

1 Domestication of different varieties in 2 the cheese-making fungus *Geotrichum* 3 *candidum*

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19

20 Abstract

21 Domestication is an excellent model for studying adaptation processes, involving
22 recent adaptation and diversification, convergence following adaptation to similar
23 conditions, as well as degeneration of unused functions. *Geotrichum candidum* is a
24 fungus used for cheese-making and is also found in other environments such as soil
25 and plants. By analyzing whole-genome data from 98 strains, we found that all
26 strains isolated from cheese formed a monophyletic clade. Within the cheese clade,
27 we identified three differentiated populations and we detected footprints of
28 recombination and admixture. The genetic diversity in the cheese clade was high,
29 indicating a lack of strong bottleneck. Commercial starter strains were scattered
30 across the cheese clade, thus not constituting a single clonal lineage. The cheese
31 populations were phenotypically differentiated from other populations, with a slower
32 growth on all media, even cheese, a prominent production of attractive cheese
33 flavors and a lower proteolytic activity. Furthermore, one of the cheese populations
34 displayed footprints of a more advanced state of domestication, with much lower
35 genetic diversity, denser and fluffier colonies and excluding more efficiently cheese

36 spoiler fungi. Cheese populations lost two beta lactamase-like genes, involved in
37 xenobiotic clearance, and displayed transposable element expansion, likely due to
38 relaxed selection. Our findings suggest the existence of genuine domestication in *G.*
39 *candidum*, which led to diversification into different varieties with contrasted
40 phenotypes. Some of the traits acquired by cheese strains indicate convergence with
41 other, distantly related fungi used for cheese maturation.

42

43 Introduction

44 Understanding how populations adapt to their environment is a key question in
45 evolutionary biology. Domestication, the change in the genetic and phenotypic make-
46 up of populations under human artificial selection, is an excellent model for studying
47 adaptation processes, as it involves recent adaptation events under strong selection
48 on known traits and rapid diversification. Numerous studies have documented the
49 specific traits acquired in domesticated animals (dog, horse, pig, cow) (Diamond,
50 2002; Frantz et al., 2015; Petersen et al., 2013; Warmuth et al., 2011) and plants
51 (cabbage, corn, wheat) (Hufford et al., 2012; Mabry et al., 2021; Peng et al., 2011),
52 as well as their genetic differentiation from wild populations and their adaptive
53 genomic changes. For example, domesticated animals (dog, horse and cattle) have
54 been selected for coat color, size, rapidity and docility (Liu et al., 2022; Plassais et
55 al., 2022; Qanbari et al., 2014). In plants too, similar traits have been selected in
56 different lineages, such as bigger grains with more nutrients and lack of dormancy
57 (Cornille et al., 2014; Hufford et al., 2012; Peng et al., 2011; Purugganan, 2019). On
58 the other hand, functions essential in wild environments but unused in anthropic
59 environments have often degenerated due to relaxed selection, for example,
60 reductions in defense mechanisms in plants (Cornille et al., 2014; Hufford et al.,
61 2012). Domestication also often leads to strong reduction in genetic diversity due to
62 bottlenecks in animals (e.g. dog) (Marsden et al., 2016) and annual plants (e.g. rice)
63 (Zhu et al., 2007).

64 Humans have domesticated several fungi for the fermentation of foods (e.g. beer,
65 bread, wine, dry-cured meat and cheese), to produce secondary metabolites used in
66 pharmaceuticals (e.g. penicillin), or for their nutritional and gustatory values (e.g.
67 button and shiitake mushrooms) (Steensels et al., 2021). Fungi are excellent models

68 for studying evolution and adaptation in eukaryotes, given their many experimental
69 assets (Gladieux et al., 2014): fungi have relatively small genomes, many are easy
70 to culture in laboratory conditions, and spores can survive long periods in the
71 freezer. However, despite their economic and industrial importance, and their utility
72 as biological models for studying adaptive divergence, the fungi used by humans
73 have yet been little studied. An exception is the budding yeast *Saccharomyces*
74 *cerevisiae* used in the production of beer, wine and bread (Bai et al., 2022; Duan et
75 al., 2018; Fay and Benavides, 2005; Gallone et al., 2016; Lahue et al., 2020; Legras
76 et al., 2018; Libkind et al., 2011; Liti et al., 2009; Peter et al., 2018), and to a lesser
77 extent the filamentous fungus *Aspergillus oryzae* used to ferment soy and rice
78 products in Asia (Galagan et al., 2005; Gibbons et al., 2012; Machida et al., 2005)
79 and the *Penicillium* species used for cheese ripening, e.g. *P. camemberti* for soft
80 cheeses (Ropars et al., 2020), and *P. roqueforti* for blue cheeses (Cheeseman et al.,
81 2014; Dumas et al., 2020; Ropars et al., 2015). Phenotypic traits beneficial for food
82 production have been acquired in fungal domesticated populations, being different
83 from wild populations. The domestication having led to *P. camemberti* occurred in
84 several steps, with the successive differentiation of several lineages displaying
85 decreasing diversity and increasing beneficial traits for cheese maturation, from the
86 wild *P. fuscoglaucum*, to *P. biforme* and then the two clonal *P. camemberti* varieties,
87 *caseifulvum* and *camemberti* (Ropars et al., 2020b). Domesticated populations of
88 fermented food microorganisms can for example better assimilate the carbon
89 sources present in the anthropic environment, e.g. lactose for *Penicillium* cheese
90 fungi (Ropars et al., 2015) and maltose for *S. cerevisiae* sourdough strains (Bigey et
91 al., 2021). Furthermore, volatile organic compounds crucial for cheese flavor are
92 more appealing in cheese populations compared to wild populations in *P. roqueforti*
93 (Caron et al., 2021).

94 The genomic processes involved in adaptation to human-made environments in
95 domesticated fungi include gene family expansion for specific metabolism pathways,
96 gene gain, inter-specific hybridization, introgression and horizontal gene transfer
97 (Almeida et al., 2014; Barros Lopes et al., 2002; Borneman et al., 2016; Cheeseman
98 et al., 2014; Gallone et al., 2016; Libkind et al., 2011; Machida et al., 2005; Naumova
99 et al., 2005; Novo et al., 2009; Ropars et al., 2015). Domesticated fungi also have
100 lost parts of genes no longer useful in the food environment; for example a cheese
101 *P. roqueforti* population and *P. camemberti* var. *caseifulvum* are no longer able to

102 produce some of their toxins due to deletions in the corresponding genes (Gillot et
103 al., 2017; Ropars et al., 2020b). Such losses are likely due to relaxed selection in
104 terms of competition ability in cheese, in which desired fungi are often inoculated in
105 large quantities compared to possible competitors. Bottlenecks and degeneration
106 have also been documented in domesticated fungi, with reduced fertility and genetic
107 diversity in the cheese fungi *P. roqueforti* and *P. camemberti* (Dumas et al., 2020;
108 Ropars et al., 2020b).

109 While several cheese-making fungi have been studied recently, it is important to add
110 study cases in additional lineages, as it allows addressing the question of whether
111 adaptation to a similar medium leads to convergent traits. In the case of cheese-
112 making fungi, one can expect convergence for example for more or less rapid growth
113 on cheese, higher proteolysis and lipolysis abilities, higher competitive abilities and
114 greater production of positive volatile compounds (Ropars et al., 2020a, 2020b).

115 *Geotrichum candidum* (teleomorph *Galactomyces candidus*) is a dimorphic fungus
116 (i.e., able to grow as a yeast or a mycelial form), commonly used for cheese-making,
117 but also thriving in other environments such as soil, plants and fruits. *Geotrichum*
118 *candidum* is naturally present in raw milk and is also often added as a starter culture
119 for the production of semi-hard, mold-ripened, smeared soft cheeses, fresh goat and
120 ewe cheeses. Analyses based on genetic markers have revealed genetic
121 differentiation between cheese and wild strains (Alper et al., 2013; Jacques et al.,
122 2017; Perkins et al., 2020; Tinsley et al., 2022). Phenotypic diversity within *G.*
123 *candidum* has been reported in terms of carbon and nitrogen assimilation, lipolysis
124 and proteolysis (Boutrou and Gueguen, 2005; Perkins et al., 2020). However, it has
125 not been tested whether *G. candidum* cheese populations have evolved specific
126 traits that could be beneficial for cheese-making.

127

128 By analyzing the genomes of 98 strains isolated from different kinds of cheeses and
129 other environments, we confirmed the genetic differentiation between cheese and
130 wild strains. Within the cheese clade, we identified three differentiated cheese
131 populations, including one with all goat cheese strains, as well as footprints of
132 recombination and admixture. The genetic diversity in the cheese clade remained
133 high indicating a lack of strong bottlenecks. Commercial strains were scattered within
134 the cheese clade, some corresponding to hybrid strains. We found phenotypic
135 differentiation between cheese and wild populations, and between cheese

136 populations, in terms of growth, proteolysis and volatile compounds. We revealed the
137 loss, in the cheese clade, of two tandem beta lactamase-like genes involved in
138 xenobiotic clearance. Altogether our findings suggest the existence of genuine
139 domestication in *G. candidum*, resulting in both the genetic and phenotypic
140 differentiation of cheese strains from their wild counterparts, and their convergence
141 with other domesticated cheese fungi. We also found diversification within the
142 cheese clade, with three genetic clusters with contrasted traits and levels of diversity.
143

144 Results

145 Genetic differentiation between wild and cheese strains in 146 *Geotrichum candidum*

147 We collected and sequenced the genomes of 88 *G. candidum* strains with Illumina
148 technology and included in our analyses ten available genomes (Illumina and
149 PacBio) (Perkins et al., 2020). Our dataset included 61 strains isolated from different
150 kinds of cheeses (semi-hard, mold-ripened, smeared soft and fresh goat cheeses),
151 16 industrial strains used for cheese-making, seven strains from dairy products, four
152 strains from other food substrates (e.g., sausage or vegetables) and all the 10 wild
153 strains available in public collections worldwide (isolated for example from soil or
154 plant) (Table S1). We identified 699,755 SNPs across the 98 strains by mapping
155 against the CLIB 918 reference genome (cheese strain, NCBI accession:
156 PRJEB5752).

157 The maximum likelihood tree, principal component analysis (PCA) and neighbor-net
158 (SplitsTree) analyses all identified the same three clades (Figure 1A), with one
159 containing mostly wild strains (corresponding to the GeoC group identified previously
160 based on genetic markers) (Perkins et al., 2020), one composed of strains of varying
161 origins (i.e. dairy products and other environments, corresponding to the group
162 previously named GeoB) and one containing mostly cheese and dairy strains
163 (previously named GeoA). The larger sampling and the genome sequencing of the
164 present study further revealed genetic subdivision in the cheese clade, with three
165 clearly differentiated populations and several admixed strains (Figure 1B).

166 We performed an admixture analysis by inferring K populations, K ranging from two
167 to ten. At $K=3$, the cheese, mixed-origin and wild clades were separated (Figure S1).
168 At $K=5$, the cheese clade was divided into three genetic clusters, corresponding to
169 monophyletic groups in the maximum likelihood tree and well-separated genetic
170 clusters in the PCA and the neighbor-net (Figure 1 B, D). At higher K , new
171 populations inferred were either too small (two individuals) or not monophyletic.
172 Some cheese strains could not be assigned to any genetic cluster with the admixture
173 analysis and were placed on the PCA between the three well-delimited cheese
174 genetic clusters (Figure 1C-D), suggesting that they resulted from admixture events.
175 To test this hypothesis, we investigated whether these strains had mosaic genomes,
176 with different genomic regions assigned to distinct clusters. We calculated pairwise
177 identity between unassigned strains and the other strains, computing mean identity
178 to the different genetic clusters along scaffolds using sliding windows. For all
179 unassigned strains in the cheese clade, we observed shifts in identity values along
180 scaffolds, confirming that these strains are the results of admixture between clusters
181 (Figure S2). In contrast, the three unassigned strains outside of the cheese clade did
182 not show changes in similarity level to the different clusters along their genome;
183 these strains may belong to yet additional genetic clusters that could not be
184 distinguished by the analyses because too few strains belonged to these clusters in
185 the sampling (Figure 1B).
186 We found no particular cheese type distribution among the three cheese populations,
187 except that all strains from goat cheeses clustered in the Cheese_1 population. The
188 wild clade was the most differentiated population from all other *G. candidum*
189 populations with F_{ST} values above 0.70 (Table S2). Its differentiation level was
190 similar to that found between the domesticated *P. camemberti* mold and its wild
191 closest relative species, *P. fuscoglaucum* ($F_{ST} = 0.83$; $d_{xy} = 6E-03$), and much higher
192 than the differentiation between the cheese Roquefort population and the
193 lumber/food spoiler population in *P. roqueforti* ($F_{ST} = 0.27$). The percentage of private
194 SNPs in the five populations was also high (Table S3). F3 tests based on the
195 number of shared sites (Table S4) supported the differentiation between these
196 populations.

197 High nucleotide diversity within cheese populations and
198 footprints of recombination

199 The overall diversity in the cheese clade ($\pi=2.82\text{E-}3$) was higher than in the wild
200 population ($\pi=2.12\text{E-}3$). Each of the three cheese populations of *G. candidum* had
201 however reduced nucleotide diversities compared to wild and mixed-origin
202 populations (Table S5), by at least a factor of two. The Cheese_2 population showed
203 the lowest genetic diversity ($\pi=4.82\text{E-}4$), by a factor of four compared to the two
204 other cheese populations (Table S5), being of the same order of magnitude as in the
205 Roquefort *P. roqueforti* population (Dumas et al., 2020). The Cheese_1 population
206 had a nucleotide diversity ($\pi=1.26\text{E-}3$) similar to that in the domesticated cheese
207 species *P. biforme* ($\pi=1.09\text{E-}3$), whereas the Cheese_3 population ($\pi=1.92\text{E-}3$)
208 was genetically as diverse as *P. fuscoglaucum* ($\pi=1.93\text{E-}3$), the closest wild
209 relative of the clonal lineage *P. camemberti* (Ropars et al., 2020b).

210 *Geotrichum candidum* is a heterothallic fungus, meaning that sexual reproduction
211 can only occur between two haploid cells carrying different mating types. Two mating
212 types have been described in *G. candidum* (Morel et al., 2015): MATA, encoded by a
213 HMG box gene homolog to the MATA2 *Kluyveromyces lactis* allele, present in CLIB
214 918 (sequence id: HF558448.1), and MATB, encoded by an alphabox gene homolog
215 to the MAT α 1 *S. cerevisiae* allele, present in the strain CBS 615.84 (sequence id:
216 HF558449.1). In the Cheese_2 population, we found a significant departure from the
217 1:1 mating-type ratio expected under regular sexual reproduction; all the 12 strains
218 carried the MATB allele, suggesting that this population is at least partly clonal
219 (Table S6). The absence of linkage disequilibrium decay with physical distance
220 between two SNPs (Figure S3), together with the absence of reticulation in the
221 neighbor-net (Figure 1), are also consistent with a lack of recombination in the
222 Cheese_2 population. However, pairwise homology index (PHI) tests, testing with
223 permutations the null hypothesis of no recombination by looking at the genealogical
224 association among adjacent sites, were significant in all the *G. candidum* populations
225 (Table S7); this indicates that recombination did occur at least in a recent past in the
226 Cheese_2 population.

227 We did not detect any accumulation of nonsense or missense mutations in any
228 population compared to silent mutations (Felsenstein, 1974; Table S8), while
229 degeneration can be expected to be particularly strong in clonally replicated

230 populations as recombination allows more efficient selection. None of the genes that
231 presented nonsense mutation had predicted functions that could be detected as
232 specific either to the wild or cheese environments (Figure S4). This also suggest that
233 the absence of sexual reproduction in the Cheese_2 population may be too recent to
234 observe degeneration.

235 In contrast to the Cheese_2 population, we found both mating-type alleles in
236 balanced proportions in both Cheese_1 and Cheese_3 populations (Table S6) and
237 we observed sharp decays in linkage disequilibrium (LD) with genomic distance,
238 although LD levels remained higher than in the mixed-origin and wild populations
239 (Figure S3). We observed reticulations in the neighbor-net network within
240 populations and, to a lesser extent, between populations (Figure 1A).

241

242 As previously mentioned, the 16 commercial starter strains in our *G. candidum*
243 dataset were scattered in the maximum likelihood tree (in yellow, Figure 1B.a.) and
244 we detected above footprints of recombination in the Cheese_1 and Cheese_3
245 populations (Figure 1A, Figure S3). We nevertheless detected a few groups of
246 clonemates, by the lack of branches in the trees and the presence of fewer than
247 1,200 SNPs between strains (Figure 1; Table S1, clonal group column). As strains
248 within these clonal lineages were isolated from different cheeses, it indicates that
249 some lineages may be clonally cultivated for cheese-making; some of the
250 commercial starter strains indeed clustered within these clonal groups ("\$" symbol on
251 Figure 1B). Within the admixed cheese strains, 19 out of 23 were part of clonal
252 lineages, suggesting that hybrid lineages may have been selected for beneficial traits
253 for cheese-making, as in other domesticated fungi (e.g. *S. pastorianus*; Gallone et
254 al., 2018).

255 Copy number variation: loss of two tandem beta lactamase-like 256 genes in the cheese populations and repeat expansion

257 Expansions of gene families involved in specific metabolism pathways, of
258 transposable elements and loss of genes no longer required in the new environment
259 can be involved in adaptation to new environments. For example, variations in gene
260 copy number were associated with the adaptation of *S. cerevisiae* to beer making,
261 with duplications of genes involved in maltose and maltotriose metabolism
262 specifically in domesticated beer strains (Gallone et al., 2016; Giannakou et al.,

263 2020; Gonçalves et al., 2016). We therefore looked for gene copy-number variation
264 (CNV) that differentiated wild and cheese populations, using 500 bp sliding windows
265 and two reference genomes, belonging to the Cheese_3 and the wild populations,
266 respectively (Table S9). Using the Cheese_3 reference, we found 61 CNV regions
267 (mean length of 1515 bp and 45 non-genic CNVs), encompassing in total 16 genes,
268 half having predicted functions, none being obviously related to cheese adaptation
269 (e.g. methylglyoxal reductase and tRNAs, Table S9). Using the wild genome
270 reference, we found 132 CNV regions (mean length of 1664 bp and 105 non genic
271 CNVs), encompassing 29 genes (seven with unknown functions).
272 One of these regions, 20 kb long, included only two genes, both matching the Pfam
273 hidden markov model for beta-lactamases; these two genes (g5112 and g5113)
274 were absent from all cheese populations, and were present in most wild strains
275 (except one that had partially the region) and in four strains belonging to the mixed-
276 origin population (Figure 2). The nucleotide identity between the two beta lactamase-
277 like genes was 93%. A third beta lactamase-like gene (g5111) was found
278 immediately next to this CNV region in all *G. candidum* strains, and displayed a
279 nucleotide identity of 87% with the two other beta lactamase-like genes within the
280 CNV. Surrounding these different genes, we found several *Tc1/mariner*, a
281 LINE/Tad1 and other DNA transposons, that may have contributed to the beta-
282 lactamase-like gene deletion (Figure 2). Fungal beta lactamase-like genes are
283 known to contribute to hydrolysis of microbial and plant xenobiotics, and thus may be
284 important in the wild environment to compete with other microorganisms (Gao et al.,
285 2017). The cheese populations may have lost these two copies of the beta-
286 lactamase genes due to relaxed selection; indeed, these functions may not be useful
287 in the cheese environment if *G. candidum* is inoculated in high quantity compared to
288 potential competitors.

289

290 *De novo* detection of repeats using the wild strain LMA-244 yielded a library
291 containing 107 types of repeated elements (including 15 types of DNA transposons
292 and 11 of retroelements and 3 rolling-circles). We identified 14 types of repeated
293 elements present in at least one other *G. candidum* genome with five times more
294 copies than in the LMA-244 wild strain (this threshold was set based on the fat tail of
295 the distribution; Figure S5). Among these 14 types of repeated elements, several
296 DNA transposons of the *Tc1/mariner* repeat family showed a cheese-clade specific

297 expansion (Table S10, Figure 3). Several unidentified, *Tad1* and *Helitron* repeat
298 types also showed expansions in the cheese clade, alongside a milder expansion in
299 the mixed origin clade. Such transposable element expansions in the cheese clade
300 could be due to relaxed selection (Baduel et al., 2019).

301 **Genomic footprints of adaptation: genomic islands of
302 differentiation in cheese populations and genes under positive
303 selection**

304 We looked for genomic regions with a greater differentiation or a lower genetic
305 diversity than the genomic background when comparing each of the three cheese
306 populations to the wild population, to detect footprints of divergent selection and
307 recent selective sweeps, respectively. We scanned the whole genome using–non-
308 overlapping windows and explored the windows with the 1% highest d_{xy} (high
309 differentiation) or 5% lowest π (low diversity) values. Regions of high differentiation
310 appeared as outliers in the distribution of d_{xy} values, representing a small peak of
311 high d_{xy} values (Figure S6), and were often located in non-genic or in low gene-
312 density regions (Figure S7). We however detected 69 genes in the high-
313 differentiation regions across the three cheese populations, including 26 genes with
314 predicted functions. Two of them encoded proteases, one of them being an ADAM
315 metalloprotease which was an enriched function in the high-differentiation regions
316 when compared to the rest of the genome , and the only one (Table S11). Proteases
317 are important in cheese-making as the breakdown of milk caseins greatly contributes
318 to cheese texture and decreases water activity by degrading proteins into molecules
319 with free carboxyl and amino groups (McSweeney, 2004). *Geotrichum candidum* is
320 prevalent during the amino-acid catabolism ripening step of Pelardon fresh cheese
321 (Penland et al., 2021), suggesting that *G. candidum* plays an important role in
322 proteolysis in cheese-making.

323 In the 198 windows representing the pooled set of the 5% lowest π values in the
324 three cheese populations, we detected 497 genes, 323 of which had predicted
325 functions Among the 323 annotated genes, five predicted proteases or lipases.
326 Although these functions were not enriched compared to the rest of the genome
327 (Table S11), this could still represent footprints of selection on some of these
328 individual genes. Lipases are key enzymes for cheese flavor as they enable the

329 breakdown of milk fats through fatty acid production (Collins et al., 2003), and are
330 thus crucial for cheese-making.

331 We searched for genes evolving under positive selection in terms of high rates of
332 non-synonymous substitutions by performing McDonald and Kreitman (MK) tests
333 (Table S12), comparing the mixed-origin population to each cheese population and
334 to the cheese clade as a whole. We detected 25 genes as evolving under positive
335 selection in at least one cheese population (9 for Cheese_1, 18 for Cheese_2, two in
336 Cheese_3 and one in all three cheese populations at once; Table S12). Among
337 them, a metalloendopeptidase evolved under positive selection in all three cheese
338 populations, likely playing a role in casein degradation through cell lysis (Dugat-Bony
339 et al., 2015; KUMURA et al., 2002). A Glucan 1,3-beta-glucosidase was also
340 detected as evolving under positive selection in the Cheese_2 population; this
341 enzyme could be involved in fungal inhibition through fungal cell degradation
342 (Adams, 2004). The other genes under positive selection had either no predicted
343 function or putative functions that could not be related to cheese adaptation (Table
344 S12).

345 Phenotypic differentiation between cheese and wild populations

346 Denser mycelial growth and/or faster proteolysis in cheese populations
347 of *Geotrichum candidum*

348 Strains selected by humans are expected to display specific traits beneficial for
349 cheese-making, such as faster growth in cheese at cave temperature or colonies of
350 attractive aspect or color. For example, the *P. camemberti* strains used for soft
351 cheese production were selected for their white and fluffy aspect, to make cheeses
352 more attractive to consumers compared to the blue-grey crust produced by the *P.*
353 *camemberti* ancestor (Pitt et al., 1986). In contrast, the ability to grow in harsh
354 conditions may have been lost in cheese strains due to relaxed selection, as often
355 reported for unused traits in human-made environments in domesticated organisms
356 (Gallone et al., 2018; Price, 2002; Ropars et al., 2015).

357 We therefore measured colony radial growth of 31 strains from the five *G. candidum*
358 populations on different agar media (cheese, rich and poor media) at different
359 temperatures. Wild populations grew faster than cheese populations on all media at
360 all temperatures, with a more pronounced difference at 25°C (Table S13, Figure S8).

361 This may result from trade-offs with other traits, such as a fluffier mycelium, i.e. more
362 vertical growth at the expense of less radial growth.

363 To test whether cheese populations had a denser mycelium or had become whiter
364 and/or fluffier, we compared the opacity of populations on cheese agar at cave
365 temperature (10°C), which integrates the brightness and fluffiness of a colony. The
366 Cheese_1 and Cheese_3 populations were not more opaque than wild populations
367 (Figure 4B). The Cheese_2 population had a significantly higher opacity than all
368 other *G. candidum* populations, except the mixed-origin population (post-hoc Tukey
369 test in Table S13). This represents a convergence with *P. camemberti* var.
370 *camemberti*, with independent evolution of similar phenotypes in two distantly related
371 cheese fungi.

372 Lipolysis and proteolysis are crucial biochemical processes during cheese ripening,
373 that influences flavor and texture of the final product; lipolysis and proteolysis
374 contribute to energy and nutrient uptake, and they affect the production of volatile
375 compounds, which are key flavor factors in cheeses (McSweeney, 2004). All
376 populations of *G. candidum* had similar lipolysis rates. The wild and mixed-origin
377 populations had degraded a significantly higher amount of proteins than the cheese
378 populations and we did not detect any proteolysis in the Cheese_2 population in our
379 experiment (Figure S9; Table S14).

380 No adaptation to high salt concentration or milk origin in cheese
381 populations

382 Cheese is a salty medium, with the percentage of salt varying from 0.5 g / 100 g for
383 Emmental to 3 g / 100 g for Roquefort. Salt is added on the surface of cheeses to
384 prevent the growth of contaminants, and cheese populations of *G. candidum* may
385 thus have adapted to high salt concentrations. Cheeses display a wide range of salt
386 concentrations so we tested four cheese media: unsalted, 1% salt as St Nectaire and
387 cream cheeses, 2% as Camembert and goat cheeses and 4% as Roquefort blue
388 cheeses. Wild populations grew faster than cheese populations in all salt
389 concentrations tested, as on YPD and minimal media (Figure S10A ;Table S13).

390 Because all strains sampled from goat cheeses belonged to the Cheese_1
391 population, we tested whether this population was able to grow faster on goat
392 cheese medium (1% salt) compared to other populations. We however found no
393 significant interaction between population and media on radial growth effects, i.e. no

394 specific adaptation to any particular kind of milk by the different populations (Figure
395 S10B).

396 Contrasting volatile compound production between wild and cheese
397 populations

398 Cheese ripening fungi, including *G. candidum*, contribute to cheese flavor through
399 the production of volatile compounds (McSweeney, 2004). Flavor is a crucial
400 criterion for cheese consumers and the cheese populations may have been selected
401 for desirable and specific volatile compounds. We grew 14 *G. candidum* strains on a
402 sterilized Camembert curd for 21 days at 10°C, *i.e.*, the ripening conditions of a
403 Camembert. On average across compounds, the wild population produced five times
404 higher quantities of volatiles than cheese populations. In order to compare the
405 relative proportions of the different compounds, which is also an important aspect for
406 flavor, we standardized the values by dividing all compound quantities by the total
407 quantity of volatiles per sample. The PCA indicated a differentiation between wild
408 and cheese strains in terms of volatile relative proportions (Figure 4D). The wild
409 population thus produced combinations of volatile compounds different from cheese
410 populations, with a high proportion of ethyl esters and ethyl acetates (Figure S10C),
411 known to be key compounds in fermented beverages such as wine and beer.
412 However, the impact of ethyl acetate on flavor is rather negative because it brings
413 solvent type notes. In cheese, these esters are never predominant (Liu et al., 2004;
414 Urbach, 1997). Ethyl esters are involved in anaerobic metabolism and may be
415 important for survival in the wild. By contrast, cheese strains produced many
416 alcohols, ketones, aldehydes and sulfur compounds (Figure S10C), known for
417 producing attractive flavors such as buttery, cheesy, fermented and aldehydic notes
418 (Curioni and Bosset, 2002). These volatile compounds, attractive in cheese, were
419 present in similar absolute quantities in wild strains but were in minor proportions
420 compared to other volatile compounds (Table S13), suggesting that cheese
421 populations evolved a lower production of undesirable and unused volatiles. The
422 overall balance between different volatile compounds is as important as volatile
423 absolute quantities for flavor perception (Liu et al., 2004). The dimethyl sulfone, a
424 compound previously reported to be produced during the catabolism of L-methionine
425 in *G. candidum*, is actually specifically produced by the cheese populations
426 (Bonarme et al., 2001; Penland et al., 2021).

427 Cheese populations inhibit more the growth of food spoilers than wild
428 populations
429 Cheese is a protein- and fat-rich medium, where many microorganisms, including
430 desired microbes, but also spoilers, can thrive and thus compete for nutrients; for
431 example, iron is limiting in cheese (Mayo et al., 2021; Monnet et al., 2015, 2012).
432 Cheese *G. candidum* populations may have been selected for excluding competitors
433 by inhibiting their growth (Boutrou and Gueguen, 2005). This fungus is known to
434 inhibit fungal and bacterial food spoilers, such as *Aspergillus* species and *Listeria*
435 *monocytogenes*, but these inhibitory activities have only been investigated in cheese
436 *G. candidum* strains so far (Dieuleveux et al., 1998; Nielsen et al., 1998; Omeike et
437 al., 2021). We therefore tested whether cheese populations displayed better growth
438 inhibition abilities than the wild population, using common fungal food spoilers as
439 competitors: *Debaryomyces hansenii*, *Penicillium biforme*, *P. roqueforti* and
440 *Scopulariopsis asperula*. We also tested whether growth inhibition of challengers
441 occurred via secreted and/or volatile compounds.

442 ***Inhibition by a mycelium lawn*** - In the first experiment, we grew challengers in a
443 central spot for 24h, alone or after spreading out *G. candidum* to let it grow as a
444 lawn; growth inhibition could occur in this setting by secreted molecules in the
445 medium, volatile compounds and/or a physical barrier to reach nutrients and grow.
446 The growth of *D. hansenii* was completely inhibited by all populations of *G.*
447 *candidum*. *Penicillium roqueforti* was strongly inhibited by *G. candidum*, in particular
448 by the Cheese_2 population that completely prevented *P. roqueforti* growth (Figure
449 5; Table S13). The growth of *Scopulariopsis asperula* and *P. biforme* was also
450 inhibited by *G. candidum*, with a significant difference between competitor growth
451 when spread alone or on a *G. candidum* lawn; the Cheese_2 population again
452 inhibited better competitors than any other population (Figure 5; Table S13). The
453 Cheese_2 population was the most opaque population on cheese and had a beta-
454 glucanase gene under positive selection, suggesting that challenger inhibition would
455 be due to either mycelium density as a physical barrier or degradation of competitor
456 cell wall.

457 ***Inhibition by volatile compounds*** - In a second experiment, we used splitted Petri
458 dishes (the two parts being separated by a plastic barrier) to test whether cheese
459 populations inhibited competitors to a greater extent than the wild population when
460 only volatile compounds can reach challengers. No significant growth difference was

461 observed between the growth alone and at the side of *G. candidum* for neither *S.*
462 *asperula* nor *P. roqueforti* (Figure 5B, Table S13). Only *P. biforme* showed a
463 significant growth inhibition by *G. candidum* in this setup (Table S13); such a growth
464 inhibition by *G. candidum* from an isolated Petri dish compartment indicates that
465 volatile compounds produced by *G. candidum* are able to impair the growth of some
466 competitors.

467 The two sets of experiments enabled us to assess by which mechanism *G.*
468 *candidum* can inhibit competitors: *P. biforme* growth was inhibited by *G. candidum* in
469 the splitted Petri dishes, suggesting that volatile compounds are able to impair its
470 growth. On the contrary, *P. roqueforti* and *S. asperula* were only inhibited by *G.*
471 *candidum* when molecules could diffuse in their medium and *G. candidum* mycelium
472 could form a physical barrier. The Cheese_2 population had a stronger inhibition
473 ability than the other *G. candidum* populations only when molecules could diffuse in
474 the medium and the mycelium could act as a barrier.

475

476 Discussion

477 Analyzing the genomes of 98 *G. candidum* strains isolated from different kinds of
478 cheeses, other food substrates and other environments revealed three monophyletic
479 clades, corresponding to strains isolated from cheese, mixed-origins (dairy and other
480 environments) and the wild, respectively. Within the cheese clade, we found three
481 distinct clusters and several admixed strains. In terms of genetic diversity, the mixed-
482 origin clade contained the highest diversity level, followed by the wild clade and then
483 the distinct cheese populations. However, the nucleotide diversity within each of the
484 cheese populations was still relatively high compared to other cheese fungi. Indeed,
485 the Cheese_2 population, while being four times less diverse than the two other
486 cheese populations, was as diverse as the Roquefort *P. roqueforti* cheese
487 population. The low diversity, the presence of a single mating type, a high level of
488 linkage disequilibrium and the absence of reticulation in the neighbor-net network
489 indicated a lack of recombination in the Cheese_2 population, that may thus
490 correspond to a clonally cultivated line for cheese-making. Additional, less
491 widespread clonal lineages may be cultivated for cheese-making, as we found
492 clonemates in all cheese populations, even in the clusters of intra-specific hybrids,

493 and including some commercial starter strains. This presence of commercial starter
494 strains in the clusters of intra-specific hybrids suggests that hybrid lineages may
495 have been selected for beneficial traits for cheese-making, as in other domesticated
496 fungi (e.g. *Saccharomyces pastorianus* used for the production of lager beer) but this
497 needs further investigation (Rainieri et al., 2006). The Cheese_1 population was as
498 diverse as the domesticated cheese species *P. biforme* and the Cheese_3
499 population as its wild relative *P. fuscoglaucum*. The genetic diversity of the cheese
500 clade as a whole was even higher than that in the wild population, which may be due
501 to the relatively low number of wild strains available and to the diversification of the
502 cheese clade into three varieties.

503 The genetic relationships between *G. candidum* populations and their contrasting
504 levels of diversity suggest that domestication occurred in several steps, with an
505 ancient domestication event separating the mixed-origin and the wild clades, then
506 the cheese and the mixed-origin clades, and yet more recently the three cheese
507 clusters. The domestication of *P. camemberti* similarly occurred in several steps, the
508 last steps involving the selection of a white and fluffy clonal lineage (Ropars et al.,
509 2020b). Considering the genetic diversity, the situation in *G. candidum* is however
510 very different from that of *P. camemberti* and *P. roqueforti*, for which a single or a
511 few clonal lineages are sold by spore producers for all kinds of cheeses (Ropars et
512 al., 2020b). The domestication of *G. candidum* did not involve strong bottlenecks that
513 occurred in other domesticated cheese fungi, such as *P. camemberti*, *P. roqueforti*
514 and *S. cerevisiae*, perhaps because it is more abundant spontaneously in raw milk
515 and because there has been a diversification into three genetically differentiated
516 varieties. It may also be that the domestication of the three *G. candidum* varieties is
517 more recent or has not involved a selection as strong as in other cheese fungi,
518 except perhaps in the Chhese_2 lineage. Sampling further cheese types, geographic
519 regions and wild environnements may reveal further genetic clusters.

520

521

522 We found evidence of phenotypic adaptation to cheese-making in *G. candidum*
523 cheese populations, with a slower growth on all media, even cheese, a prominent
524 production of attractive cheese flavors and a lower proteolytic activity compared to
525 the wild population. The slower growth and proteolysis activity may allow to prevent
526 a too fast degradation of products during maturation, as found in the Roquefort *P.*

527 *roqueforti* population (Dumas et al. 2020). The lack of adaptation to salt was also
528 found in the Roquefort *P. roqueforti* population and in dry-cured meat *Penicillium*
529 fungi and may be due to evolutionary constraints (Lo et al., 2022). We also found
530 genomic footprints of adaptation to cheese, with the presence of genomic islands of
531 differentiation in cheese populations and the loss of genes no longer required in the
532 human-made environment, i.e. tandem beta lactamase-like genes. This may
533 correspond to a first step of domestication.

534 The Cheese_2 population appeared to represent a more advanced state of
535 domestication than the other cheese populations, with much lower genetic diversity,
536 a fluffier mycelium, a higher competitive ability and a complete lack of proteolysis
537 activity. Denser mycelial growth leading to a fluffy aspect at the expense of less rapid
538 radial growth has also been selected in *P. camemberti* var. *camemberti* (Ropars et
539 al., 2020b), thus representing a convergent phenotype between two distantly related
540 cheese fungi. *Geotrichum candidum* is increasingly inoculated in milk in the place of
541 *P. camemberti* for industrial soft cheese production, as it provides the fluffy desired
542 aspect without the disadvantage of *P. camemberti* that browns the surface of
543 Camembert cheeses at the end of the ripening process (Carreira et al., 2002).
544 Proteolysis activity was also found lower in the Roquefort *P. roqueforti* population,
545 which may be beneficial to obtain not too degraded cheeses (Dumas et al. 2020).
546 The volatile proportions produced by cheese strains corresponded to attractive flavor
547 for cheese-making, in contrast to wild strains, as also documented in *P. roqueforti*
548 (Caron et al., 2021; Dumas et al., 2020). *Geotrichum candidum* is able to efficiently
549 inhibit the growth of common food spoilers, in particular *P. biforme* and *P. roqueforti*,
550 and the clonal Cheese_2 population is the most efficient competitor.

551

552 Our study shows that it is of fundamental importance to study further domestication
553 in various cheese fungi as it allows assessing whether independent adaptation
554 events to similar media and usage lead to evolutionary convergence, as this is an
555 important question in evolutionary biology (Alberto et al., 2018; Cresko et al., 2004;
556 Dyer et al., 2012; Elmer et al., 2014, 2010; Lin et al., 2012; Macías et al., 2021;
557 O’Quin et al., 2010; Thorpe et al., 2015). We found here both similarities
558 (convergence) and differences in the adaptation of *G. candidum* to cheese compared
559 to other cheese fungi. One of the most striking convergence was the evolution of a
560 fluffy and white mycelium as in *P. camemberti* with a trade-off with radial growth

561 (Ropars et al., 2020b). The higher competitive ability and lower proteolysis activity,
562 as well as the greater production of positive volatile compounds, also represent
563 interesting convergence events between multiple very distant fungal lineages,
564 indicating that evolution can be repeatable.

565

566 Our findings also have industrial implications, as they reveal high genetic diversity
567 and subdivision in a fungus widely used in the cheese industry, and the existence of
568 different varieties, *i.e.*, genetically and phenotypically different populations used for
569 cheese-making, with specific and contrasted traits beneficial for cheese-making. The
570 most fluffy and most competitive cheese population corresponded to a clonal lineage
571 which may represent the most recent selection event. The occurrence of
572 recombination between cheese strains is highly relevant for cheese producers as it
573 opens possibilities for further improvement for the agrofood sector. It is crucial to
574 maintain the larger genetic diversity in cheese *G. candidum* populations as genetic
575 diversity is essential in domesticated organisms for variety improvement and
576 diversification and to avoid degeneration (Harlan et al., 2012).

577

578 Material and Methods

579 Sampling

580 We isolated 53 strains from different kinds of cheeses (e.g. Camembert, Brie, Saint
581 Nectaire, Ossau Iraty, comté, bleu de chèvre) from five European countries, Canada
582 and the USA. Cheese crusts were left in the freezer for 24h to kill acarians. Then, we
583 diluted a piece of each crust in sterile water and spread 50 μ L of the suspension on a
584 malt agar Petri dish. When colonies appeared on the Petri dish, typically after three
585 days, we isolated the different morphotypes with a sterile toothpick and inoculated
586 them on new Petri dishes. After seven days of growth, we performed monospore
587 isolation by several dilution steps, in order to obtain separated colonies arising each
588 from a single spore. We identified the species of these pure strains after DNA
589 extraction by sequencing the 5' end of the nuclear ribosomal large subunit (LSU
590 rDNA) using the LROR/LR6 oligonucleotide primers (Vilgalys and Hester, 1990). We
591 also gathered 24 strains from INRAE, isolated from cheeses but also other

592 environments (e.g. sand, hay, rainforest) and 15 strains from a French spore seller.
593 We gathered all the wild strains available in public collections. For each strain, single
594 spore cultures were generated to ensure the presence of a single genotype before
595 DNA extraction.

596 The LMA-244 strain were inoculated on Yeast Extract Glucose (YEG) agar plates
597 (10 g.L-1 of yeast extract (Fischer Scientific), 10 g.L-1 of D-glucose (EMD
598 Chemicals) and 15 g.L-1 of Bacto agar (BD Diagnostics)) directly from 15% glycerol
599 (v/v) stock cultures stored at -80°C. The plates were incubated in the dark for five
600 days at 25°C.

601 DNA extraction, genome sequencing, assembly, annotation and
602 mapping

603 We used the Nucleospin Soil Kit (Macherey-Nagel, Düren, Germany) to extract DNA
604 from 88 *G. candidum* strains cultured for five days on malt agar. Sequencing was
605 performed with Illumina HiSeq 3000 paired-end technology (Illumina Inc.), 2x150 bp.
606 For the eight LMA strains, sequencing was performed using the Illumina HiSeq
607 paired-end technology.

608 All Illumina reads were trimmed and adapters cleaned with Trimmomatic v0.36
609 (Bolger et al., 2014). Leading or trailing low quality or N bases below a quality score
610 of three were removed. For each read, only parts that had an average quality score
611 higher than 20 on a four base window are kept. After these steps, only reads with a
612 length of at least 36 bp were kept.

613 Cleaned Illumina reads were assembled with SPAdes v3.15.3 not using unpaired
614 reads with “--careful” parameter.

615 For the LMA-244 strain, Genomic DNA was extracted using the Fungi/Yeast
616 Genomic DNA Isolation Kit (Norgen Biotek Corp.) with the following modifications.
617 Thirty milligrams of frozen grounded mycelium were thawed and homogenized in
618 500 µL of a 0.9% NaCl solution. The elution buffer was replaced by a Tris 10 mM
619 buffer (pH 8). Following the extraction step, gDNA suspensions were purified and
620 concentrated using Agencourt AMPure XP magnetic beads (Beckman-Coulter),
621 according to the manufacturer’s protocol.

622 DNA concentration and purity were measured using a NanoDrop ND-1000
623 spectrophotometer (Thermo Fisher Scientific Inc., Wilmington, U.S.A.) and a Qubit
624 Fluorometer 3.0 (Thermo Fisher Scientific Inc., Wilmington, U.S.A.).
625 The DNA library was prepared following the Pacific Biosciences 20 kb template
626 preparation using BluePippin Size-Selection System protocol and the Pacific
627 Biosciences Procedure & Checklist – Preparing Multiplexed Microbial Libraries Using
628 SMRTbell Express Template Prep Kit 2.0 protocol. No DNA shearing was performed.
629 The DNA damage repair, end repair and SMRT bell ligation steps were performed as
630 described in the template preparation protocol with the SMRTbell Template Prep Kit
631 1.0 reagents and the SMRTbell Express Template Prep Kit 2.0 reagents (Pacific
632 Biosciences, Menlo Park, CA, USA). The DNA library was size selected on a
633 BluePippin system (Sage Science Inc., Beverly, MA, USA) using a cut-off range of
634 10 kb to 50 kb. The sequencing primer was annealed at a final concentration of 0.83
635 nM and the P6 v2 polymerase was bound at 0.50 nM while the sequencing primer
636 was annealed with sequencing primer v4 at a final concentration of 1 nM and the
637 Sequel 3.0 polymerase was bound at 0.5 nM.. The libraries were sequenced on a
638 PacBio RS II instrument at a loading concentration (on-plate) of 160 pM using the
639 MagBead OneCellPerWell loading protocol, DNA sequencing kit 4.0 v2, SMRT cells
640 v3 and 4 hours movies.

641
642 Raw PacBio reads were corrected using Illumina reads already available and
643 described in a previous article (Perkins et al., 2020), with the default parameters of
644 the LoRDEC software and trimmed with Canu v1.6 (Koren et al., 2017; Salmela and
645 Rivals, 2014). Corrected and trimmed PacBio reads were then assembled using
646 Canu v1.6. Illumina polishing of the Canu assembly was performed using Pilon v1.22
647 (Walker et al., 2014). A final assembly step was then performed with the hybrid
648 assembler SPAdes v3.11.1 using the trimmed PacBio reads, the Illumina reads and
649 the Pilon corrected assembly as trusted contigs (Antipov et al., 2016; Prjibelski et al.,
650 2020) . Additionally, the CLIB 918 assembly (Bioproject PRJEB5752) was used as a
651 reference in the SPAdes script for the assembly of each *G. candidum* genome
652 (Morel et al., 2015). Scaffolds were filtered using the khmer software with a length
653 cut-off of 1,000 bp (Crusoe et al., 2015).

654

655 The LMA-244 PacBio assembly and reads have been deposited in GenBank:
656 nbPROJECT. To annotate short read assemblies and the LMA-244 genome, gene
657 prediction was performed using Augustus v3.4.0 (Stanke et al., 2008). The training
658 annotation file “*saccharomyces*” was used, with parameters as follows: “*--gff3=on*”,
659 “*--protein=on*”, “*--codingseq=on*”, “*--exonnames=on*”, “*--cds=on*” and “*--*
660 *uniqueGenelid=true*”. The output of Augustus and the CLIB 918 gff was provided to
661 Funannotate v1.8.9 (ref DOI:10.5281/zenodo.4054262) for functional annotation.
662 InterProscan was used under Funannotate pipeline locally (Blum et al., 2021).
663 Funannotate then searched in the Pfam database v34.0 and dbCAN database
664 version 10.0 with Hmmer v3.3.2 (Eddy, 2011; Huang et al., 2018; Mistry et al., 2021),
665 in database UniProt version 2021_03 and database MEROPS version 12.0 with
666 diamond blastp v2.0.11 (Rawlings et al., 2018; The UniProt Consortium et al., 2021),
667 eggNOG-mapper v2 on the database eggNOG 5.0 (Cantalapiedra et al., n.d.;
668 Huerta-Cepas et al., 2019).

669 Cleaned reads were mapped on the reference genomes CLIB 918 and LMA-244
670 using Bowtie2 v2.4.2 (Langmead and Salzberg, 2012). Maximum fragment length
671 was set to 1000 and the preset “very-sensitive-local” was used.
672 SAMtools v1.7 (Li et al., 2009) was used to filter out duplicate reads and reads with a
673 mapping quality score above ten for SNP calling and above one for CNV analyses.
674

675 In total, we have a dataset of 98 genomes, 88 being sequenced, eight from the
676 University of Laval (LMA strains: Bioproject PRJNA482576, PRJNA482605,
677 PRJNA482610, PRJNA482613, PRJNA482616, PRJNA482619, PRJNA490507,
678 PRJNA490528), one strain CLIB 918 from the Collection de Levures d'Intérêt
679 Biotechnologique (Bioproject PRJEB5752), and one of the strain Phaff72-186 from
680 the 1000 Fungal Genomes project (Bioproject PRJNA334358 NCBI).

681 SNP calling

682 Single nucleotide polymorphisms (SNPs) were called using GATK v4.1.2.0
683 HaplotypeCaller, which provides one gVCF per strain (option -ERC GVCF). GVCFs
684 were combined using GATK CombineGVCFs, genotypes with GATK
685 GenotypeGVCFs, SNPs were selected using GATK SelectVariants (option -select-
686 type SNP). SNPs were filtered using GATK VariantFiltration and options QUAL < 30,
687 DP < 10, QD < 2.0, FS > 60.0, MQ < 40.0, SOR > 3.0, QRankSum < -12.5,

688 ReadPosRankSum < -8.0. All processes from cleaning to variant calling were
689 performed with Snakemake v5.3.0 (script available at
690 https://github.com/BastienBennetot/Article_Geotrichum_2022).

691 Phylogenetic analysis

692 We inferred phylogenetic relationships among the 98 isolates using the dataset of
693 699,755 SNPs in a maximum likelihood framework using IQ-Tree2 v2.1.1 (Minh et
694 al., 2020). The tree has been midpoint rooted. The best-fit model chosen according
695 to Bayesian information criterion (BIC) was TVMe+R2 . Branch supports are ultrafast
696 bootstrap support (1000 bootstrap replicates, Minh et al., 2013).

697 Genetic structure

698 We used the dataset of 699,755 SNPs to infer population structure based on the
699 mapping on the CLIB 918 reference genome. We used Splitstree v4.16.2 (Huson
700 and Bryant, 2006) for the neighbor-net analysis. We used the R package Ade4
701 (Bougeard and Dray, 2018; Chessel et al., 2004; Dray et al., 2007; Dray and Dufour,
702 2007; Thioulouse et al., 2018) for principal component analyses (PCA, centered and
703 unscaled). We used NGSadmix v.33 (Jørsboe et al., 2017) from the ANGSD
704 (Korneliussen et al., 2014) package (version 0.933-110-g6921bc6) to infer individual
705 ancestry from genotype likelihoods based on realigned reads, by assuming a given
706 number of populations. A Beagle file was first prepared from bam using ANGSD with
707 the following parameters: “-uniqueOnly 1 -remove_bads 1 -only_proper_pairs 1 -GL
708 1 -doMajorMinor 1 -doMaf 1 -doGIf 2 -SNP_pval 1e-6”. The Beagle file was used to
709 run NGSadmix with 4 as the minimum number of informative individuals. Given the
710 high number of strains genetically highly similar among cheese strains (that may
711 represent clonal lineages), we randomly sampled one of the individuals for each
712 group of clonemates identified on the ML tree as having fewer than 90,000 SNPs
713 and filtered out the other strains (N=64 strains kept) to avoid biasing the analysis.
714 The analysis was run for different K values, ranging from 2 to 10. A hundred
715 independent runs were carried out for each number of clusters (K).
716 The nucleotide diversity π (Nei's Pi; Hudson et al., 1992; Nei and Li, 1979), the
717 Watterson's θ (Watterson, 1975), the fixation index F_{ST} (Hudson et al., 1992) and the
718 absolute divergence d_{XY} (Nei and Li, 1979) were calculated using the *popgenome*
719 package in R (Pfeifer et al., 2014). Fixed, private and shared sites were counted

720 using custom scripts available at
721 https://github.com/BastienBennetot/fixed_shared_private_count, with bcftools
722 version 1.11 (using htslib 1.13+ds). F3 tests were computed using the *admixr*
723 package v0.9.1. The pairwise homology index (PHI) test was performed using
724 PhiPack v1.1 and CLIB 918 genome as reference.
725 Linkage disequilibrium was calculated using vcftools v0.1.17 with the --hap-r2
726 parameter and a minimum distance between SNPs of 15,000 bp. Values were
727 averaged when SNPs had the same distance.
728 Pairwise identity between an admixed strain and each non-admixed strain was
729 calculated using overlapping sliding windows of 30 kb span and 5 kb step. Admixed
730 clusters are indicated in Table S1. The custom script is available on
731 https://github.com/BastienBennetot/Article_Geotrichum_2022

732 Copy number variation and identification of premature stop codons in
733 CDS
734 Copy number variation (CNV) was analyzed using Control-FREEC v11.6 with the
735 following parameters: ploidy was set to 1, non-overlapping windows of 500 bp,
736 telomeric and centromeric regions were excluded, expected GC content was set
737 between 0.25 and 0.55, minimum of consecutive windows to call a CNV set to 1.
738 This analysis was performed using as references the CLIB 918 (cheese_3) and
739 LMA-244 (wild) genome sequences. CNVs were classified in different groups when
740 the median of copy number was different between populations. We defined three
741 groups: regions for which copy number was different between wild and cheese
742 populations, between mixed-origin and cheese populations and when at least one
743 cheese population differed from another population. For each InterPro term present
744 in these regions, we performed enrichment tests, i.e., a fisher exact test comparing
745 the number of a particular InterPro term found in these regions and the whole
746 genome (Table S9).

747
748 We used snpeff (Cingolani et al., 2012) to assess how each SNP affected the coding
749 sequence of predicted proteins, in the vcf file containing all SNPs and all genomes of
750 our dataset. We detected premature stop codons in the 7,150 CDS of the CLIB 918
751 genome and the 5,576 CDS of the LMA-244 genome using a custom script and
752 bcftools v1.11.

753 Analyzing the repeat landscape

754 In order to *de novo* detect repeats within *G. candidum*, RepeatModeler (v2.0.2; [Flynn](#)
755 [et al., 2020](#)), using the ncbi engine (-engine ncbi) and the option -LTRStruct, was run
756 on the pacbio genome assembly of LMA 244 generating a library of 176 repeats. The
757 repeat redundancy was reduced using cd-hit-est, as described in Goubert et al.,
758 giving a final library of 108 repeats ([Goubert et al., 2022](#)). To estimate the per strain
759 copy number of each repeat, illumina reads were aligned using bwa mem (v0.7.17;
760 [Li, 2013](#)) to the repeat library and the median coverage for each repeat was then
761 normalized by the LMA 244 genome wide median coverage.

762 Detecting positive selection

763 The assemblies LMA-317, LMA-77 and LMA-563 have been excluded for this
764 analysis because of a N50 under ten kb. All the 437441 predicted protein sequences
765 from the 66 genomes of all cheese clades and mixed-origin clade were searched
766 against each other with BLASTP using diamond v0.9.36 and clustered into
767 orthologous groups using Orthogog v1.0.3 ([Ekseth et al., 2014](#)). For these analyses,
768 we only kept single-copy orthologs shared between two populations. We compared
769 the mixed origin population to each cheese population and the cheese clade.
770 Multiple nucleotide sequence alignments with predicted gene sequences were then
771 constructed using MACSE v2.0.3 with default parameters ([Ranwez et al., 2018](#)). We
772 performed an approximative MacDonald Kreitman tests using the R package
773 PopGenome ([Pfeifer et al., 2014](#)). The approximation comes from the fact that only
774 codons with a single SNP are examined. The assumption of this version of the test is
775 that the probability that two SNPs will appear in the same codon is very low. To
776 identify genes evolving under positive selection in *G. candidum* genomes, a, i.e. the
777 representation of the proportion of substitutions driven by positive selection was
778 used. Genes with an alpha under 0 were filtered out. Of these genes, only those with
779 a Fisher's test p-value under 0.05 were kept.

780 Phenotypic characterization

781 Sampling and strain calibration

782 We used 36 *Geotrichum candidum* strains for laboratory experiments: seven from
783 the Cheese_1 population, five from the Cheese_2 population, eleven from the
784 Cheese_3 population, eight from the mixed-origin population and five from the wild
785 population (Table S1). This set encompassed 26 strains isolated from dairies, one
786 from other food environments and nine isolated from environments other than food.
787 Experiments were initiated with spore suspensions calibrated to 1.10^6 spores/mL
788 with a hemocytometer.

789 Media preparation

790 All media were sterilized in an autoclave at 121°C for 20 minutes except those with
791 cheese or milk for which the autoclave was run at 110°C for 15 minutes to avoid

792 curdling. Each 94mm-diameter Petri dish was filled with 25mL of the appropriate
793 medium. Cheese medium was prepared as follows for 800mL: 300g of unsalted
794 cream cheese from La Doudou farm in Cheptainville, 16g agar, 8g NaCl dissolved in
795 200mL of deionized water. Deionized water was added to reach 800mL. pH was
796 adjusted to 6.5 and drops of blue food dyes were added to enable fungal colony
797 measures (white medium and white colonies are not distinguishable). Yeast Peptone
798 Dextrose (YPD) medium was prepared as follows for 1L: 10g Yeast extract, 10g
799 Bacto Peptone, 10g glucose, 14g agar powder. Minimal medium was prepared as
800 described in “Improved protocols for *Aspergillus* minimal medium: trace element and
801 minimal medium salt stock solutions”, Terry W. Hill, Rhodes College, Etta Kafer,
802 Simon Fraser University. Tributyrin agar was prepared as follows: Tributyrin medium
803 33 g/L, neutral Tributyrin 10 g/L, Bacto Agar 15 g/L. Ingredients were bought at Nutri-
804 Bact company, Québec, Canada. Caseinate agar was prepared according to Frazier
805 and Rupp, modified as follows: Calcium caseinate medium 37.2 g/L, Bacto Agar 15
806 g/L. Ingredients were bought at Nutri-Bact company, Québec, Canada. For yogurt
807 media we used three different types of raw milk, i.e. sheep, goat and cow milks,
808 coming from d’Armenon farm near Les Molières (Esonne, France), Noue farm in
809 Celle les Bordes and Coubertin farm in Saint-Rémy-lès-Chevreuse respectively.
810 Each medium was prepared following the same procedure: 1L of milk was mixed
811 with 62.5g of Danone brand yogurt, heated for 5 hour at 43°C and stored in a fridge
812 before use. A subset of 300g of this preparation was used with 16g of agar powder,
813 8g of NaCl, 4 drops of blue food dye and filled up with deionized water to reach
814 800mL.

815 *Growth in different conditions and different media*

816 Petri dishes were inoculated with 10 μ L of the 1.10⁶ cells/mL in a 10% glycerol
817 solution. Inoculated Petri dishes were wrapped with plastic film before letting them
818 grow in the dark. A millimeter rule was used to measure two opposite diameters of
819 fungal colonies to estimate their growth. Means of these two measures were used for
820 statistical analyses.

821 To test media and temperature effect on growth, *G. candidum* strains were grown on
822 minimal, YPD and cheese media. We took pictures and measured their growth at
823 seven, 11 and 14 days for minimal, YPD and cheese media at 10°C (ripening cellar

824 temperature), at seven and 11 days for the cheese medium at 15°C and at seven
825 days for minimal, YPD and cheese media at 25°C (Figure S8).

826 To test salt tolerance, *G. candidum* strains were grown at 10°C on cheese media of
827 different salt concentrations: unsalted media, 1% salt as St Nectaire and cream
828 cheeses, 2% as Camembert and goat cheeses and 4% as Roquefort blue cheeses.
829 We took pictures and measured colony diameters after 14 days of growth.

830 To test adaptation of *G. candidum* populations to different milk origins, growth was
831 measured on different yogurt media made from goat, sheep and cow raw milk for
832 seven days at 25°C.

833 To test lipolytic and proteolytic activities of *G. candidum* populations, we grew strains
834 on tributyrin agar and caseinate agar, respectively. Each strain was inoculated in
835 triplicate Petri dishes that were let grow at 25°C for 14 days. The radius of lysis was
836 measured and the mean between triplicates was used for the analysis.

837

838 Pictures were taken using a Scan 1200 (Interscience). Petri dishes grown on cheese
839 were analyzed using IRIS (Kritikos et al., 2017) which measured Integral opacity
840 scores, defined as the sum of the brightness values for all the pixels within the
841 colony bounds.

842 *Volatile compounds analysis using Gas-chromatography mass-spectrometry (GC-
843 MS)*

844 Volatile compounds produced by *G. candidum* were analyzed using gas-
845 chromatography mass-spectrometry (GC-MS). Compounds were extracted and
846 concentrated by using a dynamic headspace (DHS) combined with a thermal
847 desorption unit (TDU). Strains were grown for 21 days at 10°C (minimum
848 Camembert ripening time) on a cheese agar medium made with Camembert-type
849 curds. After 21 days, each Petri dish content, with its medium and *G. candidum*
850 mycelium, was mixed with a fork for one minute, gathered in vials and immediately
851 frozen in liquid nitrogen. For each sample, three grams of frozen cultured media
852 were weighted and stored in vials with septum caps at -80°C. Sixteen hours before
853 analysis, samples were stored at 4°C. The Cheese_2 population was not tested in
854 this experiment because population delineation was not known at this time.

855 Dynamic headspace (DHS) conditions were as follows: Inert gas: He; Incubation:
856 30°C for 3min; Needle temperature: 120°C; Trap: nature tenax, 30°C, 450 mL He;

857 He flow: 30 mL/min; Dry purge : temperature 30°C, 850 mL He, He flow 50 mL/ min.
858 Thermal Desorption Unit (TDU) conditions were as follows: inert gas : He; Initial
859 temperature: 30°C, then 60°C/min until 290°C kept for 7 minutes; Transfer
860 temperature: 300°C. Cool Injection System (CIS) conditions were as follows: inert
861 gas : He; Initial temperature: -100°C, then 12°C/s until 270°C kept for 5 minutes. Gas
862 chromatograph (brand Agilent 7890B) was used with a polyethylene glycol (PEG)
863 type polar phase column (HP-Innowax, ref. Agilent 19091N-116I, 60mx0.32mm,
864 0.25µm film thickness). Helium flow was set at 1.6mL/min. Samples were injected in
865 splitless mode with a holding time of 1 minute. To optimize separation of
866 compounds, a specific program of the gas chromatography oven was used, with
867 initial temperature at 40°C for 5 minutes, rising temperature from 40°C to 155°C with
868 a slope of 4°C/min, rising temperature from 155°C to 250°C with a slope of 20°C/min
869 and then temperature was kept at 250°C for 5 minutes. A single quadrupole mass
870 spectrometer was used to determine m/z of sample molecules (Agilent, référence
871 5977B MSD). Molecules were identified using NIST libraries (NIST 2017 Mass
872 Spectral Library).

873 *Competition experiments*

874 To test the abilities of *G. candidum* populations to exclude other fungi by secreting
875 molecules or volatile compounds, we compared the growth of competitors when
876 grown alone and on a lawn of an already grown *G. candidum* mycelium. We
877 inoculated a cheese medium with 150µL of a *G. candidum* calibrated spore solution
878 (1.10⁶ spores/mL), spread evenly on the Petri dish. After 24h of growth, we
879 inoculated 10µL of a competitor spore solution (1.10⁶ spores/mL) in a single spot, in
880 the middle of the Petri dish. We used as competitors the following species and
881 strains: *Penicillium biforme* (ESE00018, ESE00023, ESE00125, ESE00222),
882 *Penicillium roqueforti* (ESE00645, ESE00925, LCP06040), *Scopulariopsis asperula*
883 (ESE00044, ESE00102, ESE00835, ESE01287, ESE01324) and *Debaryomyces*
884 *hansenii* (ESE00284, ESE00561, ESE00576; Table S15). For each competitor, two
885 Petri dishes were inoculated without any *G. candidum* as controls for measuring
886 growth without a lawn.
887 We took pictures of the Petri dishes at 6 days, when the competitor mycelium grown
888 alone was near the Petri dishes border; we measured colony size at 7 days for *P.*
889 *biforme* and *P. roqueforti* and at 19 days for *D. hansenii*, which grows more slowly.

890 To test the abilities of *G. candidum* populations to exclude other microorganisms by
891 producing volatile compounds, we set up an experiment with splitted Petri dishes
892 where only air can be shared between the two parts. In one part of the Petri dish, we
893 spread 75 μ L of a *G. candidum* spore solution (1.10⁶ spores/mL) and let it grow
894 during 24 hours before adding on the other part of the Petri dish a drop of 5 μ L of a
895 competitor spore solution (1.10⁶ spores/mL). For each competitor, two Petri dishes
896 were inoculated without any *G. candidum* as controls. We used as competitors the
897 following species and strains: *Penicillium biforme* (ESE00018, ESE00023,
898 ESE00125, ESE00222, ESE00423), *Penicillium roqueforti* (ESE00250, ESE00631,
899 ESE00640, ESE00925) and *Scopulariopsis asperula* (ESE00044, ESE00102,
900 ESE00835, ESE01287, ESE01324; Table S15). Petri dishes were grown at 10°C,
901 measured and pictured at 11 days for *P. biforme* and *P. roqueforti* and 19 days for
902 *Scopulariopsis asperula*.

903 *Graphics and statistical analyses*

904 Plots and statistical analyses were made using *ggplot2* (Wickham, 2016), *rstatix* and
905 *ggpubr* packages in the R environment. For ANOVAs, we used standard linear
906 models in which all explanatory variables were discrete, with explained variables
907 being radial growth for growth conditions (for media, temperature, salt content and
908 adaptation to milk experiments), integral opacity score (for opacity experiment),
909 relative proportions of volatiles compounds (for volatile compounds experiment) and
910 radial growth of the competitor (for competition experiments). The explanatory
911 variable common for all analyses was the 'population' of *G. candidum*. The variables
912 'medium', 'day' and 'temperature' were explanatory variables specific to the growth
913 analysis. The 'competitor species' variable was specific to competition analyses. All
914 variables and all interactions between them were implemented in the ANOVA and
915 non-significant interactions were subsequently removed before performing post-
916 ANOVA Tukey's honest significant difference (HSD) tests. The data normality of
917 residuals was checked; when residues deviated from normality (only for the opacity
918 experiment), we also ran non-parametric tests (Wilcoxon ranking tests) using R.
919 Radius of lysis for lipolytic and proteolytic activities experiments was often discrete,
920 strains either showing lytic activity or not at all. This is why we decided to transform
921 these data into qualitative discrete data in order to fit a generalized linear model with
922 a binomial function as logit. Growth time (7, 14 and 21 days) and temperature (15

923 and 25°C) were taken as random variables because no fit could be achieved with
924 little data and we wanted to test for population effect. Tukey contrasts were used to
925 compare population means of populations when population effect was significant.
926

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935

936 Author contributions

937 J.R. designed and supervised the study, and obtained funding. B.B., V.P., J.R. and
938 A.S. generated the data. C.G. provided strains from the CIRM-Levures INRAE
939 collection. B.B., J.-P.V., R.C.d.I.V. and S.O. analyzed the genomes. B.B., S.H., J.R.
940 and A.S. performed the experiments. B.B. analyzed the data from laboratory
941 experiments. M.H.L. and St.L. supervised the lipolysis and proteolysis analyses.
942 B.B., So.L. and A.-C.P. performed the volatile compound experiment. T.G.
943 contributed to interpretation and writing; B.B. and J.R. wrote the manuscript, with
944 contributions from all the authors.

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946

947 **References**

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1484

1485 Figure legends

1486 Figure main:

1487 Figure 1: Phylogenetic relationships and population structure of 98 strains of
1488 *Geotrichum candidum*, based on whole-genome data

1489 (A) Neighbor-net analysis based on a single nucleotide polymorphism (SNP)
1490 distance matrix. The scale bar represents 0.01 substitutions per site for branch
1491 lengths.

1492 (B) Genetic relationships among strains and population structure in *Geotrichum*
1493 *candidum* based on 699,755 SNPs. a) Maximum likelihood tree showing genetic
1494 relationships among the 98 isolates used in this study. All nodes are supported by
1495 bootstrap support >98% (bootstrap analysis with 1000 resampled datasets). The
1496 scale bar represents 0.05 substitutions per site for branch lengths. We used the
1497 midpoint rooting method to root the tree. The “\$” symbol pinpoints commercial starter
1498 strains and “*” the PacBio sequences. Genomes used as reference are written in
1499 bold. b) Population subdivision inferred for $K = 5$. Colored bars represent the
1500 coefficients of membership in the five gene pools based on SNP data.

1501 (C) Principal component analysis (PCA) based on 699,755 SNPs and 98 strains.

1502 Genetic clusters are represented by the same colors on all panels: light blue for
1503 Cheese_1, dark blue for Cheese_2, pink for Cheese_3, light grey for the mixed-
1504 origin population and dark grey for the wild population. Borders of points were
1505 colored in red when multiple points were overlapping due to clonal lineages (with a
1506 threshold set at <90,000 SNP for defining clonal strains). The shape of points
1507 represents the environment from which strains were sampled: circle for cheese/dairy,
1508 square for food and triangle for wild environment.

1509 (D) PCA based on the 323,385 SNPs when the dataset was restricted to the 78
1510 strains from the cheese clade

1511 Figure 2: Synteny of the beta lactamase-like genes lost in the cheese clade of
1512 *Geotrichum candidum*
1513 Synteny of the scaffold QQZM01000080.1 of the LMA-244 (wild) assembly against
1514 the scaffold CCBN010000010.1 of the cheese CLIB 918 (Cheese_3) assembly. The
1515 two scaffolds were shortened according to the range of nucleotide position on the
1516 right of each sequence. Beta-lactamase-like genes are annotated in red while other

1517 genes are displayed in blue. Black triangles indicate positions where repeated
1518 sequences were detected by tandem repeats finder (Benson, 1999). All strains from
1519 the cheese clades and 5 from the mixed-origin populations (LMA-317, ESE00274,
1520 MUCL8652 and ESE00540) carried the 20 kb deletion containing the g5112 and
1521 g5113 genes, both encoding for beta-lactamase like.

1522 Figure 3: Heatmap of different repeats that expanded in the cheese populations
1523

1524 From the repeat database based on the LMA 244 (wild) assembly, the copy number
1525 of each repeated element was estimated by aligning illumina reads of each strain.
1526 Only repeated elements that were at least in a 5-fold copy relative to the LMA 244
1527 genome were kept on the heatmap. The total number of copies is written in the
1528 center of each cell and filled with different shadings of grey to red depending on the
1529 relative expansion from the smallest copy number for each type of repeat. The
1530 maximum likelihood (ML) tree from the figure 1 (without admixed strains) was plotted
1531 below strains name to highlight the population's delineation.

1532 Figure 4: Differences in growth, opacity and volatile compounds among the five
1533 populations of *Geotrichum candidum*

1534 Each point represents a strain, horizontal dotted lines and vertical lines represent the
1535 mean and the standard deviation of the phenotype in the population, respectively.
1536 The number n at the bottom of plots indicates the number of strains used per
1537 population for measuring the corresponding phenotypes. The pairwise Tukey tests
1538 performed to assess whether there were mean differences between populations are
1539 indicated with brackets and their p-values are given.

1540 (A) Mean radial growth of the three cheeses, mixed-origin and wild populations on
1541 cheese (1% salt), yeast peptone dextrose (YPD) and minimal media at 25°C.

1542 (B) Differences in opacity between the three cheese populations, mixed-origin and
1543 wild populations on cheese medium (1% salt) at 10°C. Integral opacity is defined as
1544 the sum of the brightness values for all the pixels within the fungal colony bounds
1545 and measures the whiteness and density of the mycelium.

1546 (C) Petri dish of a strain (ESE00182) from the Cheese_2 population showing the
1547 fluffiness of the colony

1548 (D) Principal component analysis (PCA) of *Geotrichum candidum* strains based on
1549 their relative proportions of the different volatile compounds produced. Strains are

1550 plotted using the first two PCA axes.
1551 (E) Contribution of each volatile compound to the first two PCA axes. Compounds
1552 contributing the most to the differentiation were colored in red and labeled (i.e., those
1553 distant from 0 by an Euclidean distance ≥ 0.1).

1554 Figure 5: Competitive abilities of the different populations of *Geotrichum candidum*
1555 against *Penicillium biforme*, *P. roqueforti* and *Scopulariopsis asperula* challengers.
1556 (A) At the top, radial growth abilities of the competitors on lawns of *Geotrichum*
1557 *candidum* belonging to different populations (the three cheese, the mixed-origin and
1558 the wild populations). Each point represents a combination of the growth of a
1559 competitor strain on a lawn of a *G. candidum* strain. Horizontal dotted lines and
1560 vertical lines represent the mean and the standard deviation of the competitor growth
1561 in the population, respectively. The number n at the bottom of plots indicates the
1562 number of combinations of competitor-mat used per population. The competitor was
1563 inoculated in a central point 24h later on a lawn of *G. candidum*. At the bottom, from
1564 left to right, are shown pictures of *P. biforme* ESE00023 on a *G. candidum*
1565 ESE00186 lawn and without any lawn, *P. roqueforti* ESE00645 on a *G. candidum*
1566 ESE00186 lawn and without any lawn, and *S. asperula* ESE01324 on a *G.*
1567 *candidum* ESE00198 lawn and without any lawn, all on a salted cheese medium.
1568 B: At the top, radial growth abilities of competitors, with various *G. candidum* strains
1569 belonging to different populations being grown on the other side of splitted Petri
1570 dishes. The competitor was inoculated in a central spot on one side and the *G.*
1571 *candidum* strain was spread on the other side of the splitted Petri dish (a picture is
1572 shown as example below the figure). Media is not contiguous between the two sides
1573 of Petri dishes, so that inhibition can only occur by volatile compounds. *Penicillium*
1574 *biforme* and *P. roqueforti* were grown for 11 days while *S. asperula* was grown for 19
1575 days at 25°C.
1576 Each point represents a combination of the growth of a competitor strain on a *G.*
1577 *candidum* strain. Horizontal dotted lines and vertical lines represent the mean and
1578 the standard deviation of the competitor growth in the population, respectively. The
1579 number n at the bottom of plots indicates the number of combinations of competitor-
1580 mat used per population.

1581 Supplementary Figure:

1582 Figure S1: Population structure of *Geotrichum candidum*.

1583 Population subdivision inferred for K population ranging from two to six. Colored bars
1584 represent the coefficients of membership in the K gene pools based on genomic
1585 data. Each bar represents a strain, its name being indicated at the bottom of the
1586 figure. The new color for each K increment is indicated on the right part. The
1587 second order rate of change in the likelihood (ΔK) peaked at $K=6$. However
1588 the additional population distinguished at $K=6$ only encompassed two strains that
1589 were not that differentiated in the splistree (MUCL 14462 and CBS 9194; ; FIGURE
1590 1).

1591 Therefore, we chose to set the number of populations to five, the K value at which
1592 the structure was the strongest and the clearest, with three cheese populations,
1593 several admixed or hybrid cheese strains, a population of mixed origins and a wild
1594 population. These populations are indicated on the last rows.

1595 Below the admixture plot, two rows are indicating milk from which the strains was
1596 sampled and the population delineation.

1597 Figure S2: Pairwise identity between admixed and other strains, averaged by
1598 population of *Geotrichum candidum*.

1599 In order to see traces of introgression from different populations of *Geotrichum*
1600 *candidum* in some hybrid strains we computed the pairwise identity along the
1601 genome. Only the first scaffold of the CLIB 918 genome is shown in this figure.
1602 Values were averaged by population and when admixed strains had the same
1603 genetic background (name of strains are above each subplot) across 30 kb
1604 overlapping sliding windows with 5 kb steps. If no introgression happened, we expect
1605 the admixed strain to be equally distant to the different populations along the
1606 genome. Introgression results in genomic regions being atypically closer to a single
1607 population. All admixed strains within the cheese clades had introgression imprints
1608 while the other three strains (CBS 9194^T, MUCL 14462 and ESE01080) did not,
1609 meaning that they were either from different genetic backgrounds or introgressed
1610 with genetic backgrounds different from the five populations of *G. candidum*.

1611 Figure S3: Linkage disequilibrium against distance between SNPs for the five
1612 *Geotrichum candidum* populations.

1613 The r^2 (square of the correlation coefficient between two indicator variables) varies

1614 between 0 when two markers are in perfect equilibrium and 1 when they provide
1615 identical information. Under recombination, we expect r^2 to decrease exponentially
1616 with the distance between two SNP while in non recombining lineages linkage
1617 disequilibrium remains flat. All *Geotrichum candidum* populations r^2 decay curve
1618 behaved as recombining populations except the Cheese_2 population.

1619 Figure S4: SNPs inducing a premature stop codon for each *Geotrichum candidum*
1620 strain.

1621 In order to keep genes that carried a single nucleotide polymorphism (SNP) inducing
1622 a premature STOP codon in most of a population, we only showed STOP-inducing
1623 SNP that were at least in more than three strains. Columns represent strains and
1624 strains are ordered following the maximum likelihood (ML) tree. Cells are colored in
1625 black when the corresponding SNP induces a premature stop codon, white when
1626 there is no substitution for this site compared to the reference genome and grey
1627 when the SNP status could not be attributed during SNP calling, substitution that
1628 induces other effects on the protein sequence were not present in this subset of
1629 STOP-inducing sites. Each row is a site, when multiple SNPs induced stop codons in
1630 the same gene, the corresponding rows were grouped and separated from other
1631 genes by black lines. The analysis was done using either the CLIB 918 (Cheese_3)
1632 genome (A) or the LMA-244 (Wild) genome (B) as a reference.

1633

1634 Figure S5: Density of transposable elements copy number relative to the LMA-244
1635 strain

1636 To better show the fat tail distribution, the y-axis (density) was cut at 25%. A red
1637 dashed line indicates the threshold of five times more copy number than the LMA-
1638 244 strain. This threshold was set to identify repeats expansion related to small
1639 peaks on the density curve

1640 Figure S6: Distribution of absolute divergence d_{xy} values for different pairwise
1641 populations tested.

1642 Distribution of absolute divergence (d_{xy}) values for each pairwise population
1643 comparison from the genomic scan analysis. Density is given as an overlapping
1644 window number for a specific value of d_{xy} , each window being 7.5 kb wide with a step
1645 of 5 kb (optimal values based on variants densities). A black vertical line indicates
1646 the threshold of 1% highest values kept for the enrichment test.

1647 Figure S7: Genomic scan of within-population genetic diversity and between-
1648 population differentiation in *Geotrichum candidum*.

1649 Genomic of the nucleotide diversity π , watterson's theta θ_w , absolute divergence d_{xy}
1650 and fixation index F_{ST} (Hudson et al., 1992) along the scaffold 1 of the CLIB 918
1651 reference genome. At the bottom a guide indicates genic regions in black and non
1652 genic regions in white. 7.5 kb overlapping windows with a step of 5 kb (optimal
1653 values based on variant densities). On the bottom of the figure, genic regions are
1654 shown in black (not positively selected) or red (positively selected in the MK test
1655 analysis) rectangle. On the first panel (nucleotide diversity π), 5% lowest π values in
1656 the three cheese populations were highlighted by black dots. On the third panel
1657 (absolute divergence d_{xy}), 1% highest values of d_{xy} of each pairwise comparison
1658 were highlighted by back dots. These outliers were checked for gene presence and
1659 functions that could be involved in cheese adaptation and subsequently tested for
1660 enrichment within this subset of outliers compared to the whole genome

1661 Figure S8: Differences in growth among the five populations of *Geotrichum*
1662 *candidum* populations for different media and temperature

1663 Mean radial growth of the three cheese populations, mixed-origin and wild
1664 populations on cheese (1% salt), yeast peptone dextrose (YPD) and minimal media
1665 at 10, 15 and 25°C for 7, 11 and 14 days.

1666 Each point represents a strain, horizontal dotted lines and vertical lines represent the
1667 mean and the standard deviation of the population respectively. The number n at the
1668 bottom of plots indicates the number of strains per population used for measuring
1669 these phenotypes. To assess difference in means between populations, significant
1670 pairwise Tukey tests are indicated with brackets and p-values.

1671 Figure S9: Differences in lipolytic and proteolytic activity among the five populations
1672 of *Geotrichum candidum* populations for different growing time and temperature

1673 A: Lipolytic activity of *Geotrichum candidum* at 15 and 25°C and grown for 7, 14 and
1674 21 days.

1675 B: Proteolytic activity of *G. candidum* at 15 and 25°C and grown for 7, 14 and 21
1676 days.

1677 Each point represents a strain, horizontal dotted lines and vertical lines represent the
1678 mean and the standard deviation of the population respectively. The number n at the
1679 bottom of plots indicates the number of strains per population used for measuring
1680 these phenotypes. To assess difference in means between populations, significant

1681 pairwise Tukey tests are indicated with brackets and p-values. Length of lysis was
1682 measured as a radius between the center of the colony and the limit of the lysis area
1683 when lysis happened under the colony or measured as the thickness of the lysis
1684 area when there was no lysis under the colony.

1685 Figure S10: Differences in salt tolerance, growth on different milk and volatile
1686 compounds in detail among the five populations of *Geotrichum candidum*.

1687 Each point represents a strain, horizontal dotted lines and vertical lines represent the
1688 mean and the standard deviation of the phenotype in the population, respectively.
1689 The number n at the bottom of plots indicates the number of strains used per
1690 population for measuring the corresponding phenotypes. The pairwise Tukey tests
1691 performed to assess whether there were mean differences between populations are
1692 indicated with brackets and their p-values are given.

1693 (A) Mean radial growth at 10°C of the three cheese, mixed-origin and wild
1694 populations of *Geotrichum candidum* on cheese agar medium with different salt
1695 concentrations: unsalted, 1% salt for mimicking St Nectaire and cream cheeses, 2%
1696 salt for mimicking Camembert and goat cheeses and 4% salt for mimicking blue
1697 cheeses.

1698 (B) Mean radial growth at 10°C of the three cheese populations, the mixed-origin and
1699 the wild populations on yogurt agar media made with raw cow, goat and sheep milks.

1700 (C) Relative proportions of major volatile compounds in Cheese_1, Cheese_3,
1701 mixed-origin or wild populations of *G. candidum*. The volatile compounds shown
1702 were those contributing the most to the two first PCA axes or that are important for
1703 cheese ripening. For each compound, the related corresponding descriptor from
1704 thegoodsentscompany.com was added.

1705

1706

1707 Supplementary Table:

1708 Table S1: Description of the origin, phylogenetic assignation, sequencing statistics,
1709 and phenotype tested of *Geotrichum candidum* strains used in this study.
1710 Strains: Name of the strains; ESE collection number: collection number of strains
1711 kept at the author laboratory; Population: population attributed to the strains in this
1712 study; Clonal group: strains with the same number are clonal (less than 1,200 SNP
1713 between them); Species name: species identified either based on public collection or
1714 from ITS identification for collected strains in this study; Environment of sampling
1715 simplified: broader categories for source of sampling; Milk type: if extracted from
1716 dairy, indicates species from which was made the dairy; Location: Region or country
1717 of origin; Mating type: mating type identified in *Geotrichum candidum* either MATA or
1718 MATB (Morel et al., 2015).

1719 Table S2: Population genetics statistics estimating genetic differentiation (F_{st} , d_{xy}) in
1720 the five *Geotrichum candidum* populations and among the identified population
1721 within each of two other fungal species (*Penicillium camemberti* and *Penicillium*
1722 *roqueforti*) (Dumas et al., 2020; Ropars et al., 2020b)
1723 Table of F_{st} (fixation index) and d_{xy} (absolute divergence) (Hudson et al., 1992; Nei
1724 and Li, 1979). Values for *Geotrichum candidum*, *Penicillium roqueforti* (Dumas et al.,
1725 2020), *Penicillium camemberti* (Ropars et al., 2020b) are indicated for each
1726 population. Cells are colored from the lowest (white) and the highest (red) value of
1727 each indices.

1728 Table S3: Proportions of fixed, shared and private SNPs for each pair of populations
1729 of *Geotrichum candidum* population and for each pair of populations within each of
1730 two other fungal species (*Penicillium camemberti* and *Penicillium roqueforti*) (Dumas
1731 et al., 2020; Ropars et al., 2020b).
1732 Percent and number of fixed, shared or private single nucleotide polymorphisms
1733 (SNPs) for *Geotrichum candidum*, *Penicillium roqueforti* (Dumas et al., 2020),
1734 *Penicillium camemberti* (Ropars et al., 2020b) are indicated for each populations.
1735 The method of attributions of SNPs to different categories are available on
1736 https://github.com/BastienBennetot/fixed_shared_private_count.

1737 Table S4: F3 test performed on each trio of populations of *Geotrichum candidum*
1738 populations.

1739 The F3 test is a test between three populations. It tests whether a target population
1740 (C) is admixed between two source populations (A and B) and gives a measure of
1741 shared drift between two test populations (A and B) from an outgroup (C). In case of
1742 introgression, we expect negative F3 values. A Z-score is computed based on F3
1743 value and the standard error to assess the deviation from zero of the F3 value. If the
1744 Z-score is inferior to minus three then we can conclude a significant rejection of the
1745 Null hypothesis (F3 value is not negative).

1746

1747

1748 Table S5: Population genetics statistics estimating genetic diversity (π , watterson's
1749 θ) in the five *Geotrichum candidum* populations and among the identified population
1750 of three other fungal species (*Penicillium roqueforti*, *Penicillium camemberti* and
1751 *Saccharomyces cerevisiae*) (Dumas et al., 2020; Peter et al., 2018; Ropars et al.,
1752 2020b).

1753 Nucleotide diversity statistics (π and watterson's θ) are indicated for *Geotrichum*
1754 *candidum*, *Penicillium roqueforti* (Dumas et al., 2020), *Penicillium camemberti*
1755 (Ropars et al., 2020b) and *Saccharomyces cerevisiae* (Peter et al., 2018). Cells are
1756 colored from the lowest (white) and the highest (red) value of each indices.

1757 Table S6: Distribution of the two mating types in each population and proportion test
1758 of the deviation from 1:1 ratio.

1759 Table S7: Phi test of each population of *Geotrichum candidum* using the first scaffold
1760 of CLIB 918 assembly.

1761 Pairwise homoplasy index (PHI) test helps to discriminate between the presence or
1762 absence of recombination between a population (Bruen et al., 2006). It tests with
1763 permutations the null hypothesis of no recombination by looking at the genealogical
1764 association among adjacent sites. The PHI test was performed using PhiPack v1.1
1765 and the first scaffold of the CLIB 918 assembly as reference.

1766 Table S8: Number and percentage of SNPs classified by impact, functional class,
1767 effect and genomic regions for each *Geotrichum candidum* populations.

1768 Based on the 7,150 CDS of the CLIB 918 assembly, the effect of all variants was
1769 assessed. Each variant is categorized in different functional effects on the protein

1770 sequence. Results are meaned by population and shown either as the mean number
1771 of SNP or percentage. Results were computed using snpeff (Cingolani et al., 2012).
1772 (A) Total number of single nucleotide polymorphism (SNP) within each *G. candidum*
1773 populations.
1774 (B) Putative variant impact prediction. Different impacts categories are defined in
1775 Snpeff manual in 'Input & output files' section
1776 (C) Protein sequence effect of SNPs. Variants can either not change amino acid
1777 sequence (silent), change the amino acid (missense) or induce stop codons
1778 (nonsense)
1779 (D) Functional effect of SNPs defined in Snpeff manual in 'Input & output files'
1780 section
1781 (E) Position of the SNPs compared to genes

1782 Table S9: Number of copy number variants windows that differentiated *Geotrichum*
1783 *candidum* populations and test for enrichment of gene ontologies contained within
1784 these windows.
1785 Copy number windows (non-overlapping windows of 500 bp) were subsetted and
1786 classified in three comparison when the median copy number between the two
1787 clades compared was different: wild against all other populations (mixed origin and
1788 cheese populations), mixed-origin against cheese clade, and any pairwise difference
1789 within the different cheese populations (subtable A and B). For each comparison,
1790 when subsetted windows contained genes, gene ontologies (GO) of these genes
1791 were used to perform an enrichment test compared to the rest of the genome
1792 (subtable C and D). The same methodology was used for LMA 244 (Wild) or CLIB
1793 918 (Cheese_3) as reference assembly ensuring we see regions unique to the
1794 Cheese_3 and the Wild populations.
1795 (A) Number of windows subsetted in each clade comparison using LMA 244
1796 assembly as reference
1797 (B) Number of windows subsetted in each clade comparison using CLIB 918
1798 assembly as reference
1799 (C) Enrichment test on gene ontologies (GO) present within the subsets of windows
1800 in each clade comparison using CLIB 918 assembly as reference
1801 (D) Enrichment test on gene ontologies (GO) present within the subsets of windows
1802 in each clade comparison using LMA 244 assembly as reference

1803 Table S10: Repeat copy number for the different strains of *Geotrichum candidum*.

1804 In order to de novo detect repeats within *Geotrichum candidum*, RepeatModeler
1805 v2.0.2 (Flynn et al., 2020) was run on the pacbio genome assembly of LMA 244
1806 generating a library of 176 repeats. The repeat redundancy was reduced using cd-
1807 hit-est, as described in Goubert et al., giving a final library of 108 repeats (presented
1808 in column “Clustering of repeat family”) (Goubert et al., 2022). Sometimes the type
1809 and family of these repeats was inferred (column type of repeat and repeat family).
1810 To estimate the per strain copy number of each repeat, illumina reads were aligned
1811 using bwa mem (v0.7.17; Li, 2013) to the repeat library and the median coverage for
1812 each repeat was then normalized by the LMA 244 genome wide median coverage.
1813 Strain: name of the strains studied; relative median coverage: Coverage of all
1814 genomic reads mapped to the repeated sequence normalized by genome wide
1815 coverage before taking the median of all nucleotides of the repeated sequence
1816 (gives an idea of the copy number of the repeated element genome-wide); Copy
1817 number relative to LMA-244 strains: relative median coverage of the strain divided by
1818 the one of LMA-244 (Wild) strain to better emphasize repeat expansion within the
1819 cheese clade.

1820

1821 Table S11: Test for enrichment of gene functions that showed footprints of divergent
1822 selection and recent selective sweeps.

1823 We tested gene function enrichment that were detected either by keeping 1%
1824 highest of absolute divergence (d_{xy}) between cheese and wild strains (A) or 5%
1825 lowest nucleotide diversity (π) in the cheese populations but not in the wild
1826 population (B). Only functions related to lactose, lipid, protease were kept. Windows
1827 were 7.5 kb wide and overlapping windows with a step of 5 kb.

1828 (A) Test for enrichment of gene functions within the 1% highest Dxy windows when
1829 comparing a cheese population to the Wild population

1830 The subsetted windows for each test are based on the 1% highest Dxy windows for
1831 a specific comparison between a cheese and the wild population

1832 (B) Test for enrichment of gene functions within the 5% lowest Pi windows in cheese
1833 populations. Windows are excluded when they are also in the 5% lowest Pi of the
1834 wild population.

1835 The subsetted windows for each test are based on the 5% lowest Pi windows for a
1836 specific cheese population.

1837

1838

1839 Table S12: Results of the McDonald and Kreitman (MK) test for positive selection.
1840 Genes evolving under positive selection were assessed using McDonald and
1841 Kreitman (MK) tests. Using contrasting levels of polymorphism and divergence at
1842 neutral and functional sites, MK test estimates the fraction of substitutions at the
1843 functional sites that were driven by positive selection. When fisher.P.value was lower
1844 than 0.05, we considered that the gene was under positive selection. Only genes
1845 under positive selection were shown in the table. The mixed-origin population was
1846 compared to the cheese clade (A), Cheese_1 (B), Cheese_2 (C) and Cheese_3 (D).
1847 Ortho_id: identifier of the orthologous gene; P1_nonsyn: the number of non-
1848 synonymous polymorphisms in the first population; P2_nonsyn: the number of non-
1849 synonymous polymorphisms in the second population; P1_syn: the number of
1850 synonymous polymorphisms in the first population; P2_syn: the number of
1851 synonymous polymorphisms in the second population; D_nonsyn: the number of
1852 non-synonymous substitutions; D_syn: the number of synonymous substitutions;
1853 neutrality.index: quantifies the degree of departure from neutrality; alpha: the
1854 proportion of substitutions driven by positive selection; fisher.P.value: P-value of the
1855 MK test; GenID: gene identifier in the CLIB 918 assembly annotation; Contig Start:
1856 Start of the gene sequence; Stop: Stop of the gene sequence; Name: Name of the
1857 closest orthologous annotated genes; Product: Function of the protein; PFAM: pfam
1858 database annotation; InterPro: InterPro database annotation
1859
1860
1861

1862 Table S13: Anova table of all phenotypic linear models and post-hoc test table.
1863 All outputs of analysis of variance (ANOVA) (A) and post-hoc test (B) based on
1864 different linear models that were used for phenotypic analyses. Linear models tested:
1865 Effect of media, temperature on radial growth (1); effect of media and population on
1866 radial growth of *Geotrichum candidum* at 25°C (2); effect of salt content and
1867 population on radial growth (3); effect of milk origin and population on radial growth
1868 (4); effect of media and population on opacity (5); effect of population of *Geotrichum*
1869 *candidum* on competitor growth (6); competition abilities by volatiles on splitted Petri
1870 dishes (7); effect of population on relative proportions of volatile compounds (8).

1871 In ANOVA table, columns correspond to degree of freedom (Df), sum of squares
1872 (Sum Sq), mean square (Mean Sq), the F statistic (value) and the p-value of this
1873 test.

1874 Columns in post-hoc tables before the “term column” gives the condition kept for
1875 each single test. term: variable used for pairwise comparison; group1: the group that
1876 we compare against group2; group2: a second group that we compare to group1;
1877 null.value: value of group1 - group2 under the null.hypothesis; estimate: value of
1878 group1 - group2 using the data; conf.low: Lower value of the confidence interval;
1879 conf.high: higher value of the confidence interval; p.adj: adjusted p-value; p.ad.signif:
1880 significance of the adjusted p-value (p-value >0.05:n.s.; <0.05: *; <0.01: **; <0.001: ***,
1881 <1E-04: ****). Post hoc test for testing the effect of salt content and population on
1882 radial growth of *G. candidum*.

1883

1884 Table S14: Anova table and post-hoc test of lipolysis and proteolysis analyses.
1885 All outputs of analysis of variance (ANOVA) (A) and post-hoc test (B) based on
1886 different linear models that were used for lipolysis (1) and proteolysis (2) analyses.
1887 Radius of lysis for lipolytic and proteolytic activities experiments was often discrete,
1888 strains either showing lytic activity or not at all. Thus, data were transformed into
1889 qualitative discrete data and a generalized linear model with a binomial function as
1890 logit was fitted. No post-hoc tests were computed for the lipolysis analysis because
1891 there was no population effect.

1892 In ANOVA table we find columns σ^2 : mean random effect variance of the model; τ^2_{00} :
1893 The random intercept variance of a given variable, or between-subject variance; ICC:
1894 the intraclass correlation coefficient; N variable: the number of categories of the
1895 given variable; Observations: sample size of the model; marginal R^2 : represents the
1896 variance explained by the fixed effects; conditional R^2 : interpreted as the variance
1897 explained by the entire model (i.e. the fixed and random effects).

1898 In post hoc table we find columns Linear Hypotheses: null hypothesis considered for
1899 each post-hoc test; Estimate: Measured value; Std. Error: standard error of this
1900 measure; z value: Z statistic of this test.

1901 Table S15: Description of the origin and species of strains used in the competition
1902 experiments.
1903 ESE collection number: Author collection number for this strain; Previous name in
1904 public collection: name of the strain in other public collection; Species: Species of the
1905 strain; Origin of sampling: Environment of sampling for this strain; Milk (if cheese):
1906 species from which was collected the milk that was used to make the dairy where the
1907 strain was sample; Location of sampling; Location of the sampling; Cheese shop:
1908 where the cheese was bought for cheese strains; Information on sampling date:
1909 Sampling date when known for strains sampled years before the study

Figure 1: Phylogenetic relationships and population structure of 98 strains of *Geotrichum candidum*, based on whole-genome data

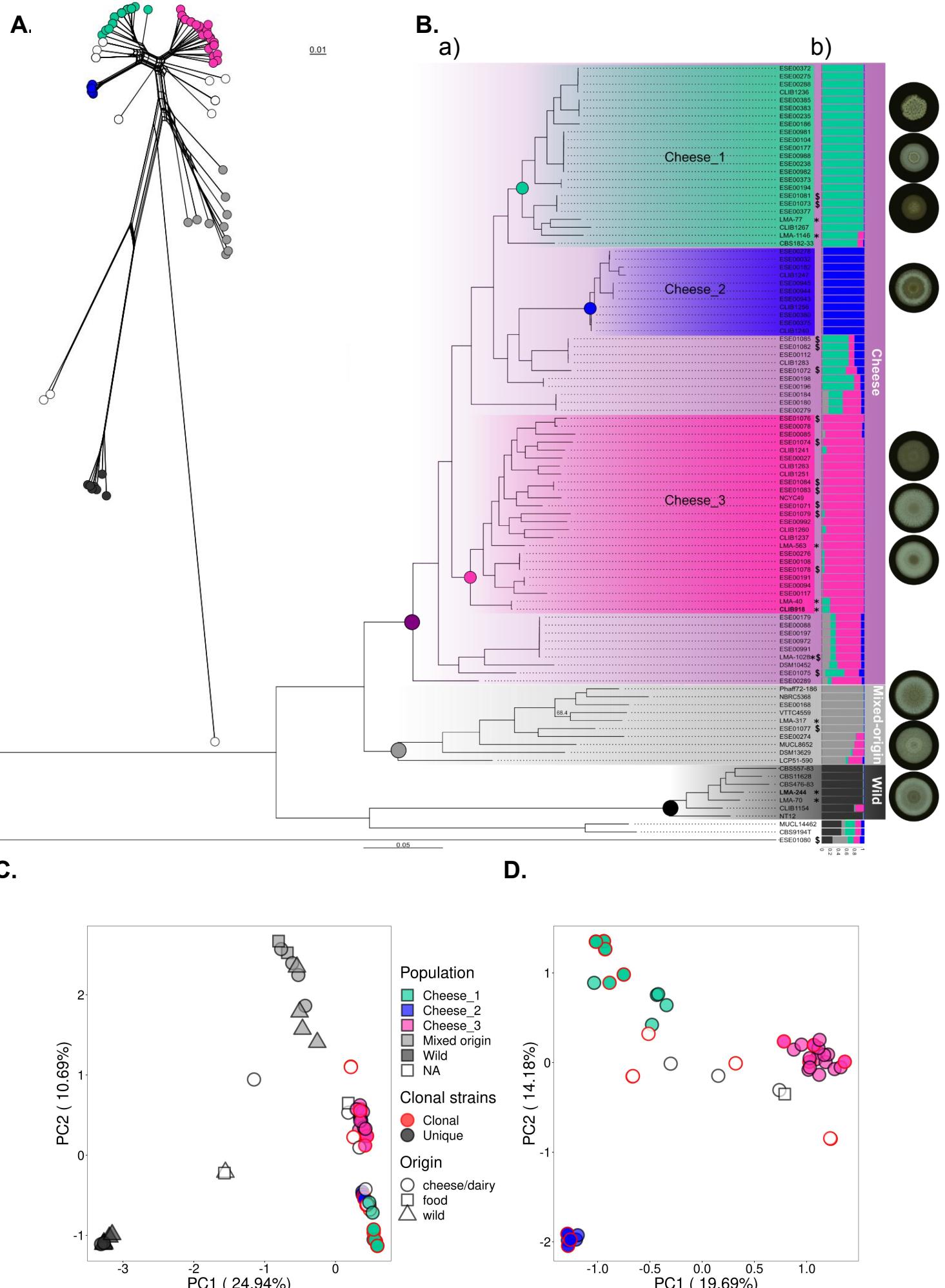


Figure 2: Synteny of the beta lactamase-like genes lost in the cheese clade of *G. candidum*

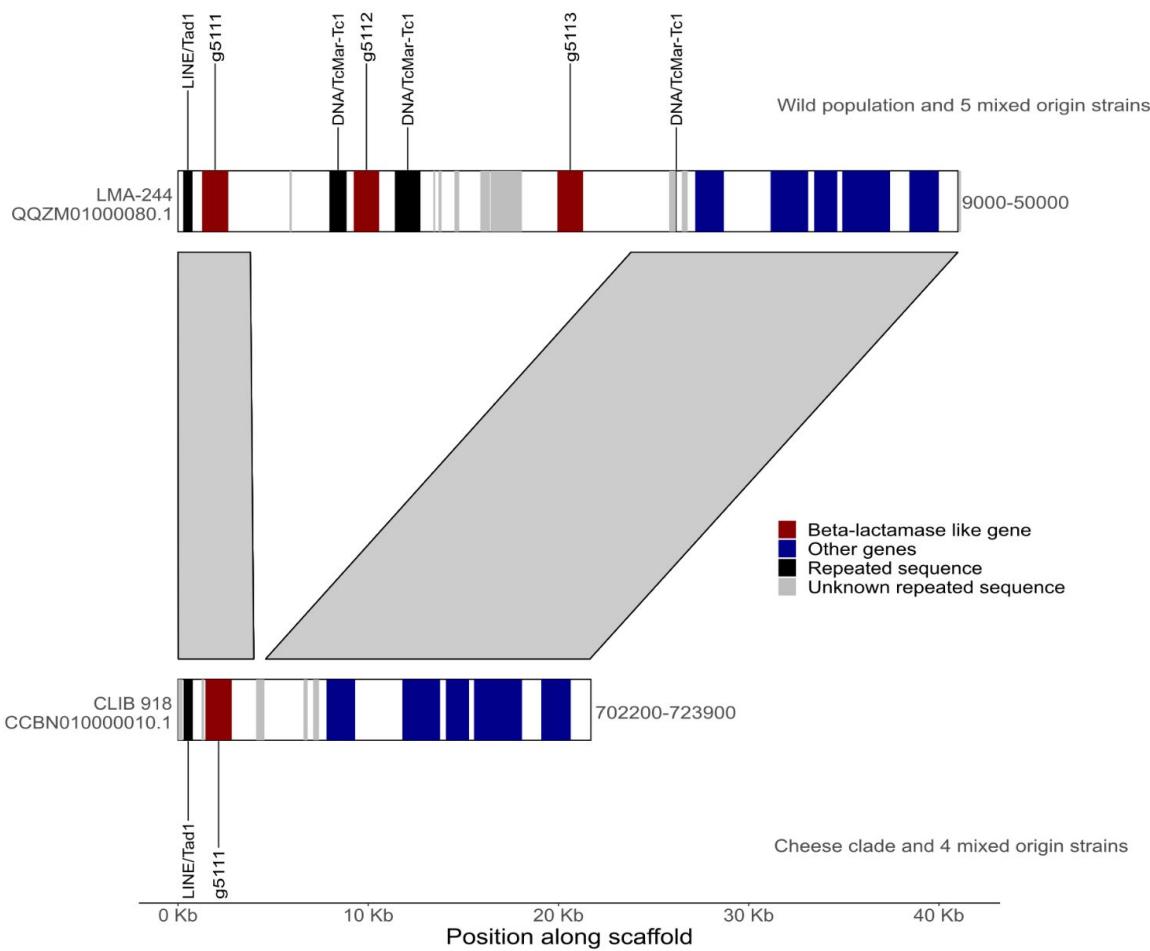


Figure 3: Heatmap of different repeats that expanded in the cheese populations

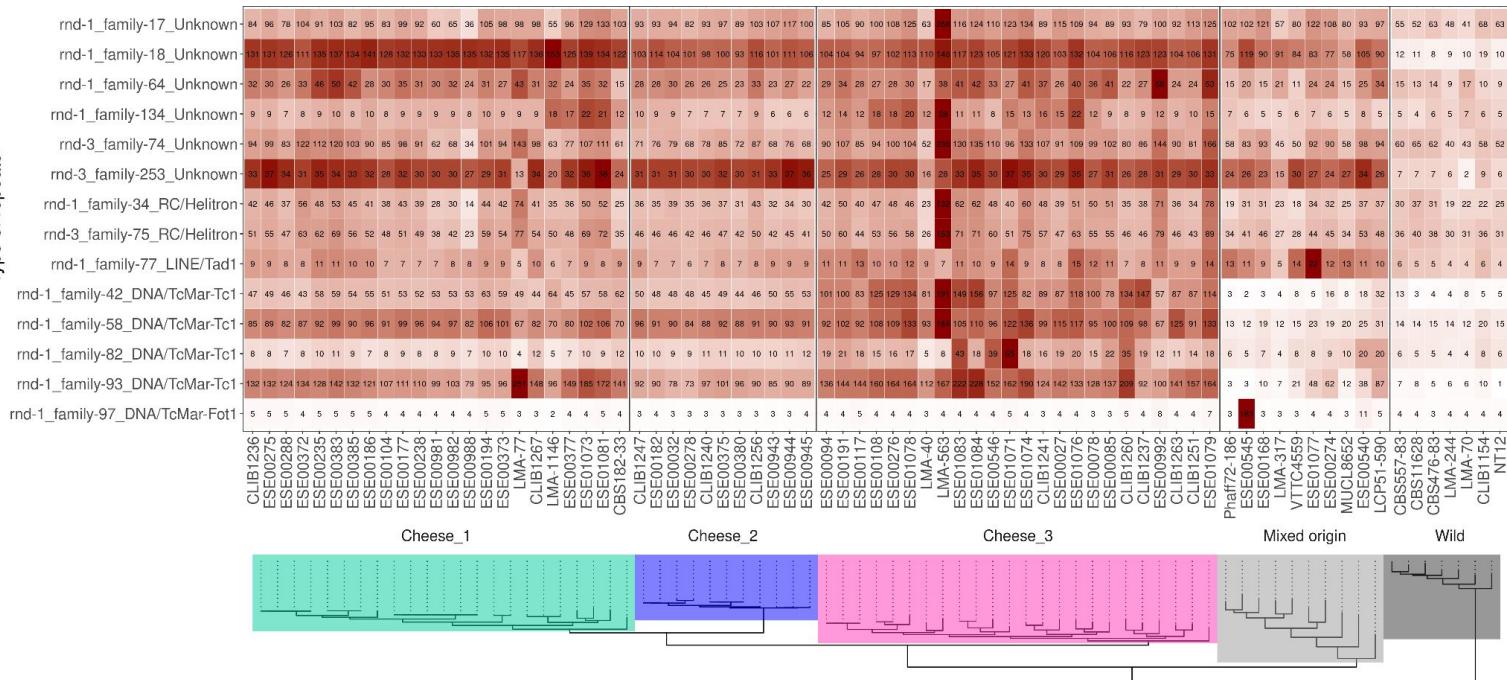
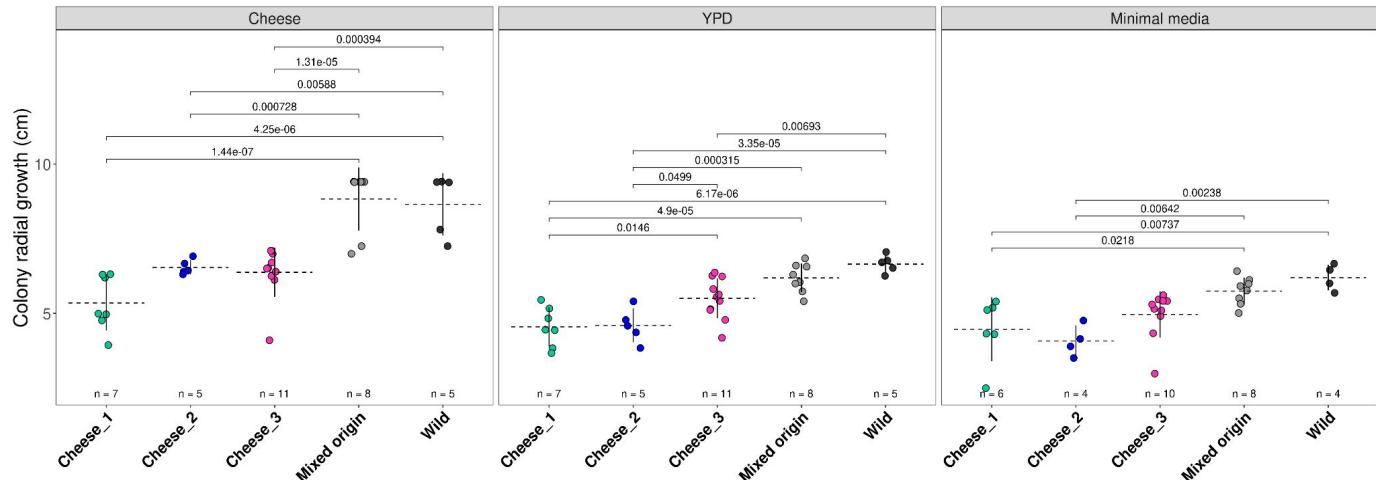
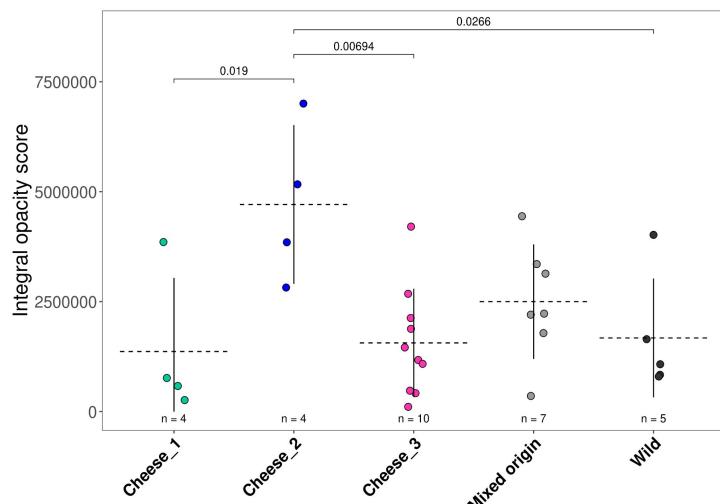


Figure 4: Differences in growth, opacity and volatile compounds among the five populations of *Geotrichum candidum*

A.



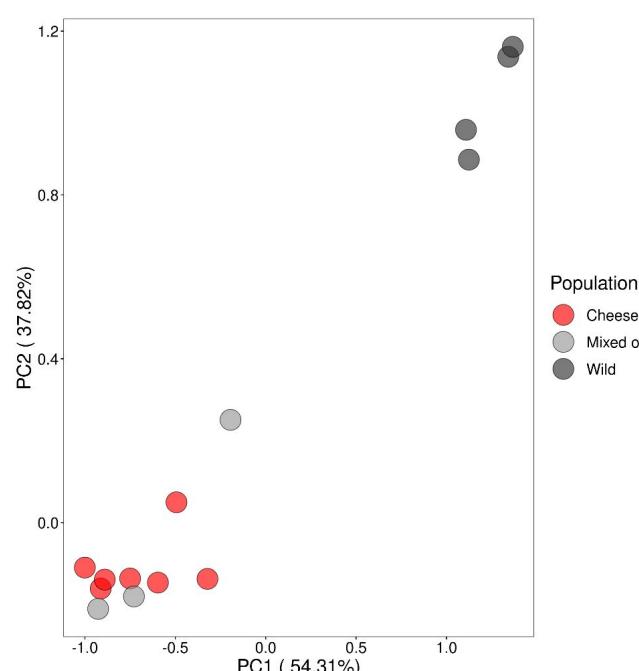
B.



C.



D.



E.

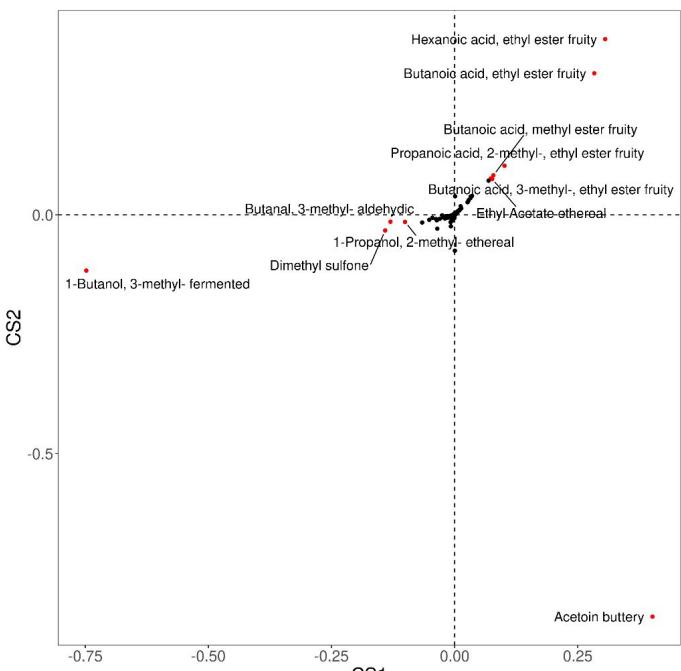
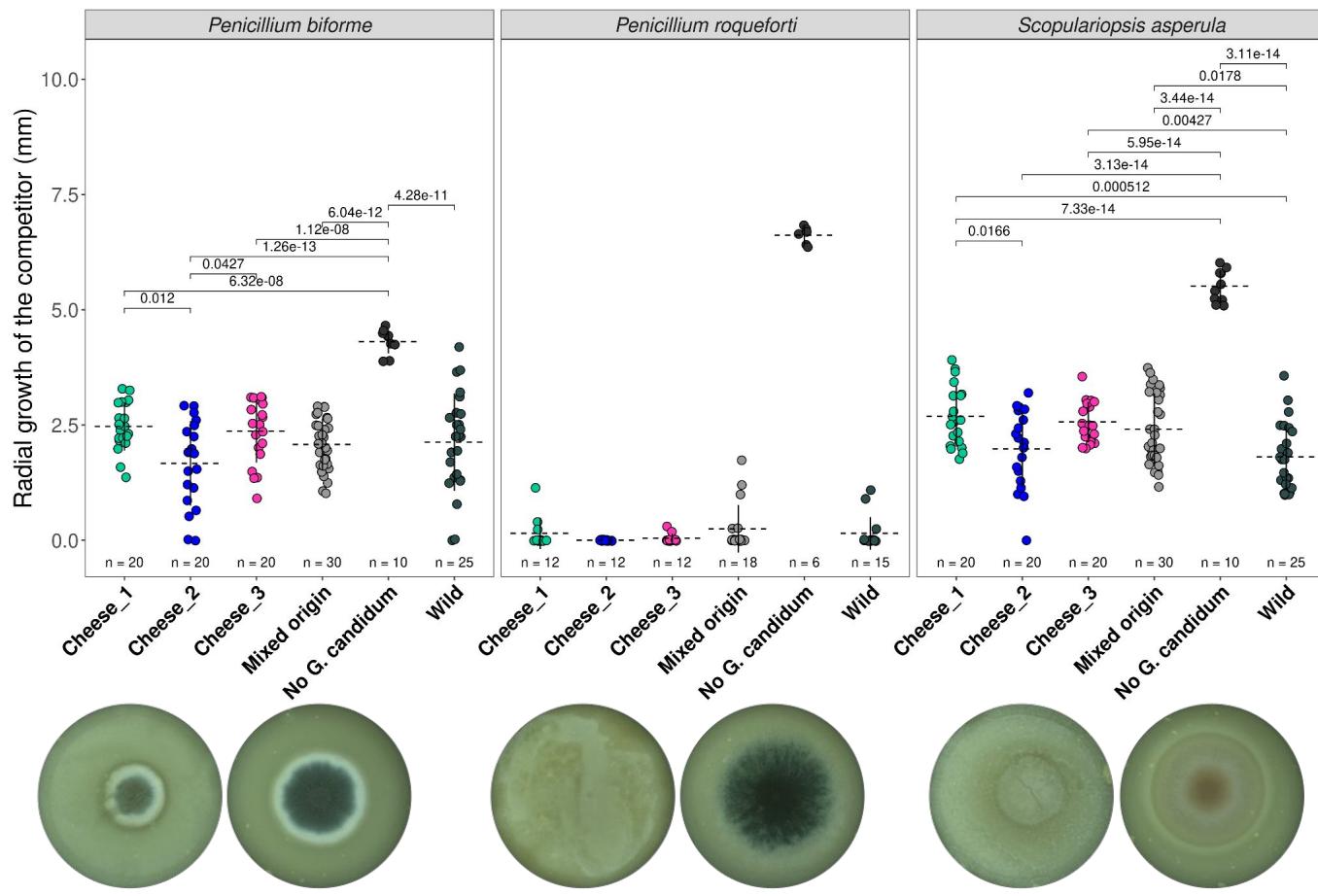


Figure 5: Competitive abilities of the different populations of *G. candidum* against *Penicillium biforme*, *P. roqueforti* and *Scopulariopsis asperula* challengers.

A.



B.

