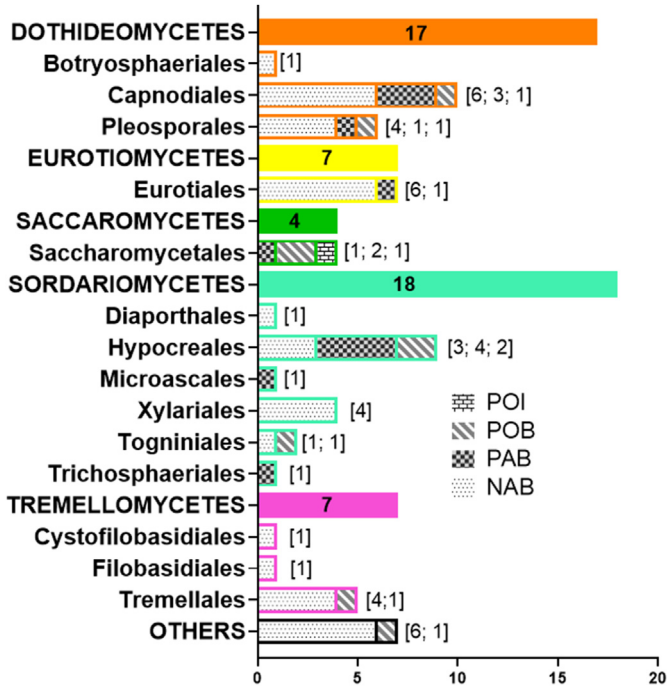

Fig. 6. The number of fungal species grouped per family and representing a new record for ambrosia beetle (NAB); previously recorded on ambrosia beetle (PAB); previously recorded on other beetles (POB); previously recorded on other insects (POI). Number in brackets = absolute frequency.

P. brevicompactum was identified. *Penicillium* spp. were frequently found in association with ambrosia beetles although they are considered 'weed' fungi, occurring in old galleries or used as a supplementary food source for the insect (Beaver et al., 1989; Ranger et al., 2018). The order Saccharomycetales contributed with the species *C. germanica*. This yeast was previously associated with ambrosia beetles by Carrillo et al. (2016). Many species of the genus *Candida* are considered ambrosia yeasts (Endoh et al., 2008; Suh and Zhou, 2010). The genus *Aureobasidium* was the only one representing the Dothideales in the core-biome. Again, these yeast-like fungi were reported as associates of ambrosia beetle such as *X. saxesenii* (Malacrinò et al., 2017; Rassati et al., 2019). About the Basidiomycota yeast *V. carnescens*, this is a common inhabitant of wood of different hosts (Behnke-Borowczyk et al., 2018; Cadete et al., 2017) and this is the first record as an associate of an ambrosia beetle.

Additional OTUs not included in the core-biome were previously recorded as associated with ambrosia beetles, other beetles, or insects as species or genus. *Phaeoacremonium prunicola* is a plant pathogen cause of dieback of several woody species in South Africa (Spies et al., 2018), an area of introduction of *X. compactus* (Wood, 1992). There are no records of *Pm. prunicola* interacting with ambrosia beetles; however, many species of *Phaeoacremonium* are reported as associated with beetle galleries, larvae, or adults (Belhoucine et al., 2011; Mohammadi and Sharifi, 2016). Another *Phaeoacremonium* species was identified, *Pm. fraxinopennsylvanicum*, frequently recorded from Europe also associated with larval galleries (Farr and Rossman, 2020). *Ramularia hydrangea-macrophyllae* is a leaf pathogen recorded from Iran and New Zealand that was intercepted in Italy on *X. saxesenii* from traps at international harbours (Malacrinò et al., 2017). An additional *Ramularia* species, *Ramularia eucalypti*, was detected as an associate of *X. compactus* in this study. *R. eucalypti* is a pathogen of *Eucalyptus* spp. foliage in different geographic areas including Europe (Farr and Rossman, 2020; Stefani et al., 2016). This finding is of interest if related to the identification of another pathogen of *Eucalyptus* spp., *Pestalotiopsis biciliata*. Although this species has not previously associated with insects, the genus *Pestalotiopsis* is reported in the literature as an associate of ambrosia beetles (Berger, 2017; McPherson et al., 2010, 2013; Rajput and Rao, 2007; Suh et al., 2011; Tuncer and Kushiyev, 2017) including *X. compactus* (Bateman et al., 2016). Moreover, *Ps. biciliata* was recently recorded from the Circeo National Park as the causal agent of leaf spots on *E. camaldulensis*, *E. globulus*, and *E. botryoides* (Morales-Rodríguez et al., 2019b). The genus *Eucalyptus* is included in the host-range of *X. compactus* (Hara and Beardsley, 1979), thus colonization by *X. compactus* cannot be ruled out, even when considering of the extensive presence of *Eucalyptus* spp. in the area of the National Park (Morales-Rodríguez et al., 2019b). The detection of yeast species within the fungal community confirms the association with ambrosia beetles reported in the literature. Hulcr and Stelinski (2017) indicated that although interaction of Saccharomycetales with galleries and mycangia of ambrosia beetles, only the genus *Ambrosiozyma* can be considered a true ambrosia yeast, while other clades such as *Candida* and *Pichia*, and considered non-specific commensals. Three yeast species not included in the core-biome, the Saccharomycetales *Clavispora lusitaniae,* and *Ca . quercitrusa*, and the Basidiomycota *Cryptococcus amylolentus*, were previously reported as associates with insects. *Cryptococcus* sp. was found associated with *X. compactus* in Florida (Bateman et al., 2016). *C. lusitaniae* and *Cs. amylolentus* were detected in association with the bark beetle *Dendroctonus ponderosae* in Canada (Lee et al., 2006), while *Ca. quercitrusa* was found in the gut of Lepidoptera (Stefanini, 2018).

Fungal taxa not included in the core-biome contributed to differences between fungal communities associated with insects from different plant hosts. Although the discrete number of bulk samples processed in the present study, the clustering of fungal communities with the insect host plants supports the hypothesis of the environmental acquisition of fungal taxa during insect invasion (Rassati et al., 2019). According to these authors, the forest type (plant hosts in the present study) has a relevant effect on fungal community composition and assemblage during insect invasion favoring new acquisitions and the rearrangement of the fungal community. In contrast, Kostovcik et al. (2014), following an analysis of mycangial fungal communities associated with three ambrosia beetles in Florida, concluded that fungal assemblages were statistically correlated with the insect species but not with the locality. However, Kostovcik et al. (2014) analyzed the fungal community within the mycangia where the true nutritional mutualists and stable commensals are supposed to be carried. In the present work and the study of Rassati et al. (2019) the fungal community from the whole insect body was analyzed, which includes both mycangial and nomycangial associates among which nutritional mutualists, commensal fungi or no-specific 'hitchhiker' sensu Six (2020), and occasional contaminants.

Based on the above considerations, the fungal community associated with *X. compactus* is biodiverse and functionally heterogeneous and includes true nutritional mutualists as the results of coevolution with the insect (i.e. *A. xilebori*), stable commensal fungi, and occasional contaminants. Persistence of the association can be determined by different factors including the ecology of the single fungal taxa. Literature records associated most of the taxa included in the core-biome with different species of beetles. It can be speculated that the ecological adaptation of these fungal taxa on a wide range of hosts and substrates, including bark and wood for some taxa such as *Fusarium*, *Geosmithia*, *Sarocladium*, might facilitate the interaction with the beetles and the opportunistic colonization of their galleries as commensals. Such behavior was claimed by Bateman et al. (2016) for the FSSC members associated to *X. compactus*, that were demonstrated to be present consistently on the surface and abdomen of the insect, but in a limited amount in mycangia. Thus, those taxa more adapted to the environment they interact with, in terms of host range and competitiveness for space and nutrients, have the chance to be consistently represented over several generations of the insect. However, during the progress on invasion and the interaction with new hosts/habitats, additional species can meet the insect and, depending on their saprotrophic/pathogenic lifestyle, be differently represented in the mycoflora of the galleries. Summarizing, it can be assumed that during the progress of invasion less adapted species will decrease in abundance over the generations and disappear with time, while some well-adapted fungal species will become more stable associates. For instance, within the large FSSC, some members have coevolved with specific ambrosia beetles as nutritional mutualists (the Ambrosia Fusarium Clade (AFC)) (Kasson et al., 2013); other nomycangial FSSC behave as commensal. Moreover, it can be speculated that the interaction of *X. compactus* with some pathogenic fungi might result in mutualistic advantages and more stable associations. *X. compactus* is considered a primary parasite affecting living branches of healthy hosts (Daehler and Dudley, 2002); pathogenic fungi carried by the insect take advantage of being vectored into the host bark/woody tissues where infection takes place. As demonstrated for FSSC members (Bosso et al., 2012; Vannini et al., 2017) some of these pathogens are the cause of extensive necrosis of the distal part of the branches above the galleries, facilitating the insect boring activity.

Whether the fungal community associated with *X. compactus* represents a potential risk for the environment during the progress of the invasion of the insect is a major point of speculation. The most relevant example of an epidemic outbreak caused by the combined activity of the vector and associated fungus is represented by the Laurel wilt. Responsible of this syndrome are the ambrosia beetle *Xyleborus glabratus* and its mycangial symbiont *Raffaelea lauricola* whose combined action caused the death of hundreds of millions of redbay trees (*Persea borbonia* sensu lato) throughout the south-eastern USA (Harrington et al., 2008). The fungus, originated in Asia, was introduced in the USA together with the insect (Harrington et al., 2011). Additional evidence is represented by the Japanese Oak Wilt caused by the mycangial fungus *Raffaelea quercivora* and the ambrosia beetle *Platypus quercivorus* in Japan (Kusumoto et al., 2012). An example of damage to host trees caused by nomycangial fungi associated with ambrosia beetles refers to *X. compactus* and FSSC members on *Q. ilex* (Bosso et al., 2012). Thus, the risk that fungal taxa introduced in new environments/hosts through the progress of the invasion of *X. compactus*, succeed in causing novel diseases outbreak cannot be ruled out. As suggested by Hulcr and Dunn (2011) the virulence of symbiosis in an invaded range is the result of the combination of several factors determined by the lack of coevolution with hosts, including the overcome of the host defenses but also possible 'olfactory mismatches' in the insect. This could match with *X. compactus* invasion process in the Mediterranean maquis where the insect displays a wide host range and the associated fungal community is highly biodiverse, possibly including both alien and native species. Indeed, the present study represents the first record from Europe of six out of sixty (10 %) fungal species. Most of these species have been previously recorded from the native or introduction range of *X. compactus* or from main hosts of *X. compactus*. One species, *Pm. prunicola* is a plant pathogen with affinities, as genus, with beetles adults and larvae (Belhoucine et al., 2011; Mohammadi and Sharifi, 2016).

The indirect effect of the ambrosia beetle–fungi complex on existing interactions in the invaded environment must also be considered. Indeed, the introduction and establishment of an alien species in a new environment result in additional ecosystems changes due to indirect effects on ecosystem functioning. Indirect interactions occur when one species influences a second via its interactions with a third species (Waser et al., 2015). McPherson et al. (2010) demonstrated that the attack by ambrosia beetles (i.e. the introduced *Xyleborinus saxeseni* and *Cyclorhipidion bodoanum*) and the associated pathogenic fungi, of *Phytophthora ramorum* infected coastal live oak trees shortened the survival of the trees by 65 %, as well as facilitated new ecological associations between fungi, beetles, and a native host tree species. The host range of *X. compactus* in the Mediterranean maquis includes trees such as *Q. ilex*, heavily challenged by the root rot oomycete *Phytophthora cinnamomi* (Scanu et al., 2013). An exacerbation of the effect of *P. cinnamomi* root rot on trees attacked by *X. compactus* and associated fungi cannot be ruled out and deserves further investigation.

5. Conclusions

The results of the present study deserve to be in somehow contextualized. Firstly, here the fungal community is described associated to the body of mature adults of *X. compactus* before flying from the galleries, including true mycangial and extramycangial symbionts, occasional commensals, 'weed fungi' and simply contaminants. Thus, this study did not aim to demonstrate symbiosis but to highlight the potential risk determined by the association of a *X. compactus* generation with a biodiverse fungal community. In fact, these results should be discussed in a context of biological invasion where an exotic organism (i.e. fungal pathogen)

can be introduced and spread in a new environment as a symbiont or as simple occasional contaminant. In such context it is not relevant the performance or the risk posed by a single insect individual, but the risk posed by a new generation challenging the hosts in a new environment. Furthermore, no statements can be done for any of these fungi to be efficiently vectored by *X. compactus*, unless for those reported in literature as nutritional mycangial symbionts or strict extra-mycangial such as *A. xilebori* and *Fusarium* spp. respectively. However, many of the *X. compactus* fungal associates in the present study are reported in current and past literature as commonly interacting with Ambrosia beetles or other beetles. In conclusion, the accurate monitoring of the fungal community associated with *X. compactus* generations along their introduction and invasion pathways is of relevance to 'early detect' potentially threatful new associations that can determine direct or indirect deleterious effects in the invaded environments.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funbio.2020.09.008.

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