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1 **Climate-induced long-term changes in the phenology of Mediterranean fungi**

2 **Running head:** Mediterranean fungi phenology

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26

27 **Abstract**

28 Long-term responses in the phenology of Mediterranean macrofungi to climatic changes are
29 poorly documented. Here, we address this issue by comparing the fruiting patterns of 159
30 fungal species in Southern France between the first half of the 19th century and the first
31 decade of the 21st century. We used a trait-based approach to assess the influence of
32 phenology and morphology of fungal fruit bodies and their site ecology and biogeography on
33 the response to climate change. We show that early autumnal fruiterers, epigeous species and
34 species with affinities for cold climates now start to fruit on average 16.4, 17.3 and 17.3 d
35 later compared to their emergence dates in the 19th century, while late fruiterers, hypogeous
36 species and Mediterranean-restricted species did not change their fruiting date. Among
37 ecological guilds, saproxylic species and pine-associated mutualists delayed their autumnal
38 emergence by 32.5 and 19.2 d, likely in response to a delayed rewetting of litter and woody
39 debris after extended summer drought. Our results suggest that long-term climate warming
40 in the Mediterranean was accompanied by contrasting changes in the emergence of fungal
41 fruit bodies according to ecological guilds, sporocarp life-forms and forest types.

42 **Index descriptors:** Climate change, ectomycorrhizal fungi, herbarium, Mediterranean
43 ecosystems, mushrooms, phenology, saprotrophic fungi, traits-based analysis.

44

45

46 **1 INTRODUCTION**

47 Documenting long-term changes in biodiversity patterns is an essential and timely issue
48 in ecology, and a particularly challenging research objective from a methodological
49 perspective (Heilmann-Clausen & Læssøe 2012). Regardless of this, the ecological plasticity
50 of ecosystems and species in response to long-term environmental changes have been
51 explored, mainly for plants (*e.g.* Chuine *et al.* 2000; Primack *et al.* 2004, see Cleland *et al.*
52 2007 and Schatz *et al.* 2016 for a review) and animals (Spark & Carey 1995; Delpon *et al.*
53 2018). In comparison, because long-term fungal datasets are particularly scarce, fungal
54 records and herbaria have only been used to document the global warming during the 20th
55 century, and mostly since 1950 (see Boddy *et al.* 2014 for a review). So far, these organisms
56 have never been used to measure the consequences of the environmental changes since the
57 19th century's temperature depression, at the end of the Little Ice Age (Pages 2013).

58 Because many macrofungi produce ephemeral reproductive structures of short
59 endurance called fruit bodies (Straatsma *et al.* 2001), in response to rainfall events,
60 sporocarps are valuable markers of the weather conditions at the collection time. This is the
61 reason why fungal herbaria and written records have been widely used in diachronic
62 approaches to document the consequences of ongoing climate change on fungal diversity
63 (*e.g.* Boddy *et al.* 2014), mostly in Europe (*e.g.* Kauserud *et al.* 2008; Büntgen *et al.* 2012a;
64 Andrew *et al.* 2018) and North America (Diez *et al.* 2013). These studies consensually
65 showed significantly delayed fruiting patterns of fungi during the 20th century in both
66 nemoral and boreal regions. However, fungi have never been used to place species-specific

67 responses to global climate change in a multi-centennial, long-term perspective, in the
68 Mediterranean region.

69 The astonishing taxonomic diversity within the fungal kingdom encompasses a wide
70 range of feeding modes, regarding the origin of the carbon they mobilize (mycorrhizal vs.
71 saprotrophic vs. parasitic, Bardgett and Wardle 2010) and within each feeding mode
72 regarding the range of substrates (*e.g.* leaves, wood, twigs, cones for decayers) and/or hosts
73 (from highly specific to wide host range for mutualists and parasites, Bruns *et al.* 2002;
74 Taudiere *et al.* 2015). Previous studies showed that in Northern Europe and North America,
75 the amplitude of fungal fruiting delay in response to climate change was related to different
76 ecological traits as the feeding mode (saprotrophic vs. mycorrhizal species, Kauserud *et al.*
77 2012), for mycorrhizal fungi, the taxonomic range of hosts (*e.g.* angio- vs. gymnosperm,
78 Gange *et al.* 2007; evergreen vs. deciduous trees, Diez *et al.* 2013) and spore dimensions
79 (Kauserud *et al.* 2011; Andrew *et al.* 2016). However, a global approach, combining
80 morphological and ecological life history traits of sporocarps, is still lacking.

81 In Mediterranean ecosystems, dry and hot summers delineate spring and fall rainfall
82 events that widely vary in intensity depending on years (Bolle 2012). In the Mediterranean
83 basin, the combination of a marked seasonality, long term fluctuations, and a diversified
84 geological mosaic, favored a concentration of biodiversity (Myers 2000), including an
85 exceptional accumulation of endemic plants (Medail *et al.* 2019) and the emergence of
86 locally adapted fungal diversity (*e.g.* Norstedt *et al.* 2001; Loizides *et al.* 2016, 2019). In this
87 part of the world, summer drought is expected to increase in amplitude and duration during
88 the current century (IPCC 2007, Giorgi & Lionello 2008), with consequences for the endemic
89 plant and fungal lineages that emerged in one of the three hottest hotspots for conservation

90 stakes (*e.g.* Loizides *et al.* 2019 for conservation stakes associated with endemic oaks and
91 their highly specific ectomycorrhizal species). In this region, the ongoing climate warming
92 increases the severity and length (Ruffault *et al.* 2013) of summer drought, with
93 consequences for fruiting phenology and productivity (Büntgen *et al.* 2015; Alday *et al.* 2017;
94 Karavani *et al.* 2018). However, previous research investigated the effect of climate change
95 on fruiting phenology in this ecoregion from a decennial perspective (Buentgen *et al.* 2015),
96 and research devoted to secular phenological responses associated with the diversity of
97 fruitbody morphologies, in a biological, ecological and evolutionary perspective is still lacking.

98 At the local scale, Mediterranean macrofungal communities bring together species
99 with contrasted biogeography, from typical Mediterranean to widely distributed species (*e.g.*
100 Norstedt *et al.* 2001; Richard *et al.* 2004). In these communities as in temperate (Smith *et al.*
101 2002; Moore *et al.* 2008) and boreal (Timling *et al.* 2014) ones, a wide range of fungal life-
102 forms co-occur, based on their morpho-anatomical (gastroid vs. agaricoid species), biological
103 (*e.g.* location relative to soil surface, epi- vs. hypogeous) and phenological (early- vs. late-
104 fruiterers) traits. In the Mediterranean, this diversity of life-forms evolved in response to
105 environmental conditions, with dry, warm environments governing the evolution of fruit
106 body morphology (Bruns *et al.* 1989). In particular, a hypogeous life-form (truffle-like fruit
107 bodies) is supposed to be an adaptation to heat and drought (Diez *et al.* 2002; Bui *et al.* 2020;
108 refer to Chevassut 1988 for a reference in the study area), and gastroid life-form (*e.g.*
109 puffballs, stinkhorns, in which enclosed spores are protected against desiccation) may have
110 recently diverged in many lineages as an adaptation to aridity (Bruns *et al.* 1989; Wilson *et*
111 *al.* 2011) and Mediterranean climate conditions (Justo *et al.* 2010). So far, the response of
112 the variety of fungal life-forms to the ongoing climate change has not been documented.
113 More generally, a comprehensive trait-based approach has not been applied to fungal long-

114 term diachronic data to measure the response of fungal life-forms to the ongoing climate
115 change in the Mediterranean area.

116 Diachronic comparison of fruiting patterns of fungi is methodologically challenging
117 and requires high-quality sampling procedures (Heilmann-Clausen & Læssøe 2012). Thus,
118 erratic fruiting of species (Richard *et al.* 2004; Baptista *et al.* 2010; Alday *et al.* 2017), cryptic
119 nature of fruit bodies with respect to their size (from flashy macromycetes to micromycetes
120 virtually invisible to the naked eye; Halme & Kotiaho 2012) or location (*i.e.* position of the
121 structures regarding soil surface), highly variable among-species lifespan of fruit bodies
122 (from perennial to ephemeral) and contrasted field identifiability (Löhmus 2009) induce high
123 variation of detectability among species. In field surveys, different detectability rates of
124 species can provide important variation in the number of records (Löhmus 2009), and
125 subsequent biases for evaluating species response in comparative approaches. In addition,
126 assessing long-term changes increases the risk of comparing highly contrasted corpus of
127 taxonomic knowledge between investigated periods, with consequences on the quality of
128 field records for poorly described species. The methodological dimension and the
129 consequences of between-species variability of detectability have been widely investigated
130 for plants (McCarthy *et al.* 2013; *e.g.* Vogt-Schilb *et al.* 2016; Schatz *et al.* 2016).
131 Contrastingly, the detectability of fungal fruit bodies remains scarcely explored (but see
132 Halme & Kotiaho 2012 for wood-inhabiting fungi), despite its importance to limit the risk of
133 under-detection of species, and to improve the quality of monitoring datasets (*e.g.* Löhmus
134 2009; Vogt-Schilb *et al.* 2016).

135 Here we used two high-resolution herbarium datasets assembled in the French
136 Mediterranean region in 1821–1852 and 2001–2011. We fully characterized 159 fungal

137 species (75 ectomycorrhizal and 84 saprotrophic) by providing information about their
138 ecology, biogeography, morphology, detectability in the field and status in the 19th century
139 regarding their presence in the taxonomic corpus (*i.e.* described in 19th century taxonomic
140 literature of the 19th century vs. not included in the available corpus). We used this matrix of
141 ecological traits to question the temporal patterns of fungal species fruiting in the French
142 Mediterranean region 170 y apart. We first hypothesized that an increased duration of
143 summer drought in the region (*i.e.* a significantly postponed restart of autumn rainfall;
144 Ruffault *et al.* 2013) preferentially delayed fruit body emergence of early- as compared late-
145 fruiting species. We secondly inferred that an increased severity of summer drought (*i.e.* an
146 increased occurrence of severe hydric stresses; Ruffault *et al.* 2013) primarily impacted
147 fungal species poorly-adapted to drought, including epigeous rather than hypogeous species,
148 agaricoid more than gastroid morphology, species with small spore sizes rather than larger
149 ones, large fruitbodies rather than small ones and wide-geographical distribution more than
150 Mediterranean-restricted species (Table S1). As previously observed in temperate Europe
151 (Kausrud *et al.* 2012; Boddy *et al.* 2014), we inferred that climate change in the
152 Mediterranean differentially impacted saprotrophic and ectomycorrhizal species, among
153 mycorrhizal species, pine- and than oak associates and among saprotrophs, litter- and wood
154 decayers. We finally assumed that differences in the detectability of species induced field
155 biases which impacted the intensity of the recorded phenological shifts of species (Löhmus
156 2009; Heilmann-Clausen & Læssøe 2012). We then specifically compared the fruiting delays
157 of species with resistant sporocarps as compared to those producing ephemeral fruit bodies,
158 less visible species (inconspicuous species) as compared to more visible species (conspicuous
159 species), and poorly known species in the 19th century, as compared to well-known species
160 in de Candolle's published corpus.

161 2. MATERIALS AND METHODS

162 *Study area and sampling sites*

163 The study was performed in the French Mediterranean region (continental France), in
164 an area centered in Montpellier, and extending from Béziers to Alès and from the
165 Mediterranean Sea coast to the Cévennes region (43°14'N–44°03'N, 2°36'E–4°28'E; Figure
166 1A). The present climate in Montpellier area is of Mediterranean type with a high seasonal
167 variability, including mean monthly precipitation ranging from 16.4 mm (in July) to 96.8 mm
168 (in October), and mean temperatures ranging from 7.2 °C (in January) to 24.1°C (in July)
169 (Météo France). Study sites correspond to a set of private parks and public forest stands of
170 at least one hectare in area each (Vogt-Schilb *et al.* 2018). Historical archives (Land registers)
171 and maps (Etat Major, available at <https://www.geoportail.gouv.fr/>) were used to locate 19th
172 century's sites.

173 In all, mycological data were collected at 285 sites, including 103 sites sampled over a
174 32-year period in the 19th century and 182 sites sampled over a 12-year period in the early
175 21st century; Figure 1, Table S2). During both sampling periods, referent mycologists
176 organized field surveys every week throughout the year. At each sampling date, 1.53 and
177 1.15 sites were visited in average, in the 19th and in the 21st century sampling periods,
178 respectively. For 71.9 and 88.4% of the sampling dates, only one site was visited in the 19th
179 and in the 21st century sampling periods, respectively. Among the 103 sites sampled during
180 the the 19th century sampling period, eight of them were discarded because they could not
181 be located with certainty. Additionally, we excluded 79 sites (40 and 39 in the 19th and in the
182 21st century sampling periods, respectively) because they were localized outside of the
183 Mediterranean climatic domain (here delineated by the distribution of *Quercus ilex*; Quézel

184 & Médail 2017). Their inclusion into the dataset would have then generated ecological
185 heterogeneity within the dataset (see Figure S1 for a schematic view of the data filtering).

186 *Analysis of 19th century herbarium*

187 In the early 19th century, de Candolle exported Persoon's unified fungal
188 nomenclature to Montpellier, where he discovered and published 67 new fungal species (de
189 Candolle 1815). As director of the Botanical Institute in Montpellier from 1808 to his
190 departure to Geneva in 1816, he initiated several talented mycologists, who successively
191 contributed to the analyzed dataset (Moreau et al. 2011). Then, the 19th century herbaria
192 consisted of 1590 fungal records assembled from 1821 to 1852, and nowadays conserved at
193 the MPU Herbarium (Service du patrimoine historique, Université de Montpellier). Each
194 analyzed bundle included watercolor paintings (*Icones Fungorum*; Node-Véran 1820-1843;
195 Figure 1B), their associated descriptive notes and dried specimens (Figure 1C) and were
196 successively assembled by Delile (A.R. Delile, *Icones Fungorum*, unpublished volume, MPU
197 Herbarium), and Dunal (M.-F. Dunal, *Flore de Montpellier*, unpublished volume, MPU
198 Herbarium) during the periods 1821-1857 and 1821- 1845, respectively (Moreau *et al.* 2011).

199 Some of the dominant taxonomic groups currently considered in mycological surveys
200 were poorly considered by the mycologists of the 19th century, including many hypogeous
201 fungi, all genera of boletes, and species producing inconspicuous fruitbodies within the
202 Corticiaceae family (*e.g. Tomentella, Sebacina*). In our analysis, we included only the records
203 that were accurately located (*i.e.* ascribed to a given collecting site) and dated (*i.e.* ascribed
204 to a given collecting date) by collectors. All included collections were morphologically
205 analyzed and microscopically checked when necessary (*e.g.* in Figure 1C, without
206 microscopic analysis - spore shape, presence of clamps- it would have been impossible to

207 name this specimen - finally identified as *Amanita echinocephala*) prior to a taxonomic
208 assignation according to the current nomenclature (MycoBank database;
209 <http://www.mycobank.org/>).

210 *Analysis of 21st century herbaria records*

211 The 21st century herbaria records consisted of weekly collected information at 182
212 sampling sites which were located around Montpellier (Figure 1) and surveyed as part of a
213 systematic mycological survey coordinated by J.-C. Malaval and the Société d'Horticulture et
214 d'Histoire Naturelle de l'Hérault (SHHNH) from 2001 to 2011. These reports include recorded
215 fungal species, their precise sampling location (GPS coordinates), their collecting date, and
216 additional notes (*e.g.* fruit body abundance, ecology within the collecting site), pictures
217 (samples and microscopy) and materials (herbarium samples) when necessary.

218 *Trait assignation of fungal species*

219 In total, 159 fungal species fruited in the selected sites during both 19th and 21st
220 century century sampling periods. Species were assigned as either ectomycorrhizal (75
221 species) or saprotrophic (84 species), using the available literature dealing with fungal
222 communities of *Quercus ilex* (*e.g.* Richard *et al.* 2004, 2005; Taudiere *et al.* 2015). For all
223 these species, we documented eight categories of life-history traits, *i.e.* fruiting seasonality,
224 life-form and habit, fruit body and spore dimensions, feeding modes, geographical range,
225 detectability and identifiability of fruitbodies, in order to relate the variations in fruiting
226 patterns of fungal species to taxonomic, biological and ecological features (Figure S1).

227 Based on the literature (*e.g.* Chevassut 1988, Richard *et al.* 2004) and two field guides
228 (Courtecuisse & Duhem 2007; Roux & Eyssartier 2011), each species was assigned as either

229 an early-fruiter (summer-early autumn fruiting, 73 species), or a late-fruiter (late autumn-
230 winter fruiting, 17 species), or a species with no marked seasonal pattern of fruiting (69
231 species, Table S3, “fruiting seasonality”). Each species was assigned to a preferential
232 phenological fruiting type as follows: early fruiters include all species with fruiting
233 preferentially occurring in summer and early autumn, while late fruiters include all species
234 with fruiting preferentially occurring in late autumn and winter (Table S3).

235 Regarding the life forms and habits, species were assigned to either above- (epigeous) or
236 below-ground (hypogeous) fruiters, according to the location of their fruitbodies related to
237 the surface of soil (Table S3, “life forms”), or to either agaricoid (all fungi from the
238 Agaricaceae family, with exposed hymenium) or gastroid (fungi with a completely closed
239 hymenium; Table S3, “fruiting habit”). Regarding fruit body and spore dimensions, the mean
240 cap diameter (*FBSize*), fruit body shape (*FBShape*, calculated as the ratio between cap
241 diameter and stem diameter), stem height (*StemHeight*), spore volume (*SSize*) and shape
242 (*Sshape*, calculated as the ratio between spore length and spore width) were calculated for
243 each species, as in Kauserud *et al.* (2011) and using the current literature (Roux & Eyssartier
244 2011). Regarding their ecology, all species were assigned to their trophic status
245 (ectomycorrhizal or saprotrophic). Ectomycorrhizal species were characterized regarding
246 their associated host tree species using a compilation of the available literature (*e.g.*
247 Taudiere *et al.* 2015). For this trait, our comparative analysis focused on pine specific (known
248 to be strictly associated with *Pinus spp.*, 10 species) and oak specific (known to be strictly
249 associated with *Quercus spp.*, 16 species) species (Table S3, “Feeding modes”). Saprotrophic
250 species were subsequently ascribed to either wood-decaying or litter-decaying, depending
251 on their known interaction with the different compartments of the necromass (Table S3,
252 “Feeding modes”) by compiling published datasets in the Mediterranean region (Malençon

253 & Bertault 1968; Laganà *et al.* 2002; Richard *et al.* 2004). The corresponding analysis
254 excluded 123 species with no clear ecology (Table S3). Regarding the bioclimatic affinities,
255 fungal species were ascribed to either Mediterranean (*i.e.* with a distribution restricted to
256 the Mediterranean bioclimatic domain; these species are hereafter called *Mediterranean*) or
257 temperate (*i.e.* for which the study area is located at the southern limit of their distribution
258 range; these species are hereafter called temperate) using the current biogeographical
259 affinities of species as a proxy (*e.g.* Courtecuisse & Duhem 2007; Roux & Eyssartier 2011;
260 Table S3, “Geographical range”). We also compared fruiting patterns among fungal families
261 of ectomycorrhizal fungi (*i.e.* Amanitaceae, Cortinariaceae, Russulaceae, Tricholomataceae)
262 and saprotrophic fungi (Agaricaceae, Mycenaceae, Psathyrellaceae, non-ectomycorrhizal
263 Tricholomataceae) (Table S3, “Taxonomy”). At the species level, we restricted the analysis to
264 the most commonly observed species (*i.e.* that were observed at least three times at both
265 sampling periods).

266 Additionally, we tested three attributes associated with the detectability and
267 identifiability of fruit bodies, that could influence the sampling in the 19th century sampling
268 period and reduce the detected phenological patterns of fungi, *i.e.* fruit body’s lifespan
269 (short vs. long lifespan before complete decaying), visibility (*i.e.* conspicuous vs.
270 inconspicuous; Figure S1, “Fruitbody visibility”) and nomenclature existence (Figure S1,
271 “Identifiability”). For the latter, we distinguished species that were previously described by
272 de Candolle (De Candolle & Lamarck 1805; De Candolle 1815) from poorly known species.

273 *Assessment of the 19th and 21st century fungal phenologies*

274 For the 159 species of fungi represented in the two sampling periods, the first fruiting date
275 (FFD) and last fruiting date (LFD) of each species was yearly recorded and averaged over

276 each sampling. For each species, a difference in fruiting time *dFFD* (or *dLFD*) was calculated
277 as the difference between the mean *FFD* (or *LFD*) in the early 21st century and the mean *FFD*
278 (or *LFD*) in the 19th century sampling period.

279 *Analysed dataset*

280 The analysed dataset consisted of two association matrices (Figure S1). The first [159 x 11]
281 matrix recorded the correspondences between 159 species and 11 attributes (including
282 eight biological and ecological attributes, and three attributes associated with their
283 detectability, hereafter called *Trait association matrix*, Figure S1). The second [159 x 4]
284 matrix associated 159 species with their *FFD* and *LFD* at each sampling period (hereafter
285 called *Phenological matrix*, Figure S1).

286 *Statistical analysis*

287 For each of the eight categories of fungal traits, averaged *FFD* values were compared
288 between the 19th and the 21st century using Wilcoxon non-parametric- tests. The correlation
289 between biometrical traits (*FBSize*, *FBShape*, *StemHeight*, *SSize*, *SShape*) and phenological
290 response (*dFFD*) were analyzed using a Kendall Rank correlation test. In the particular case of
291 fruiting seasonality, the differences of monthly distribution of fruiting diversity between
292 early- and late-fruiting species during the two periods were compared using Watson two-
293 sample tests of homogeneity (package “circular” in R; Lund & Agostinelli 2010). To represent
294 the temporal dynamics of the fruiting communities, the monthly distribution of species
295 richness was analyzed. The monthly distribution of species richness was compared between
296 the two sampling periods by calculating the Pielou’s evenness index (package “vegan” in R).
297 All analyses were performed using R software (R development core team, version 2.15.0).

298

299 **3. RESULTS**

300 **Temporal distribution of records and structure of the datasets**

301 The analysis of the temporal distribution of fruiting events showed that the
302 systematic weekly sampling carried out in 1821–1852 and 2001–2011 provided records from
303 week 1 to week 52 for both periods (Figure S2). The lowest frequency of fruit body
304 emergence was observed (1) during both periods during summer (*i.e.* mostly from week 24
305 to week 53) and (2) during the 21st century only, at the very beginning of autumn fruiting
306 season (*i.e.* weeks 40-42; Figure S2).

307 The number of observed fruiting species per sampling date per site averaged 1.29
308 (from 1 to 8) and 15.08 (from 1 to 90) in 1821–1852 and 2001–2011, respectively (data not
309 shown). When considering only those species which were recorded during both sampling
310 periods, the number of observed fruiting species per sampling date per site was significantly
311 lower on average in 1821–1852 (1.17 ± 0.03) than in 2001–2011 (4.8 ± 0.43 , $P < 0.001$ by
312 Wilcoxon test).

313 **Climatic change in the study area**

314 The analysis of the available climatic data in the Montpellier area since 1821 showed a
315 significant increase in mean June-August temperatures, from $22.8 \text{ °C} \pm 0.2$ in 1840-1852 to
316 $24.4 \text{ °C} \pm 0.5$ in 2001-2010 ($W = 12$, $P = 0.003$ by Wilcoxon test; www.meteofrance.fr; Figure
317 2). At the same time, summer precipitation slightly varied, from $68.4 \text{ mm} \pm 12.4$ on average
318 during the period 1835-1852 to $76.9 \text{ mm} \pm 16.2$ on average during the period 2001-2010 (W
319 $= 73.5$, $P=0.58$ by Wilcoxon test; www.meteofrance.fr).

320 **Fruiting seasonality**

321 Early fruiting fungi started fruiting significantly later in the early 21st century
322 compared with the 19th century (FFD delayed by 16.4 ± 3.1 d by Wilcoxon non-parametric
323 test, $P < 0.001$; Table 1; see Table S4 for LFD data). This result was consistent when
324 considering only ectomycorrhizal fungi (FFD delayed by 12.0 ± 3.2 d (mean \pm SE and
325 hereafter), $P < 0.001$ by Wilcoxon non-parametric test; Table 1) or saprotrophic (FFD delayed
326 by 25.3 ± 6.3 d, $P < 0.001$ by Wilcoxon non-parametric test; Table 1) species. Contrastingly,
327 FFDs of late fruiting species were not significantly delayed (Table 1). Early fruiting fungi
328 extended their fruiting period and the LFD was significantly delayed by 18.2 ± 3.2 days ($P <$
329 0.001 by Wilcoxon non-parametric test, Table S4).

330 Regarding the monthly distribution of diversity, a temporal shift in species richness
331 maximum was visually observable for early fruiting saprotrophic species only (Figure 3). For
332 ectomycorrhizal species, the highest number of fruiting species (accounting 43.7% of the
333 total number of species) was observed in November during the early 21st century, while a
334 more even pattern characterized the temporal distribution of diversity in the 19th century
335 sampling period ($P < 0.05$ by Watson test; Figure 3). Similarly, according to the Pielou's
336 evenness index, the temporal fruiting dynamics was also the most unevenly distributed
337 along the fruiting season for early fruiting ectomycorrhizal fungi from the early 21st century
338 (Pielou's evenness index = 0.78) compared to the monthly distribution of the
339 ectomycorrhizal and saprotrophic fruiting species from the 19th century (Pielou's evenness
340 index > 0.95). Early fruiting saprotrophic species showed a similar trend, with a delayed peak
341 of the number of fruiting species from October (in the 19th century) to December (in the
342 early 21st century), but the difference was not significant by Watson test (Figure 3). A fruiting

343 interruption between January and March was, however evidenced for early fruiting
344 saprotrophic species in the ancient period, that was absent in the early 21st century (Figure
345 3B). Late fruiting species did not show significant difference in the temporal distribution of
346 fruiting species between the 19th and 21st century, for both ectomycorrhizal (Figure 3) and
347 saprotrophic (Figure 3) species (Watson test, $P > 0.05$). However, some ectomycorrhizal (late
348 fruiters) and saprotrophic (early and late fruiters) fungi fruited 1 month later in the early 21st
349 century compared to the early 19th century (Figure 4).

350 **Life forms and habits**

351 As hypothesized, epigeous and hypogeous fungi showed contrasting phenological
352 patterns. While epigeous macromycetes currently start fruiting 17.3 ± 2.3 d later than during
353 the ancient period ($P < 0.001$ by Wilcoxon non-parametric test), hypogeous fungi did not
354 significantly change their FFD between the two sampling periods (Table 1). In addition,
355 agaricoid and gastroid species showed contrasting phenological shifts. Species producing
356 agaricoid fruit bodies significantly delayed their fruiting by 16.7 ± 2.5 d ($P < 0.001$, Wilcoxon
357 non-parametric test), while gastroid fungi did not significantly change their fruit body
358 emergence time ($P > 0.05$, Wilcoxon non-parametric test) between the two sampling periods
359 (Table 1).

360 **Morphology**

361 Regarding the correlations between the fruit body-spore dimensions and the fruiting
362 time, dFFD was slightly positively correlated with the size (FBsize) and shape of the fruit
363 body (FBshape), height (StemHeight) of fruit bodies and spore shape (Sshape), while
364 negatively correlated with spore size (Ssize) (Figure S3). These correlations were, however,
365 not significant (Kendall rank correlation test, $P > 0.05$).

366 **Feeding modes**

367 The analysis of fruiting time of fungal species with different feeding modes shows
368 that in Mediterranean forests, ectomycorrhizal species associated with pines significantly
369 delayed their fruiting start (FFD delayed by 19.2 ± 6.1 d; $P < 0.01$ by Wilcoxon non-
370 parametric test) since the early 19th century, whereas oak fungal symbionts did not change
371 their FFD (Table 1). Regarding their feeding substrate, both wood-decaying fungi and litter
372 decayers significantly shifted their fruiting start (Table 1).

373 **Geographical range**

374 Regarding the geographical range, temperate species delayed their fruiting time by
375 17.3 ± 8.4 d ($P < 0.05$, Wilcoxon non-parametric test) since the 19th century in the study area
376 (Table 1). In contrast, our analysis revealed no significant change in fruiting date for species
377 with distribution restricted to the Mediterranean ecoregion (Table 1).

378 **Taxonomy**

379 For the ectomycorrhizal families, we observed a delayed start of fruiting by 19.1 ± 8.1
380 and 18.4 ± 6.3 d for Amanitaceae ($P < 0.05$ by Wilcoxon non-parametric test) and
381 Russulaceae ($P < 0.01$ by Wilcoxon non-parametric test), respectively, since the 19th century
382 (Table 1). Contrastingly, FFD did not significantly differ between the two sampling periods
383 for the families Cortinariaceae and Tricholomataceae (Table 1). At the species level, and
384 regarding the most common species, six species within basidiomycete families (*i.e.* *Astraeus*
385 *hygrometricus*, *Cantharellus cibarius*, *Clavulina cinerea*, *Gyroporus castaneus*, *Hebeloma*
386 *sinapizans*, *Phellodon niger*) and one species in the ascomycetes (*i.e.* *Helvella crispa*) fruited
387 later in the early 21st century compared to the 19th century (Figure 4). Among saprotrophic

388 families, significant changes in the start of fruiting were evidenced for Agaricaceae, with a
389 34.3 ± 12.5 d delayed FFD during the early 21st century as compared to the 19th century ($P <$
390 0.01 by Wilcoxon non-parametric test, Table 1). Other families, including Mycenaceae,
391 Psathyrellaceae and non-ectomycorrhizal Tricholomataceae did not significantly change their
392 phenology of fruiting since the 19th century (Table 1). At the species level, delayed starts of
393 fruiting occurred in seven saprotrophic species (*i.e.* *Auricularia auriculae-judae*, *Auricularia*
394 *mesenterica*, *Hypholoma fasciculare*, *Lepista sordida*, *Mycena pura*, *Psathyrella candolleana*,
395 *Tapinella panuoides*), whereas three species (*Collybia butyracea*, *Lepista nuda*, *Psathyrella*
396 *prona*) currently start to fruit earlier compared to the ancient period (Figure 4).

397 **Fruit body detectability and identifiability**

398 All the six categories of fungal species based on their detectability and identifiability
399 significantly changed their FFD (Table 1) and their LFD (Table S3) between the 19th and the
400 21st century. The FFD of both species with long and short lifespan was significantly delayed
401 by 20.6 ± 5.9 d (Wilcoxon non-parametric test $P < 0.01$) and 15.9 ± 2.4 d (Wilcoxon non-
402 parametric test $P < 0.01$), respectively (Table 1). Significant shifts in FFD were also found
403 regarding the detectability, for conspicuous (14.9 ± 2.2 d) and inconspicuous species ($22.4 \pm$
404 3.6 d) (Wilcoxon non-parametric test, $P < 0.01$, Table 1), and the identifiability of fungi with
405 well described (20.5 ± 3.1 d) and poorly known (11.8 ± 3.3 d) fungal species (Wilcoxon non-
406 parametric test, $P < 0.001$, Table 1).

407

408 **4 DISCUSSION**

409 This study, based on the oldest fungal dataset in the Mediterranean, reveals that a close
410 interaction between the ongoing climate change and the various facets of fungal diversity
411 shapes the phenological response of fungal species to temperature increase and extension
412 of summer drought length in the studied region. In the French Mediterranean region,
413 climate warming increases the severity of summer drought, with consequences for the
414 phenology of early fruiterers, but also for species with affinities for cold climates and/or
415 producing epigeous fruit bodies which delayed their fruiting time since the 19th century's last
416 temperature minimum. Contrastingly, Mediterranean species and/or species
417 morphologically adapted to drought did not change their fruiting phenology over time.
418 Our analysis of potential detectability biases supports the use of ancient fungal herbarium
419 records as a valuable source of phenological data.

420 **Fungal herbaria: opportunities and challenges for diachronic analyses**

421 Herbaria are considered as relevant tools to track changes in phenological patterns of
422 organisms in response to climate changes (Lavoie & Lachance 2006; Diez *et al.* 2013) as they
423 provide high resolution temporal datasets (Meineke *et al.* 2018). Nevertheless, the use of
424 raw biological recording dates in long term diachronic analyses is challenging, particularly for
425 macrofungi (Halme & Kotiaho, 2012; Diez *et al.* 2013; Boddy *et al.* 2014; Chapman *et al.* 2015;
426 Daru *et al.* 2018; Andrew *et al.* 2018), as fruit body production can vary markedly between
427 years (Straatsma *et al.* 2001; Boddy *et al.* 2014) in particular in Mediterranean regions
428 (Richard *et al.* 2004; Baptista *et al.* 2010). Indeed, Diez *et al.* (2013) and Chapman *et al.*
429 (2015) showed respectively that uneven recording periods or too short recording duration
430 could bias the apparent fruiting periods. In our study, the effect of erratic fruiting patterns

431 was limited by the length (12 and 32 y of sampling in the 19th century and the 21st century)
432 and the systematic weekly sampling. In addition, we limited the influence of potential
433 methodological biases on the phenological response of species by: (1) focusing the analysis
434 on species which were recorded at the two sampling periods and (2) restricting the sampling
435 area to a homogenous bioclimatic domain of Mediterranean oaks, including a set of
436 common sites (Figure 1). However, this site selection induced an incomplete overlap of areas
437 sampled in the 19th and the 21st century, with sampling of ancient study sites concentrated
438 in a restricted area, as compared to the distribution of recent study sites.

439 When testing the influence of sporocarp detectability and identifiability on their recorded
440 fruiting patterns, we found that these sampling biases impact neither the significance nor
441 the direction of the effect, with slight differences in the amplitude of the measured delay
442 (Table 1). This result suggests that species producing poorly detectable sporocarps may be
443 considered as an integral part of fungal datasets used in diachronic surveys. However, using
444 five estimators of the detectability of polypores, previous research showed that longevity
445 and identifiability of fruit bodies strongly affect the occurrence of species in datasets, and
446 highlighted the strong influence of the quality of sampling on the estimation of the
447 abundance of poorly detectable species (Löhmus 2009). As a consequence, poorly
448 detectable species should be considered with caution, to limit potential biases for evaluating
449 species response in comparative approaches.

450 We found a significant fruiting delay for both species forming resistant and fragile fruit
451 bodies, for both species producing inconspicuous and conspicuous fruit bodies, for both
452 poorly known and well described species in the ancient sampling period (Table 1).
453 Interestingly, we highlighted a markedly lower fruiting shift for poorly documented species

454 during the 19th century than for species described by De Candolle and Lamarck (De Candolle
455 & Lamarck 1805; De Candolle 1815). This result suggests that species identifiability may be
456 used as a species trait which potentially biases the assessment of fruiting shift in long-term
457 diachronic surveys. Our finding also highlights the substantial taxonomic upsets within the
458 fungal kingdom during the 20th and the early 21st centuries (*e.g.* Vesterholt 2012), and its
459 consequence for the quality of the sampling by fungal forayers (Heilmann-Clausen & Læssøe
460 2012).

461 **The influence of species seasonality on fruiting phenology**

462 In the study area, early fruiters significantly delayed their fruiting period between the 19th
463 and 21st century, in contrast to late-fruiters (Table 1). This result is in accordance with our
464 hypotheses concerning preferential effects of an extended drought on early-fruiting species
465 that first produce their fruit bodies at the end of summer. Thus, in the study area, the
466 severity of summer drought increased since the 19th century through the combined effects
467 of significant temperature increase (Figure 2) and extended drought duration (Ruffault *et al.*
468 2013). Our results in the Mediterranean area are consistent with the response of fungi
469 documented by Kauserud *et al.* (2008) in temperate areas. These authors evidenced a 30 d
470 fruiting shift of early-fruiting species with no shift for late-fruiting species. Interestingly, and
471 even if averaged values have to be considered with caution because of the above-mentioned
472 methodological biases, we observed a fruiting shift at the secular scale of similar amplitude
473 to previous studies investigating the same question at decennial scales (Gange *et al.* 2007;
474 Kauserud *et al.* 2008; Moore *et al.* 2008). This finding suggests that either most phenological
475 shifts are recent and similar in duration across Europe, or changes in the Mediterranean area
476 during recent decades were less pronounced than in temperate regions. Tracking fungal

477 datasets of the intermediate period (*i.e.* early 20th, *e.g.* from de Seyne; Moreau *et al.* 2011)
478 may help to understand the temporal dynamics of phenological changes in the
479 Mediterranean area from 1820 to 2010.

480 **Contrasting fruiting responses depending on feeding modes**

481 When considering only early-fruiting fungi, the amplitude of fruiting delay for saprotrophic
482 species was almost twice that of ectomycorrhizal species (Figure 3). This confirms a previous
483 study of Kauserud *et al.* (2012) indicating that saprotrophic guilds were much more
484 influenced by climatic variations than ectomycorrhizal fungi. The mechanisms underlying this
485 pattern remains unclear. Saprotrophic fungi acquire their nutrients from inert organic matter,
486 especially from tree litter and dead wood (Smith & Read 2010) lying on forest floor, and are
487 then particularly exposed to environmental fluctuation, as well as to the highly variable
488 availability and recalcitrant nature of soil organic matter (Courty *et al.* 2016) by comparison
489 to ectomycorrhizal species. Alternatively, this result may reflect differences in fruit body size
490 between saprotrophic and ectomycorrhizal species, and then differential carbon cost for
491 reproductive investment between trophic modes (Bässler *et al.* 2015). We cannot exclude a
492 combined effect of fruit body size, but it is unlikely when considering the weak and not
493 significant relationship between phenological shift of species and the size of fruit bodies
494 (Figure S3).

495 When considering both early- and late-fruiting fungal species, both wood- and litter decaying
496 fungi delayed their FFD (Table 1). The factors explaining this pattern are unclear, but may
497 include different mechanisms such as water infiltration and evaporation limiting water
498 storage in both wood and litter. It takes longer for wood than litter to rewet after drought, as
499 shown in Harmon & Sexton (1995), while the water is less well stored in litter than in wood.

500 Based on 29-y-observations, Sato *et al.* (2012) found that wood-decaying fungi and litter-
501 decaying fungi respond differently to environmental conditions, with more variable fruiting
502 phenology among genera of wood-decaying fungi. Regarding phenological patterns, more
503 research is needed to understand the mechanisms underlying these contrasting patterns,
504 and their consequences for nutrient turnover and soil functioning. In particular,
505 complementary research focusing on the guild of wood decayer fungi, and distinguishing
506 among contrasting fruit body morphologies (*i.e.* polypores vs. corticioids vs. discomycetes vs.
507 pyrenomycetes vs. agarics vs. jelly fungi) and/or nutritional profiles based on enzymatic
508 diversity (*e.g.* cellulolytic vs. ligninolytic) may advantageously complete the available
509 corpus, by providing valuable data about adaptative traits in response to drought (*e.g.*
510 Purhonen et al. 2017).

511 In the case of ectomycorrhizal fungi, we observed that fungi associated with *Pinus* spp.
512 significantly delayed their fruiting period while fungi associated with *Quercus* spp. poorly
513 responded (Table 1). This influence of tree host on phenological shifts of fungi has been
514 previously documented by Diez *et al.* (2013), who found that the fruiting period of species
515 associated with evergreen trees is more delayed than deciduous species. The process
516 underlying host effect is not clear, but one may argue that under *Pinus* spp. canopies, soil is
517 more exposed to environmental fluctuations including higher water evaporation and
518 temperature variation as compared to evergreen oak forests. Thus, *Q. ilex* canopies provide
519 a particularly dense protection against incident light and favor moisture retention in soil
520 (Gass & Barnes 1998). These forest conditions may differently influence fruiting patterns of
521 ectomycorrhizal fungi depending on their associated host. Other factors can explain these
522 differences in phenological fruiting patterns, including the contrasting distribution of oak

523 and pine ecosystems regarding topography and soil properties. Further investigations should
524 be carried out in the future to disentangle these factors.

525 **Fruit body anatomy and life-form induced phenological response**

526 As postulated, in our study, hypogeous fungi did not significantly delay their fruiting period,
527 while epigeous species showed a significant temporal shift (Table 1). Our findings suggest
528 that the higher protection against drought of hypogeous fungi may balance a phenological
529 shift due to increased drought, the epigeous habit of macromycetes enabling long distance
530 dispersion of spores but exposing the reproductive structure to desiccation in contrast to
531 hypogeous species (Hibbett *et al.* 1997). Some studies investigated relationships between
532 occurrence of hypogeous fungi and environmental conditions (Fogel 1976; Claridge *et al.*
533 2000; Buntgen *et al.* 2012b;), but comparison between epi- and hypogeous fruiting patterns
534 in response to environmental fluctuations remain scarce (Hawker 1954).

535 We also considered the fruit body form in distinguishing agaricoid-type from gastroid-type
536 fruit bodies. It has been hypothesized that gastroid fruit body has evolved as an adaptation
537 to arid climates (Thiers 1984). From a mechanistic point of view, this enclosed hymenium
538 enables a low surface to volume ratio that minimizes water loss during drought. The findings
539 of our study is in line with this hypothesis, as no significant phenological shift was observed
540 for gastroid compared to agaricoid species (Table 1). In addition, macroscopical
541 morphological traits, related to the fruit body and stalk (FBSize, FBShape, StemHeight) did
542 not show any correlation with fruiting patterns (Figure S3), agreeing with Kausrud *et al.*
543 (2011). Although it has been shown that morphological traits (*e.g.* cap size of fungi) are
544 related to hygrometric indexes (Gange *et al.* 2018), these traits seem not to be linked to a
545 fruiting response to climate change. From temperate to Mediterranean ecosystems, these

546 morphological traits thus consistently appear as poorly predictive proxies of the sensitivity of
547 species to drought.

548 At the microscopical scale, we observed a non-significant negative relationship between
549 SporeSize and dFFD (Figure S3). This finding contrasts with the pattern reported by Kauserud
550 *et al.* (2011) who observed that once spore volume doubles, fruiting time advances 3 d
551 earlier. Our result then poorly supports the hypothesis of Kauserud *et al.* (2011), who
552 postulates that the higher spore volume, the higher the volume of stored water, and the
553 higher the probability of spore germination success in dry environments.

554 **Conservation challenges and fungal diversity**

555 In our study, contrasting patterns of phenological response to climate change was evidenced
556 among taxonomic groups of fungi. For the ectomycorrhizal guild, Russulaceae and
557 Amanitaceae demonstrated a marked delay, whilst no significant shift was observed in
558 Cortinariaceae and Tricholomataceae (Table 1). Interestingly, a rainfall exclusion experiment
559 installed in the same sampling area showed a similar contrasting pattern when considering
560 the below-ground apparatus (*i.e.* ectomycorrhizal root tips) of Russulaceae and
561 Cortinariaceae, the two dominant families of macromycetes (Richard *et al.* 2011). Thus, after
562 9 y of increased drought, a consistent response pattern was found for Cortinariaceae, which
563 significantly increased in relative abundance on *Q. ilex* root systems, while Russulaceae
564 slightly decreased (Richard *et al.* 2011). Moreover, Buée *et al.* (2005) evidenced drought
565 resistance traits of Cortinariaceae species, such as higher abundance and metabolic activity
566 in summer when compared to winter periods. Considered altogether, these results suggest
567 that Cortinariaceae may be less sensitive to the ongoing climate change than Russulaceae,

568 and questions concerning possible effects on soil nutrient turnover, in relation to their
569 contrasting ability to hydrolyze complex sources of organic carbon (Courty et al. 2005).

570 These results suggest that some families, such as Cortinariaceae, weakly respond both
571 above- and below-ground to short and long-term environmental fluctuations and remain
572 inefficient candidates for indicating climate change cascading effect. Contrastingly,
573 Russulaceae may be considered as potential integrative indicators of the consequences of
574 climate change on soil biota.

575 Within families, fruiting shifts varied markedly among species. In Cortinariaceae,
576 *Cortinarius torvus* fruited significantly later in the early 21st century as compared to the 19th
577 century, in contrast to *Cortinarius castaneus*. These results are in accordance with the
578 picture obtained below-ground by Richard *et al.* (2011), and above-ground by Diez *et al.*
579 (2013), who highlighted high inter-specific differences in phenology within families and
580 genera of fungi.

581 Our study detected that a few fungal species may be considered as potential
582 candidates to monitor the effect of climate change on fruiting of fungi in the Mediterranean.
583 Candidates include *Helvella crispa* (ectomycorrhizal fungi), *Auricularia mesenterica*
584 (saprotrophic fungi) or *Auricularia auriculae-judae* (saprotrophic fungi) (Figure 4) which were
585 (1) highly responsive, (2) frequent and widespread enough to be observed several years
586 during the monitoring period and (3) easily identifiable in the field. The responsiveness to
587 climatic change of *Auricularia auriculae-judae* has been previously observed since 1980 in
588 southern England (Gange *et al.* 2011), but the respective influence of global warming and
589 methodological biases remain under debate (Heilmann-Clausen & Læssøe 2012). Indeed,
590 long-lived and resistant *Auricularia auriculae-judae* fruit bodies make it difficult to

591 distinguish between fresh and old reproductive structures, and then compromise attempts
592 for homogeneous sampling in diachronic surveys.

593 As suggested by Diez *et al.* (2013), concomitant factors combine their effect with those of
594 climatic changes, including land-use changes, and influence fruiting patterns of fungi. In the
595 study area, marked temporal changes in land cover converted open vegetation, inherited
596 from centuries of intensive grazing into a mosaic of secondary oak (*Quercus ilex*) forests and
597 urban areas (Sirami *et al.* 2010; Vogt-Schilb *et al.* 2018). This change may have favored
598 mycorrhizal species associated with oaks, such as the late-fruiting *Leccinellum lepidum*
599 (Loizides *et al.* 2019). Interestingly, the fruiting frequency of this species increased during the
600 21st century compared to 19th century (data not shown). The observed patterns of this
601 Mediterranean species strictly associated with oaks may be related to the increasing of holm
602 oak covering the studied Mediterranean ecosystems under secondary succession (*e.g.* Sirami
603 *et al.* 2010; Vogt-Schilb *et al.* 2018), and not only a positive response to climate change.

604

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613

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833 Legends of figures

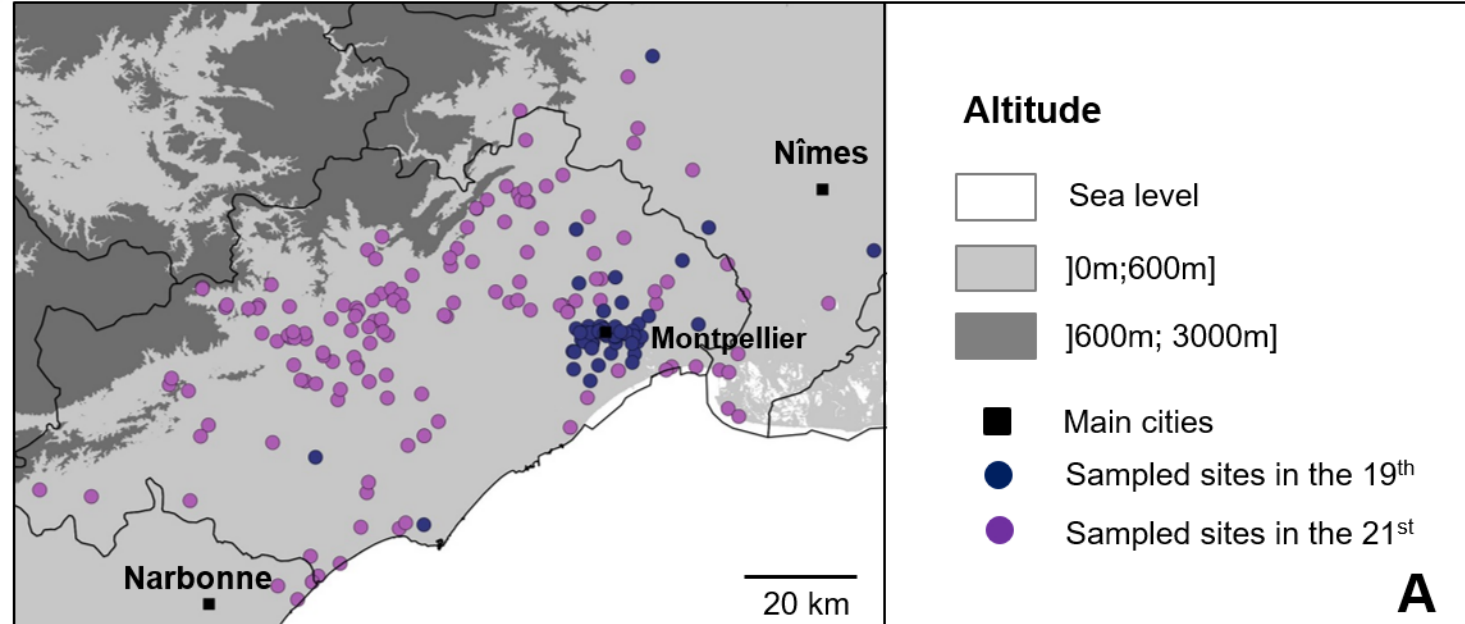
834 **Figure 1.** Sampling design and historical overview of the 19th century. (A) Localization of the
835 19th (1821-1852) and the 21st (2001-2011) century field records around Montpellier. The
836 grey colours in the left map delineate the altitudinal range of the study area. (B) Painting of
837 *Agaricus erythrosarcos* Dunal (*Lactarius deliciosus*), Fontfroide, 28/10/1836, coll. Dunal,
838 Herbar MPU–UM, (C) Dried specimen of “Agaric tout blanc” (*Amanita echinocephala*),
839 Grammont, 11/1823, coll. Touchy, Herbar général MPU–UM. (D) Picture of *Omphalotus*
840 *olearius*, a typical Mediterranean species.

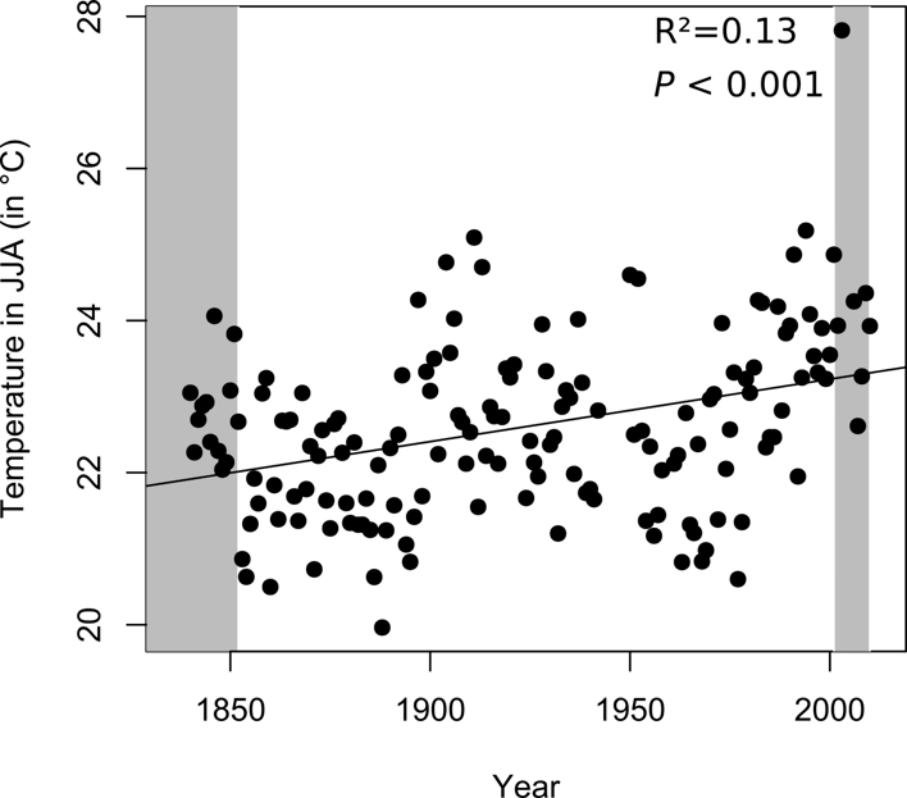
841 **Figure 2.** Mean Summer temperatures (June-July-August) in downtown Montpellier since
842 1840. Shades represent the two field sampling periods. R^2 and p-value of the linear
843 regression model is indicated.

844

845 **Figure 3.** Monthly distribution of fungal diversity in 1821–1852 and 2001–2011, according to
846 the two ecological guilds: ectomycorrhizal (ECM) vs. saprotroph (SAPRO) and fruiting
847 seasonality (early- vs. late-fruiting). The mean annual number of fruiting species is
848 expressed in percentages.

849 **Figure 4.** Comparison of the first fruiting day of (A) ectomycorrhizal (ECM) guild and (B)
850 saprotrophic (SAPRO) guild between the 19th century (1821-1852) and the 21st century
851 (2001-2011), which are the most commonly observed in both periods (occurred in ≥ 3 years).
852 Each point represents the averaged first fruiting day of a species \pm standard deviation.



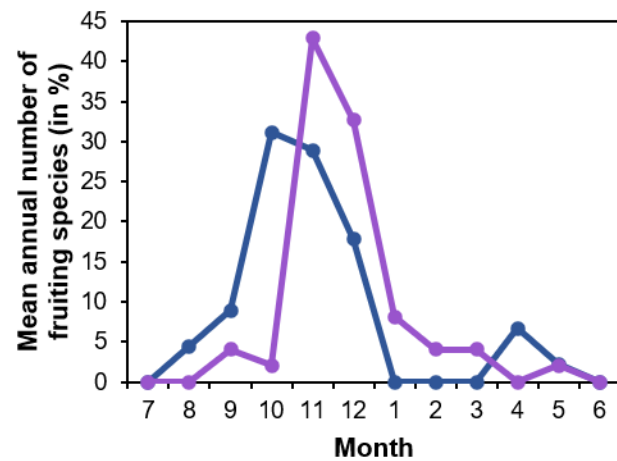
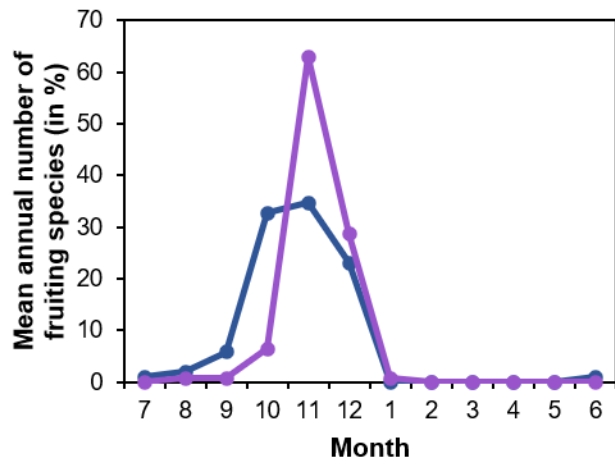


19th
21st

ECM

SAPRO

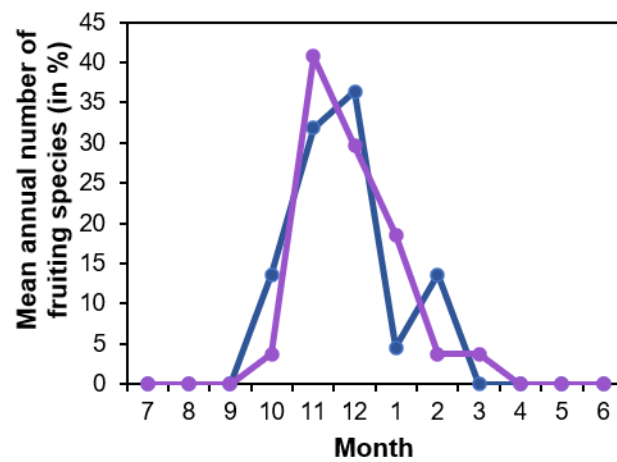
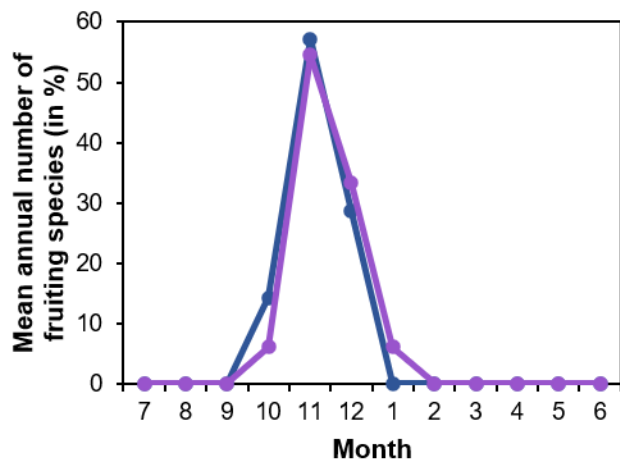
Early-fruiting



A

B

Late-fruiting



C

D

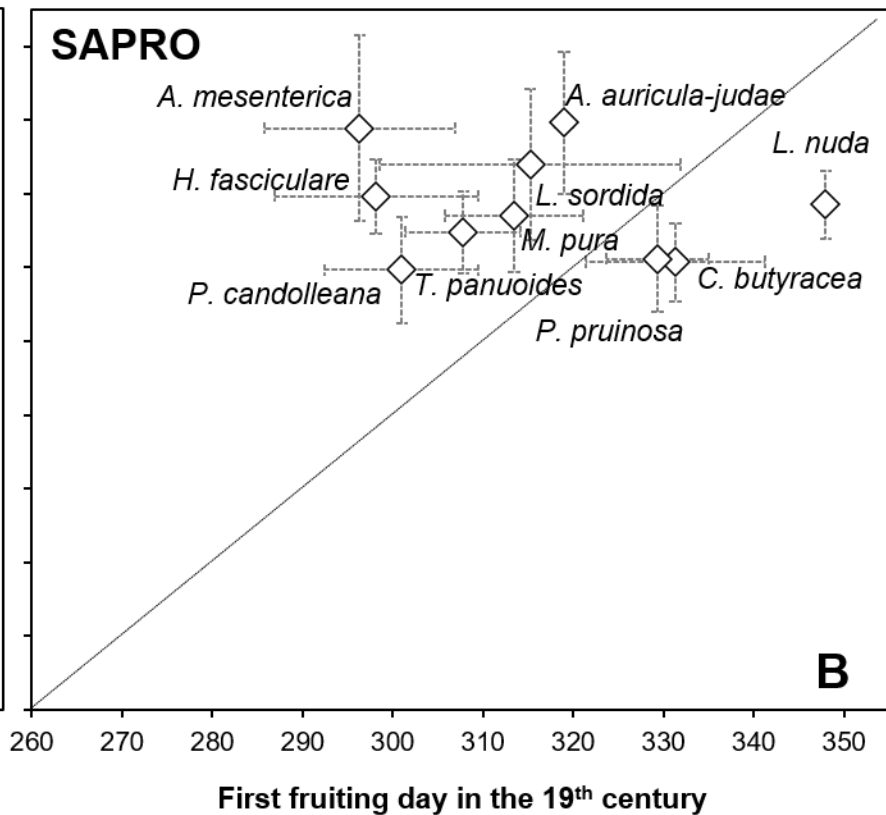
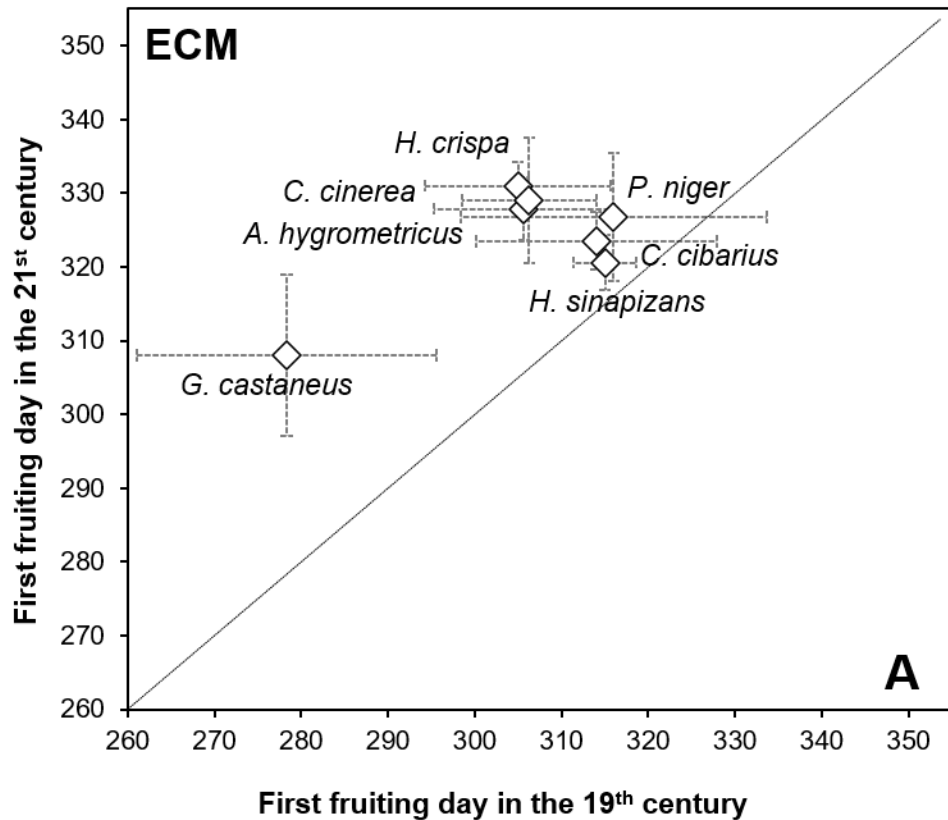


Table 1. Mean and standard error of the first fruiting day (FFD) and difference of FFD between the 21st and the 19th century (dFFD) of fungal species, depending on the taxonomy, fruiting seasonality, life-form and habit, ecology geographical range, detectability and identifiability of species. Statistical significance by Wilcoxon non-parametric test at P < 0.001, 0.01 and 0.05 is indicated by ***, ** and *, respectively. NS: not significant. The number (N) of species per category is indicated. ECM, ectomycorrhizal; sapro, saprotroph.

Trait	N	FFD				dFFD		Wilcoxon test		
		in the 19 th		in the 21 st		Mean	SE	W	P	
		Mean	SE	Mean	SE	Mean	SE			
Taxonomy	Amanitaceae	11	295.7 ± 4.7	314.8 ± 4.6	19.1 ± 8.1	22	0.012	*		
	Cortinariaceae	7	319.8 ± 7.8	319.4 ± 2.9	-0.4 ± 8.9	29	0.609	NS		
	Russulaceae	10	304.8 ± 3.5	323.1 ± 3.7	18.4 ± 6.3	11	0.004	**		
	Tricholomataceae (ECM)	8	320.6 ± 5.4	326.7 ± 3.8	6.1 ± 6.7	26	0.563	NS		
	Agaricaceae	7	290.4 ± 6.0	324.7 ± 9.6	34.3 ± 12.5	7	0.007	**		
	Mycenaceae	8	322.1 ± 7.4	328.5 ± 4.5	6.4 ± 7.9	23	0.370	NS		
	Psathyrellaceae	9	313.2 ± 5.4	327.9 ± 8.1	14.7 ± 10.7	26	0.222	NS		
	Tricholomataceae (Sapro)	11	312.3 ± 5.9	325 ± 5	12.7 ± 7.3	46.5	0.148	NS		
Fruiting seasonality	Early-fruiting	73	307.6 ± 2.6	323.9 ± 2	16.4 ± 3.1	1421.5	< 0.001	***		
	Late-fruiting	17	324.9 ± 4.6	327.5 ± 3.8	2.6 ± 6.3	134	0.730	NS		
	Early-fruiting (ECM)	49	308.9 ± 2.8	320.9 ± 1.5	12.0 ± 3.2	662.5	< 0.001	***		
	Late-fruiting (ECM)	8	323.8 ± 3.0	324.4 ± 3.3	0.5 ± 5.4	30.5	0.916	NS		
	Early-fruiting (Sapro)	24	304.9 ± 5.5	330.2 ± 5.3	25.3 ± 6.3	136	0.002	**		
	Late-fruiting (Sapro)	9	325.8 ± 8.4	330.3 ± 6.6	4.5 ± 11.3	39.5	0.965	NS		
Life-form and habit	Epigeous	153	310.5 ± 1.9	327.9 ± 1.6	17.3 ± 2.3	6500.5	< 0.001	***		
	Hypogeous	6	317.4 ± 10	324.5 ± 3.6	7 ± 12.4	13	0.485	NS		
	Agaricoid	129	308.9 ± 2	325.6 ± 1.6	16.7 ± 2.5	4627	< 0.001	***		
	Gastroid	11	311.9 ± 7	330.1 ± 3.6	18.3 ± 9.8	30.5	0.053	NS		
Feeding modes	<i>Pinus spp.</i> (ECM)	10	306.5 ± 4.4	325.7 ± 3.2	19.2 ± 6.1	14.5	0.008	**		
	<i>Quercus spp.</i> (ECM)	16	312.7 ± 5.1	321.8 ± 2.5	9.1 ± 6.2	79	0.067	NS		
	Litter decaying (Sapro)	52	307.6 ± 3.6	324.6 ± 2.2	17.0 ± 4.4	767	< 0.001	***		
	Wood decaying (Sapro)	28	316.8 ± 4.6	348.3 ± 5.1	31.43 ± 5.9	143	< 0.001	***		
Geographical range	Temperate	15	309.1 ± 6.2	326.3 ± 5.3	17.3 ± 8.4	59.5	0.029	*		
	Mediterranean restricted	22	311.6 ± 5.1	319.9 ± 2.6	8.3 ± 6.3	176.5	0.127	NS		
Fruitbody lifespan	Short duration	129	309.4 ± 2.1	325.3 ± 1.4	15.9 ± 2.4	4699	< 0.001	***		
	Long duration	29	316.4 ± 4	336.9 ± 5.1	20.6 ± 5.9	231	0.003	**		
Detectability	Conspicuous	121	309.5 ± 1.9	324.4 ± 1.5	14.9 ± 2.2	4005.5	< 0.001	***		
	Inconspicuous	38	314.7 ± 5	338 ± 3.9	22.4 ± 3.6	437.5	0.003	**		
Identifiability	Described	91	307.6 ± 2.6	328.1 ± 2.1	20.5 ± 3.1	2005.5	< 0.001	***		
	Undescribed	64	313.5 ± 2.6	325.3 ± 2.1	11.8 ± 3.3	1348	< 0.001	***		