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## Biogeography and shape of fungal fairy rings in the Apennine mountains, Italy

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1 **Biogeography and shapes of fungal fairy rings in the Apennine mountains, Italy**

2

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25

26 **Abstract**

27 Fungal “fairy rings” (FR) are regular bands of vegetation caused by a centrifugal expansion of fungal  
28 mycelia. It is well established that FR affect both soil chemistry and microbiome, promoting plant  
29 coexistence at community scale. However, nothing is known about the distribution of these peculiar  
30 patterns at regional scale. Here, we report on the FR biogeography of in the Apennine mountains  
31 across a 300 km latitudinal gradient, comparing twelve sites with different elevation, geomorphology,  
32 and climate. From high-resolution images we gathered data concerning FR shape, colonial density,  
33 and distribution. Overall, 1,163 FR structures were found across the study area. Three type of spatial  
34 patterns could be identified, proper rings, i.e. circular vegetation structures, arcs representing circle  
35 sections, and rotors where an arc was showing narrower circular distortions at its end points. Arcs  
36 were the most common shape followed by rings, while rotors were rare, accounting for less than 2%  
37 of all observations. Fungal colony density varied largely both among and within sites, averaging 6.7  
38 arcs, 2.2 rings and only 0.1 rotors per ha. On average, arcs (18.8 m) were similar in size compared to  
39 rotors (18.4 m) while rings were smaller (11.7 m). Notably, arcs present a higher frequency of  
40 occurrence on steeper slopes while rings are mostly found on flat and moderate slopes. In relation to  
41 climate, FR occur within the altitudinal range between 546 m and 2,148 m a.s.l., corresponding to  
42 temperature between 3.4°C and 12.7°C. and rainfall between 1,100 and 1,300 mm per year. No  
43 colonies were found with an annual rainfall lower than 800 mm. Based on this study, FR are common  
44 elements of the Apennine grasslands landscape contributing to the maintenance of plant and microbial  
45 diversity. A better systematic identification of the fungal species involved in the FR formation is  
46 necessary in relation to the different environmental gradients observed in the study area. Furthermore,  
47 other investigations and modelling demonstrations are required to understand the dynamic processes  
48 behind the development of the different FR forms..

49

50 **Keywords:** Plant-soil feedback, Autotoxicity, Arcs and rotors, *Agaricus arvensis*, Basidiomycota,  
51 Ecosystem engineer,.

52

## 53 **1. Introduction**

54 Fungal “fairy rings” (FR) are circular bands of vegetation caused by the centrifugal expansion of  
55 fungi (Edwards, 1984, 1988). More than 50 species of basidiomycetes and few ascomycetes have  
56 been reported to be able to create FRs (Fox, 2006; Halisky & Peterson, 1970) in different ecosystems,  
57 including sand dunes (Abesha, Caetano-Anollés, & Høiland, 2003), woodlands (Dowson, Rayner, &  
58 Boddy, 1989; Peter, 2006), and grasslands (Karst, Dralle, & Thompson, 2016; Yang, Li, Liu, &  
59 Zhang, 2019). FRs, spreading radially in the soil as fronts of dense mats of fungal mycelia, only  
60 become evident above ground because of the sporadic appearance of the fungal fruiting bodies or  
61 because of their effect on vegetation (Gregory, 1982). Shantz and Piemeisel (1917) classified  
62 grassland FRs into three types based on the response of vegetation: Type-1 formed by an external belt  
63 of bare soil or dead vegetation surrounding a second belt of luxuriant vegetation; Type-2 recognizable  
64 for the presence of a luxuriant belt without any dead zone; Type-3 periodically revealed only by the  
65 presence of fungal carpophores with no detectable changes in vegetation color and floristic  
66 composition.

67 The occurrence of FRs in grasslands has been the subject of scientific studies since the end of  
68 the 19th century (Elliott, 1926; Evershed, 1884; Lawes, Gilbert, & Warington, 1883; Shantz &  
69 Piemeisel, 1917), particularly in the context of turfs management where they are considered  
70 destructive phenomena (Fidanza, Colbaugh, & Davis, 2000; Filer, 1965). Several attempts have been  
71 made to explain the detrimental effect of FR fungi on vegetation. The most cited hypotheses are the  
72 local increase in soil hydrophobicity causing the dry out of the soil (Gramss, Voigt, & Bergmann,  
73 2005), the immobilization of nutrients in the mycelium body (Fisher, 1977), the direct pathogenic  
74 behavior (Fidanza et al., 2007; Terashima, Fukiharu, & Fujiie, 2004), and the release of phytotoxic  
75 compounds like cyanide (Blenis, Chow, Duncan, & Knowles, 2004; Caspar & Spitteller, 2015).  
76 Differently, the mechanisms triggering the formation of luxuriant vegetation in FRs were ascribed to  
77 the flush of mineral nutrients after the fungal passage, the formation of vacant niches, the release into  
78 the soil of molecules with hormone-like activity also called “fairy chemicals”, or the stimulation of a  
79 symbiotic microbiome with a positive effect for the plants (Choi et al., 2010; Suzuki et al., 2016;  
80 Yang, Li, Zhang, Liu, & Zhang, 2018; Zotti et al., 2020).

81 In the last decade, several studies also revealed the impact of FRs at ecosystem level. Type-1  
82 FRs, by killing the established vegetation, create gaps that are filled by short-lived plants, thus  
83 enhancing species coexistence and plant diversity at community level (Bonanomi, Mingo, Incerti,  
84 Mazzoleni, & Allegranza, 2012). More recently, the extensive use of next generation sequencing  
85 provided the means to study the impact of FRs on soil microbiome in terms of bacteria and fungi  
86 composition (Oh, Fong, Park, & Lim, 2016; Xing et al., 2018). Recently, Zotti et al. (2020) revealed

87 that the passage of Type-1 FRs, caused by *Agaricus avernsis*, causes profound changes in the  
88 microbiota composition with an overall increase in taxa diversity. In fact, the passage of the FRs wipe  
89 out the established bacterial and fungal communities, promoting the recolonization of disturbance  
90 related taxa. Taken together, available evidence indicates that FRs fungi are crucial for the  
91 maintenance of plant and microbial diversity in grasslands acting as ecosystem engineers in  
92 grasslands.

93 Most of the previous studies investigated the impact of FRs at community scale, focusing on  
94 soil chemistry (Edwards, 1984), plant communities (Yang et al., 2019), and soil microbes (Espeland,  
95 Caesar, Sainju, Lartey, & Gaskin, 2013). However, very little is known about the factors controlling  
96 the distribution of FRs at regional scale. Recently, Karst and coauthors (Karst et al., 2016), using  
97 high-resolution aerial imagery, documented that in United States the FRs colonies can develop in  
98 different shapes, i.e. complete ring, arc-shaped, and rotor. The same paper reported , on mathematical  
99 simulations reproducing the observed spatial patterns without investigating the link between  
100 ecological factors and geographical distribution of the observed different shapes of FRs. In this work,  
101 we attempt to describe the biogeography of fairy rings at regional scale and propose a mechanistic  
102 explanation for the induction of the FR types. To this aim, we carried out a study on twelve sites in  
103 the Italian Apennine mountains, ranging across high geomorphological, climatic and latitudinal  
104 variability, of ecosystems in which FRs exist. This allowed us to set the biological limits of  
105 occurrence of such peculiar phenomenon.

106 We collected, from high-resolution images, data concerning FR shape, colonial density and  
107 distribution. Thereafter, we analyzed the relationships between fungal colonies data with selected  
108 climatic and geomorphological variables to explore the factors that affect FR distribution. The  
109 specific objectives of our study were:

- 110 (i) to assess the abundance and relative occurrences of different FR types, i.e. rings, arcs,  
111 and rotors;
- 112 (ii) to explore the association between geomorphology and FR types;
- 113 (iii) to reveal the distribution of FR in relation to temperature and rainfall;
- 114 (iv) to define a new hypothesis on the causal process explaining the occurrence of different  
115 FR types

## 117 **2. Material and Methods**

### 119 *2.1 Study area*

120 The Apennines is a ~1,000 km long mountain chain that span in latitude from 38°N to 44°N  
121 accounting 261 peaks above 2,000 m a.s.l. and The Apennine rock is mainly composed by limestone  
122 substrata, with arenaceous-pelitic flysch present only in the Laga groups (Bonanomi et al., 2020). The  
123 climate is a mountain variant of the Mediterranean type, with mean annual temperature that range  
124 from 0 °C to 8 °C in January and from 20 °C to 28 °C in the hottest month, July. Total annual  
125 precipitation also largely varies, from less than 600 and more than 3,000 mm, with abundant winter  
126 snowfall above 1000 m a.s.l.

127 The current treeline, dominated by the deciduous tree *F. sylvatica*, occur at elevation that  
128 range from ~1,000 m a.s.l. to ~2,100 m a.s.l. (Bonanomi et al. 2020). Because of past intensively  
129 human exploitation for agricultural purposes (i.e. cultivation, livestock, wood, charcoal production),  
130 the current treeline stay several hundred meters below its potential climatic limit that in Central and  
131 Southern Italy is above 2,000 m a.s.l. Consequently, grassland under ~2,000 m a.s.l. are considered  
132 secondary i.e. created by past human activity, with only high-elevation grassland being primary or of  
133 natural origin (ref\_marina).

134

## 135 2.2 Study sites and survey design

136 To identify the study sites we capitalized from our recent survey of *F. sylvatica* distribution across  
137 all Apennine peaks where we examined 3,622 km of treeline and adjacent grasslands (Bonanomi et  
138 al., 2018). Based on this survey, we identified twelve mountains where FR were present and clearly  
139 visible from satellite images (Figures 1, 2).

140 A first data set build with the aims of assessing the FRs density in terms of number of fungal  
141 colonies per ha, and the relative occurrence of different forms, i.e. ring, arc, rotor. To achieve this  
142 aim, in each of the twelve mountains, and in grasslands where FRs were present, we randomly  
143 selected five 1 ha plots. A total of 60 ha was surveyed: 5 plots for each of the 12 mountains. The  
144 selected sites fulfilled the following requirements: i) grassland are not subject to extensive shrub  
145 encroachment, i.e. less than 30% cover of either *Juniperus communis* or *Pinus mugo*; ii) rocks do not  
146 cover more than 50% of the surface. In each plot, using Google Earth Pro™ (Google, Inc. Mountain  
147 View, CA, USA) images dating 2004-2018, we counted all occurring FRs and identified their forms  
148 for a total number of observations of 547 FRs (Figure 2).

149 A second data set was built to assess the relationships between FRs occurrences with local  
150 geomorphology and climate. In detail, we selected additional sites located in the surrounding of the  
151 twelve mountains (Supplementary Table S1). Here, we extensively searched for all occurring FRs  
152 that was mapped in Google Earth Pro™ (Google, Inc. Mountain View, CA, USA) images dating  
153 2004-2018. The geographical coordinate, the shape, the size (diameter in m), and the elevation of

154 each FR were recorded for a total of 616 observations (Table 1). The vertical accuracy of the Google  
155 Earth-measured data was further checked in the field on 100 FR, corresponding to 16.2% of  
156 geolocated waypoints, distributed along the Apennines, with a Garmin Montana® 600 GPS device  
157 equipped with a barometric altimeter. For each FR the slope was measured as average slope of the  
158 transect crossing them. In addition, for each fragmented forms of FR (arcs and rotors) we assessed if  
159 the convexity was upslope or downslope.

160

### 161 *2.3 Climatic variables*

162 Based on the literature concerning higher plants biogeography in Apennines (Bonanomi et al., 2018),  
163 we selected 10 variables to evaluate their ability to explain FR distribution (Table 1). Climatic data  
164 were gathered from the global climate database WorldClim 2.0 <http://www.worldclim.org>; (Hijmans,  
165 Cameron, Parra, Jones, & Jarvis, 2005) at a spatial scale resolution of 1 km<sup>2</sup>. In the WorldClim  
166 database, temperature variables are calculated as the spatial average of grid squares that include the  
167 selected point and adjusted according to their average elevation. Data were then adjusted at the  
168 elevation of each study sites by using a 0.006°C m<sup>-1</sup> adiabatic lapse rate (Barry, 1992). For rainfall  
169 variables, data were gathered from the Bioclimates of Italy because of the higher spatial resolution  
170 compared with WorldClim for the Apennines. Shortly, rainfall data were obtained with a calibration  
171 process, via regression kriging, of the WorldClim (1.4), with a large data set from local  
172 meteorological stations (Pesaresi, Biondi, & Casavecchia, 2017).

173

### 174 *2.4 Colonies migration*

175 To assess FRs migration, we used the diachronic approach using satellite images of 2006 and 2012  
176 available in Geoportale Nazionale ([www.pcn.minambiente.it](http://www.pcn.minambiente.it)). Despite extensive searching, we found  
177 only a limited number of FR ( $N=10$ ) where high-resolution images were available at both dates. For  
178 each FR we measured the diameter in 2006 and 2012 and the annual increment was calculated.

179

### 180 *2.5 Data analysis*

181 Density in colonies per ha across the twelve mountain ranges selected were assessed by average  
182 values on five replicates in the same study site. Comparison of FRs density were made by FRs forms  
183 if were rings, arcs or rotors for the totality of the Apennine region and between each study site. With  
184 the same approach we compare data of relative abundance between the different forms and between  
185 the different study site across the Apennine. To obtain and evaluation of the more frequent diameter  
186 by which arcs, ring and rotor are observed we assess separately their distribution by applying normal  
187 fitting distribution curves. Distribution of rings, arcs and rotors were also visualized by the relation

188 with climatic variables including temperature and precipitation variables. Comparison of the highest  
189 frequency of occurrence for rings and arcs were tested for the range of slope values observed in the  
190 different study sites. To emphasize the relation between slope, elevation and diameter of rings and  
191 arcs we performed bubble-plots between slope and elevation with labels proportional to the diameter  
192 of the FRs sampled. We also visualized the occurrence of all the FRs sampled and divided by rings  
193 and arcs by linear regression between slope and annual cumulated rainfall. The last three analysis  
194 were conducted uniquely on arcs and rings because the lower contribution of rotors and the rarity of  
195 this particular formations. Statistical analyses and plotting were carried out using Statistica 10  
196 software (StatSoft, Tulsa, OK, USA).

197

### 198 **3. Results**

199

#### 200 *3.1 Form, size, and density*

201 Overall, 1,163 FRs were recorded across the Apennines. Arcs were largely the most common shape  
202 (75.1%) followed by ring (23.5%) (Figure 3). Rotors, although present, were rare accounting for only  
203 1.4% of all observations. The relative abundance of different FR forms largely varied among  
204 mountains, with arcs being the most common in ten sites (**elencare siti**) while rings only in two  
205 (Montiego and Fiegni). Rotors, instead, were found only at three sites (**elencare siti**). Considering all  
206 study sites, we found an average density of 6.7 arcs, 2.2 rings and only 0.1 rotors per ha. Colonies  
207 density varied amount mountains, with the highest values at Vettore (19.2 colonies per ha), followed  
208 by four sites where the density ranged between 10 and 15 colonies per ha, and the other sites where  
209 we found a density between 5 and 10 colonies (Figure 3).

210 On average, rings have smaller diameters (11.7 m) compared to arcs (18.8 m) and rotors (18.4  
211 m). However, the size of all shapes largely varies with most of the rings falling in the diameter classes  
212 between 5 and 15 m, with the largest ring having a diameter of 51.9 m. The majority of arcs are in  
213 the diameter classes between 10 and 20 m, but reaching the notable maximum size of 137.1 m, while  
214 the population of rotors is limited, ranging in size between 4.2 and 33.0 m (Figure 4).

215 The annual average migration of the FRs was  $64.7 \pm 17.5$  cm per year, with the highest values  
216 of  $151.3 \text{ cm year}^{-1}$  and the lowest of  $40.3 \text{ cm year}^{-1}$ . For arcs, we always observed that the fungal  
217 colonies migrate upslope (Supplementary Figure S4).

218

#### 219 *3.2 Elevation, latitude and climate*

220 Rings, arcs and rotors showed a similar distribution in relation to elevation and climatic variables.  
221 Arcs showed a bimodal distribution in relation to elevation, with peaks between 1,000-1,200 m a.s.l.



222 and 1,600-1,800 m a.s.l. and had a slightly larger elevation range than rings and rotors (Figure 5a),  
223 but no FRs were recorded below 546 m a.s.l. and above 2,148 m a.s.l. Concerning latitude, we found  
224 a significant negative relation between FR altitude and latitudinal position (Pearson  $r = -0.82$ ;  
225 Supplementary Figure S1).

226 FR distribution was bimodal also in relation to mean annual temperature (Figure 5b). Arcs  
227 showed the largest amplitude, ranging from a minimum of 3.4 °C to a maximum of 12.7 °C of mean  
228 annual temperature. The distribution of FR to other temperature variables was similar to that observed  
229 for mean annual temperature (Supplementary Figure S2).

230 FR distribution in relation to annual rainfall was unimodal, slightly skewed on the left (Figure  
231 5c). Most FRs occurs in the class of precipitation between 1,200 and 1,300 mm per year, with no  
232 cases below 813 mm and above 1,668 mm. Also in this case, arcs showed a larger ecological  
233 amplitude compared to rings and rotors. Monthly and seasonal rainfall relationships with FR  
234 distribution was similar to that of annual cumulated data (Supplementary Figure S3).

235

### 236 3.3 *Slope and fairy rings*

237 Rings and arcs showed a different distribution in relation to mountain slope (Figure 6). Overall, rings  
238 were more common in flat and moderately sloped areas while arcs were common also on very steep  
239 slopes. In detail, 55.7% of the rings were found in areas with a slope lower than 10%, with only 2.7%  
240 occurring in steep areas (slope >30%). Instead, 57.2% of the arcs were found in areas with slopes  
241 between 10% and 30%, with 13.2% of the cases in steep slope. Notably, 99.7% of the recorded arcs  
242 showed an upslope convexity.

243 Moreover, we found different relationships between slope, elevation and the size of rings and arcs  
244 (Figure 7). Specifically, we found that large rings are mainly present at low elevation (<1,400 m a.s.l.)  
245 and in flat or moderately sloped areas. Instead, we found that very large arcs also occur at high  
246 elevation and in steep areas. Finally, we observed a positive correlation between slope and annual  
247 cumulated rainfall (Figure 8a). Notably, the correlation was steeper for rings than for arcs (Figure  
248 8b).

## 249 **4. Discussion**

250 Previous studies showed that fungal FR exert major effects on soil chemistry (Yang et al., 2019),  
251 microbial populations (Zotti et al., 2020), and plant diversity (Bonanomi et al., 2012). Here, we  
252 provide the first assessment of FR biogeography at regional scale. We found that rings, arcs and rotors  
253 occur with different densities and relative abundances across the Apennine mountain range, with  
254 climate and slope playing an important role in explaining the observed variability.

255

### 256 *4.1. Variation in size, form and density of fairy ring*

257 FR density, size and forms varied greatly within and among sites. Rings are more common on flat  
258 areas, while arcs are more frequent in steep slopes. Rotors, on the other hand, are always very rare.  
259 However, in some sites (i.e. Montiego, Ocre and Vettore) rings, arcs and rotors coexist in close  
260 proximity, suggesting that local factors could explain their cooccurrence. Commonly, colonization  
261 strategies of fungi are divided in vegetative strategies or production of spores (Dix, 2012). As  
262 demonstrated for *M. oreades* in sand dunes (Abesha et al., 2003), the initiation of FRs probably  
263 derives from fungal spores that, after germination, spread centrifugally. The relative low density of  
264 FRs in the field coupled with the long-lived nature of these structures and the high amount of spores  
265 produced by basidiomycetes suggest that spore establishment is a rare event (De Groot et al., 2012).  
266 In the very early phases of development, FRs are not noticeable aboveground, also after careful  
267 inspection in the field, probably because the mycelium does not reach a sufficient biomass to affect  
268 plants. Concerning FRs population structure, in the smallest size class (i.e. 0 to 5 m in diameter), rings  
269 are far more common than arcs. On the contrary, arcs are much more common than rings in the size  
270 class over 10 m in diameter. The shifting of FRs population structure, i.e. more common rings of  
271 small size compared to arcs, suggest that arcs may generate from rings during their ontogenetic  
272 expansion. Here, we propose two possible mode of arcs generation. In the first model, a complete and  
273 regular ring brakes during its expansion due to the encounter with an obstacle of physical (i.e. a rock  
274 or unsuitable soil patches) or biological nature (e.g. mycoparasites or another fungal front). We found  
275 several FRs with circular shape but with a missing short portion (Supplementary Figure S4a),  
276 suggesting that some factors generated a rupture of the fungal front. Thereafter, as the fungal front  
277 expands, the break becomes progressively larger generating the arcs. In this regard, we believe that  
278 the encounter of different fungal fronts, i.e. FR coalescence, would be a common event leading to the  
279 emergence of irregular shapes. However, the coalescence of two rings, while creating new shapes  
280 departing in time from a regular circle, would not justify the rupture of the ring continuity and the  
281 appearance of partial rings or arcs. (Supplementary Figure 4b).

282 At microscopic level the fate of fungal hyphae that belong to different genets during colonies  
283 coalescence is largely unknown although often described as repulsion (Deacon, 2013), but at  
284 macroscopic level the rings indeed can lose their integrity (Parker-Rhodes, 1955; Stevenson &  
285 Thompson, 1976). A similar effect resulting from rings coalescence was also presented by Carteni et  
286 al (2012) in the context of ring forming clonal plants. Accordingly, Karst et al. (2016) showed how  
287 different structures can rise by the intersection of different expanding simulated colonies. The  
288 “obstacle” hypothesis is consistent with the observation that large rings (>20 m in diameter) are rare  
289 while arcs can often reach diameter >50 m, with some cases where the diameter are over 100 m.  
290 A Fairy ring can spread at a rate of about 60 cm per year, then an arc of 50 m would be ~75 years old,  
291 and the largest observed arc (137 m) would have more than 200 years. These are not exceptional size  
292 and age for basydiomicota colonies, e.g. *Armillaria spp.* clones can cover hundreds of ha aging than  
293 1,000 years (Bendel, Kienast, & Rigling, 2006). Such lifespan suggest that a fungal front is likely to  
294 encounter obstacles thus generating arcs from rings.

295 Although the “obstacle” hypothesis seems plausible and probably is operative in many cases,  
296 it does not explain the prevalence of arcs over rings in steep slope, and the case of low density of the  
297 colonies corresponding to low probability of crossing trajectories between different structures.

298 Our hypothesis to explain the formation of arc structures from initial smaller complete rings  
299 is based on the effect of autotoxic compounds in interaction with their leaching. Autotoxicity is a  
300 phenomenon reported for microbes (Berne, Kysela, & Brun, 2010) and higher plants (Singh, Batish,  
301 & Kohli, 1999) caused by localized accumulation of chemical compounds either actively produced  
302 by the considered organism, or released during decomposition of its parts likelitter and fine roots.  
303 For fungi, autotoxicity has been reported to control spore germination, and impair hyphal growth and  
304 proliferation (Bottone, Nagarsheth, & Chiu, 1998; Chitarra, Abee, Rombouts, Posthumus, &  
305 Dijksterhuis, 2004). Several classes of chemicals have been considered as putative autotoxic  
306 compounds, including fatty acids, alkaloids, and phenols, but none of these justifies a species  
307 specificity of the effect. Recently, Mazzoleni *et al.* (2015) discovered the species-specific inhibitory  
308 effect of extracellular DNA on plants and confirmed that the phenomenon was generally occurring  
309 across a broad range of organisms of different kingdoms, including plants, insects, bacteria and fungi  
310 (Mazzoleni et al 2015b, Carteni et al. 2016). The inhibition by extracellular self-DNA released into  
311 the soil by the decomposition of organic matter has unique features to provide a mechanistic  
312 explanation for the formation of FRs and also for their differentiation into different shapes. In fact,  
313 DNA is soluble in water and so it is spatially distributed according to main water flows. In the FR  
314 context, this logically support the theoretical framework of the formation of arcs. In flat areas, the  
315 local accumulation of autotoxic compounds due to the mycelium turnover, would trigger, in

316 interaction with depletion of resources, the centrifugal hyphae growth with the development of  
317 circular structures. A similar dynamics has been described for tussock grasses and plants capable of  
318 vegetative propagation that forms the so called hollow crowns, central dieback or monk's tonsure like  
319 gaps (Bonanomi et al., 2014). In the absence of slope, the autotoxic compound is mostly leached  
320 vertically along the soil profile, according to soil texture and hydraulic properties (Heuvelink,  
321 Burgers, Tiktak, & Van Den Berg, 2010). Under such conditions, modelling exercise demonstrate the  
322 creation of ring structures and their possible coalescence into continuous waves across the landscape  
323 (Carteni et al JTB). Differently, on slopes the directional water movement creates a down slope  
324 diffusion of the putative hydrosoluble autotoxic factor (with accumulation of the adverse effect on  
325 the lower section of the ring. If the autotoxic effect is strong enough, the lower fungal front would be  
326 inhibited, and arcs would arise. This hypothesis is consistent with the observation that 99.7% of the  
327 arcs move upslope, with no cases of colonies moving downslope (Supplementary Figure 4c). On the  
328 other hands, we found few rings in very steep slopes, with the few cases occurring in areas with  
329 substantial annual rainfall over 1,300 mm per years. We suggest that in these slopes, the co-  
330 occurrence of abundant rain and rocky, porous soils may have promoted a faster vertical leaching of  
331 the autotoxic compound, thus explaining the persistence of some rings also on slopes. Theoretically,  
332 the prevalence of vertical versus lateral water flow can be the causal factor for the maintenance of a  
333 ring structure, whereas a dominance of down slope directional flow of water will cause the lower ring  
334 rupture with the creation of the arc pattern. The Vettore site (Figure 2 and Supplementary Figure 4)  
335 is characterized by the co-presence of all these features, i.e. abundant annual rainfall, rocky and  
336 heterogeneous soil and very steep slopes, and, consistently with our model, here arcs and rings largely  
337 coexist. Further field work is ongoing to assess within FRs and arc structures the gradients of  
338 concentration of the fungal DNA to observe its consistency with the proposed model of autotoxicity  
339 in both flat and sloped areas. This study will use next generation sequencing, including shotgun  
340 methods (Mendes, de Lima Brossi, Kuramae, & Tsai, 2015) to investigate the self-DNA hypothesis.

341 Finally, we found that rotors are rare (1.4% of all cases) and occurs only in few places at very  
342 low density (less than 0.1 colonies per ha). Karst and coauthors (Karst et al., 2016) also noticed that  
343 rotors occurs far less frequently than rings and arcs in US grasslands. Moreover, the author's  
344 simulation model suggested that soil patches with low resources could promote rotation in the  
345 advancing fungal front. Probably conditions suitable for rotors development are very special and  
346 occur infrequently in nature, in this regard fine-scale investigation of soil heterogeneity is required to  
347 test the Karst's hypothesis.

348

349 *4.2. Climate, geomorphology and fairy ring*

350 At a global scale climate is the primary factor controlling the distribution of living organisms, with  
351 mean annual temperature that is considered a key parameter to explain biological distribution along  
352 latitudinal and altitudinal gradients (Bennie, Duffy, Inger, & Gaston, 2014; Körner, 2012). However,  
353 much less is known about fungal biogeographic distribution (Tedersoo et al., 2014), and few  
354 concerning FRs (Shantz & Piemeisel, 1917). In this context, our study provides a wider description  
355 of FR distribution in relation to temperature and rainfall. In general, we found that FR mostly occurs  
356 within the temperature range between 4°C and 12°C, with altitudinal upper distribution likely limited  
357 by low temperature. In our survey, the highest FR occur at 2,148 a.s.l. where the mean annual  
358 temperature of ~3.4°C likely poses a climatic constraint upon the growth of FRs. In addition, at this  
359 elevation in Apennine a substantial shift in grasslands plant composition and structure occurs (ref.  
360 Marina), with a possible reduction of the relative abundance of the plant species that the fungus use  
361 as a substrate. It will be interesting to further investigate the different fungal species altitudinal  
362 distribution and their interactions with the plant communities. Our current knowledge of fungal  
363 species forming FR is sparse, based on either morphological and molecular methods we were capable  
364 to identify *Agaricus arvensis* at the Puro-Rogedano site (Zotti et al., 2020). Here, the bi-modal  
365 distribution of FR in respect to mean annual temperature with two peaks at 5-6°C and 10-11°C  
366 suggest that different fungal species may form FR in cold and mild climatic conditions. Indeed,  
367 further studies are urgently required to assess the taxonomy of species that forms arcs and ring along  
368 the investigated altitudinal and latitudinal gradient.

369 FRs rarely occurs below 800 m, with the lowest occurrence at 546 m where the mean annual  
370 temperature is ~12.7°C. Moreover, with found a strong negative correlation between altitude and  
371 latitudinal occurrences of FR, meaning that in Central Italy we found arcs and ring at lower elevation  
372 compared to Southern Italy. such altitudinal range and its shift with with latitude suggest that  
373 temperature plays a critical role on FR distribution. First, the absence of FR below ~500 m could be  
374 related to a shift of fungal colony spreading mode. We suggest that when the fungi lives in optimal  
375 temperature condition , their mycelium show a “phalanx like strategy” (ref.), producing the circular  
376 pattern, reflecting vigorous growth of the fungal front. Instead, at the edge of the ecological niches  
377 where growth conditions are not optimal, e.g. at low altitude with high temperature, the fungi are  
378 unable to form a compact fungal front showing a weaker spread by single hyphae, classifiable as  
379 “guerrilla strategy”. Thus not producing FR structures. A second hypothesis to explain the lacks of  
380 FR at lower altitudes is related to land-use in Apennine mountains. In fact, at lower elevation these  
381 landscape are heavily managed with both pastures and grassland being replaced by intensive  
382 agricultural system and urban areas (ref\_marina). This, indeed, could contribute to the rarity of FR  
383 but cannot explain their absence in the residual grasslands present at low elevation.

384 Alongside temperature, precipitation also affects FRs distribution with most of the cases that  
385 occurs where rainfall is between 1,100 and 1,300 mm, with no cases below 800 mm. This indicate  
386 that FRs cannot proliferate in arid and semi-arid climates. On the other hands, we do not found FRs  
387 where rainfall exceed 1,700 m. In the field we observed that FR do not occur in flat area subject to  
388 periodical flooding, suggesting that basidiomycetes fungi cannot tolerate prolonged anoxic soil  
389 conditions (Tavzes, Pohleven, & Koestler, 2001). According, we found that ring and arcs occurs both  
390 in flat and sloped areas in the range between 800 and 1,400 mm of annual rainfall, whereas over the  
391 1,400 threshold we mainly found FRs only where the slope exceed 20%. In general terms, many  
392 basidiomycetes including wood degrading species are less abundant and perform poorly under anoxic  
393 condition (ref, ref). Overall, our data indicate that both shortage and excessive rainfall, below 800  
394 mm and above 1,700 mm, respectively, could hamper FR development. However, in flat areas subject  
395 to flooding, because of poor drainage conditions, a reduction of the upper limit of annual rainfall was  
396 recorded, corresponding in this case to 1,400 mm per year.

397

## 398 **5. Implications for management and future directions**

399 FRs are notable features of grassland ecosystems and available evidence demonstrate that these fungi  
400 promote plant and microbe coexistence at local scale. This study, recording the presence of FR across  
401 a whole Mountain range, albeit within a specific set of environmental conditions. FR occur at density  
402 of several colonies per hectare, highlight their importance for maintenance of biodiversity in  
403 Mediterranean grassland. In this regard, FR fungi operate as ecosystem engineers and by killing the  
404 established vegetation and microbiome, allow the periodical flourishing of life by ecosystem  
405 rejuvenation. However, FR occurs only in permanent grassland and moved pastures and we observed  
406 that they disappear after shrub encroachment, a comment vegetation dynamics in Apennine because  
407 of land abandonment (Bonanomi, Incerti, & Allegranza, 2013; Malandra, Vitali, Urbinati, &  
408 Garbarino, 2018). Specific management plan could be applied in some sites of special values (e.g.  
409 Puro-Rogedano, Fiegna, Montiego) to maintain summer moving and avoid *J. communis* establishment  
410 and encroachment.

411 Further advances in understanding FR dynamics are needed to explain the formation or arcs,  
412 ring and rotors. The combination of long-term field manipulative experiments and modeling work  
413 would help to falsify the “obstacle” and the “autotoxic” hypotheses proposed to explain the formation  
414 of arcs from rings during the ontogenetic development of fungal fronts. Finally, a substantial  
415 knowledge gap still requires the taxonomic identification of fungal species that forms FR across  
416 altitudinal and latitude gradients in Apennine.

417

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537

**Table 1.** Variables accounted for the analysis of FR across the Apennines range.

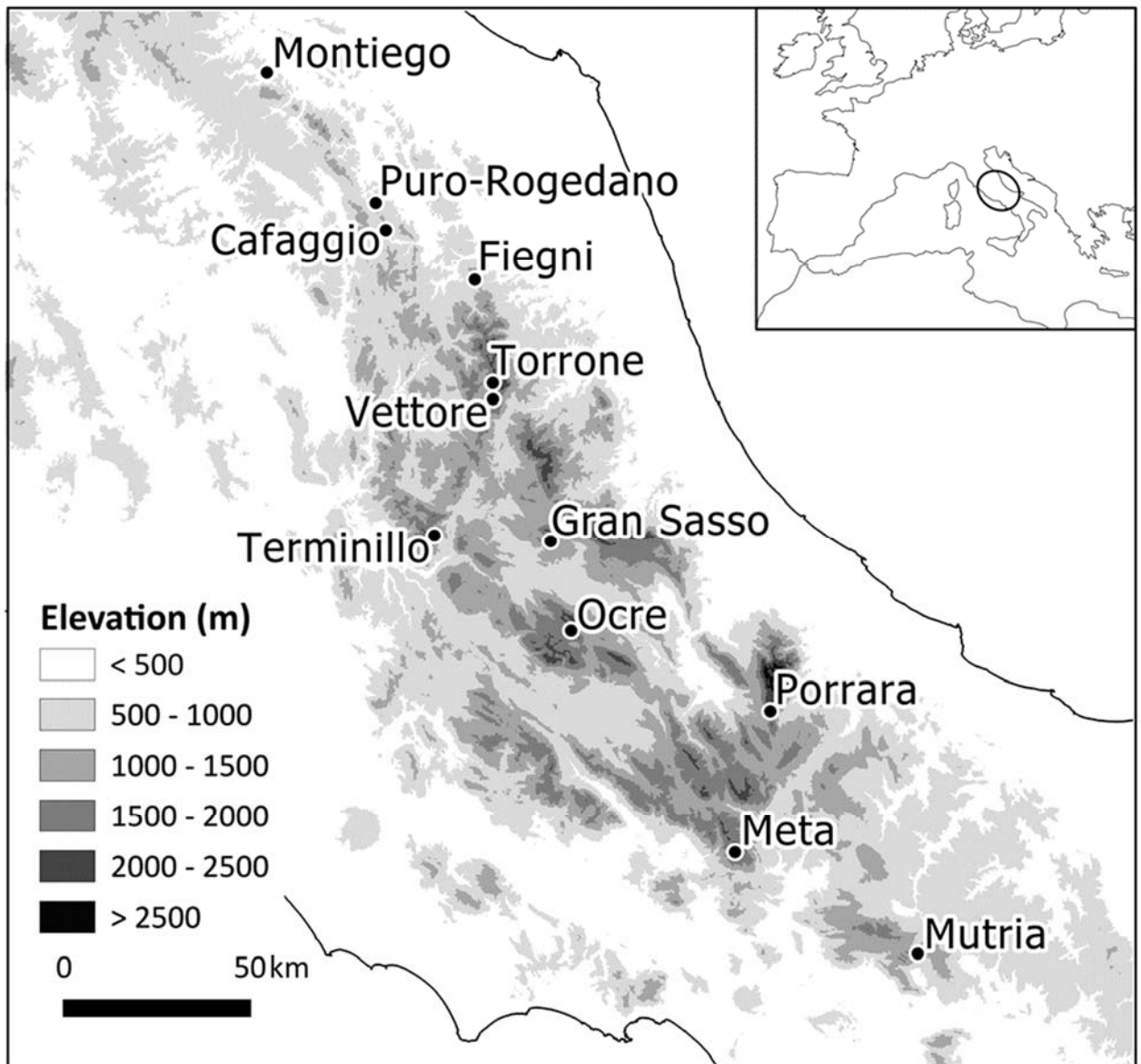
<b>Variable</b>	<b>Unit</b>
<i>Geographical</i>	
Latitude	degree
Elevation	m a.s.l.
Slope‡	%
<i>Climatic</i>	
Mean annual temperature (MAT)	°C
Mean monthly temperature*	°C
Max temperature of warmest month	°C
Min temperature of coldest month	°C
Temperature annual range	°C
Mean temperature of warmest quarter	°C
Mean temperature of coldest quarter	°C
Mean cumulated annual rainfall	mm y <sup>-1</sup>
Mean cumulated monthly rainfall†	mm mo <sup>-1</sup>

‡ Slope measured above, across, and below the treeline.

\* Monthly mean temperature from January to December.

† Monthly cumulated rainfall from January to December.

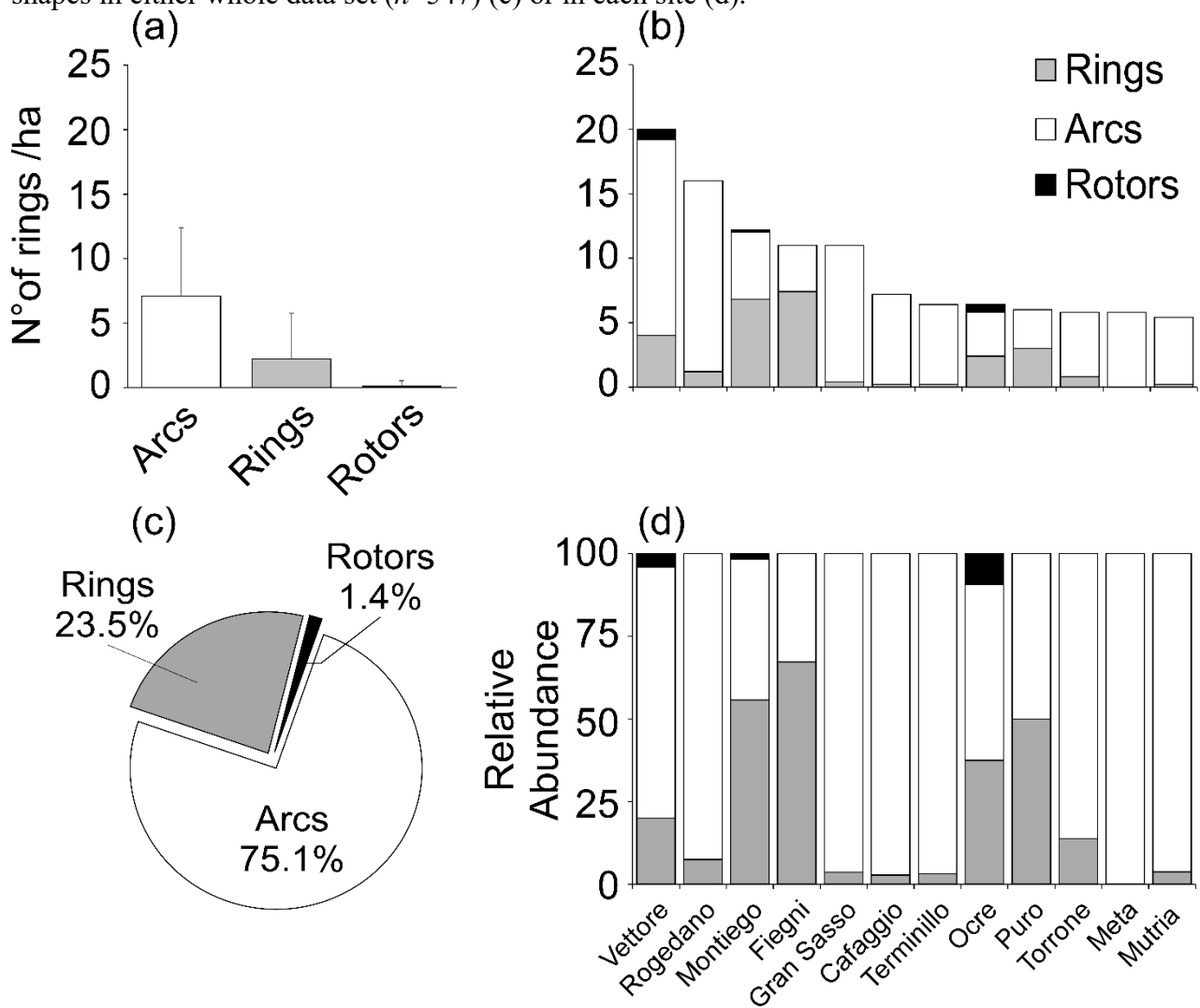
**Figure 1.** The twelve study sites (black dots) selected across the Apennine Mountains range (Italy).



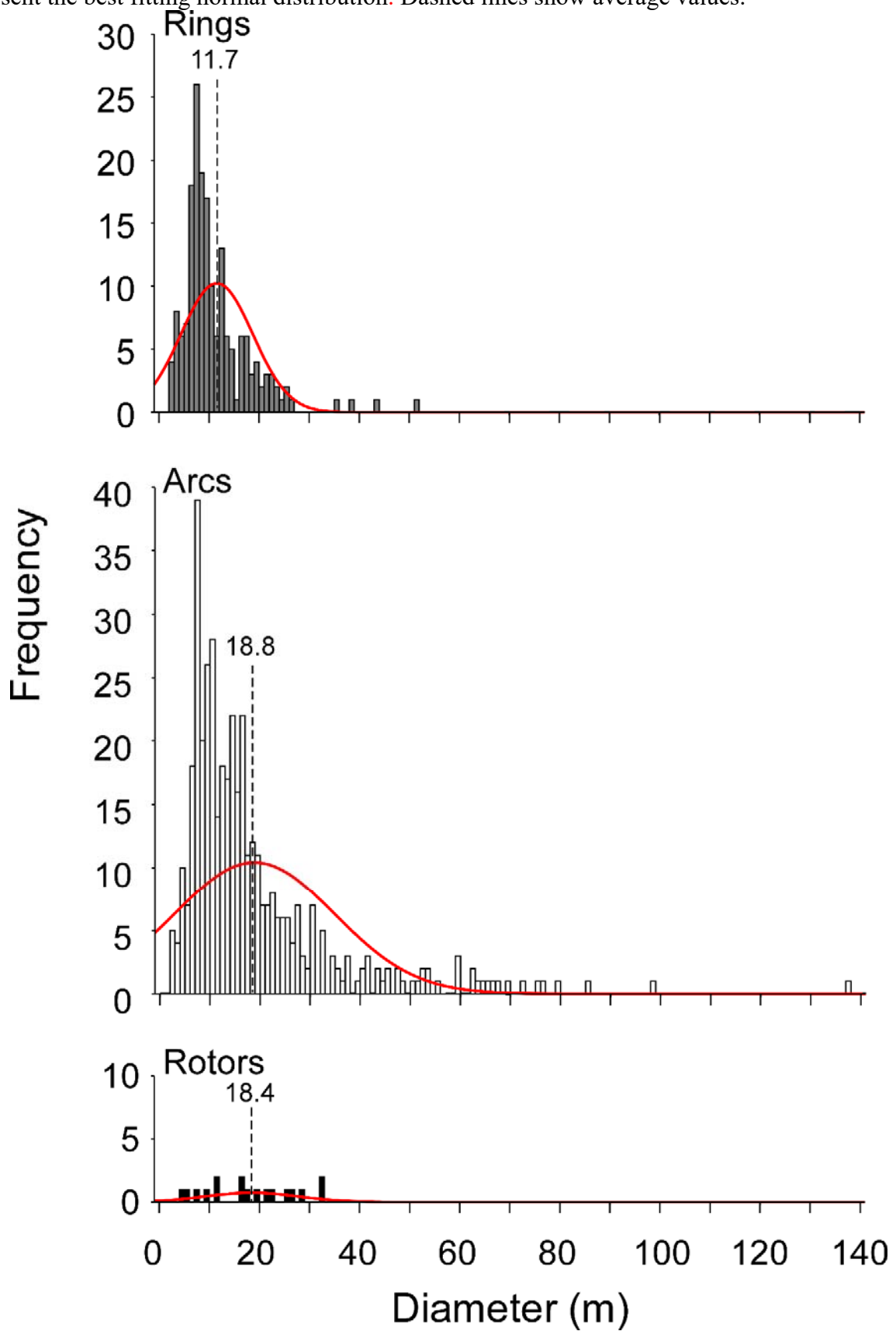
**Figure 2.** Selected satellite images of three study sites (Fiegni, Montiego, and Vettore) with photostitched examples of a ring, an arc and a rotor. Bars for scale.



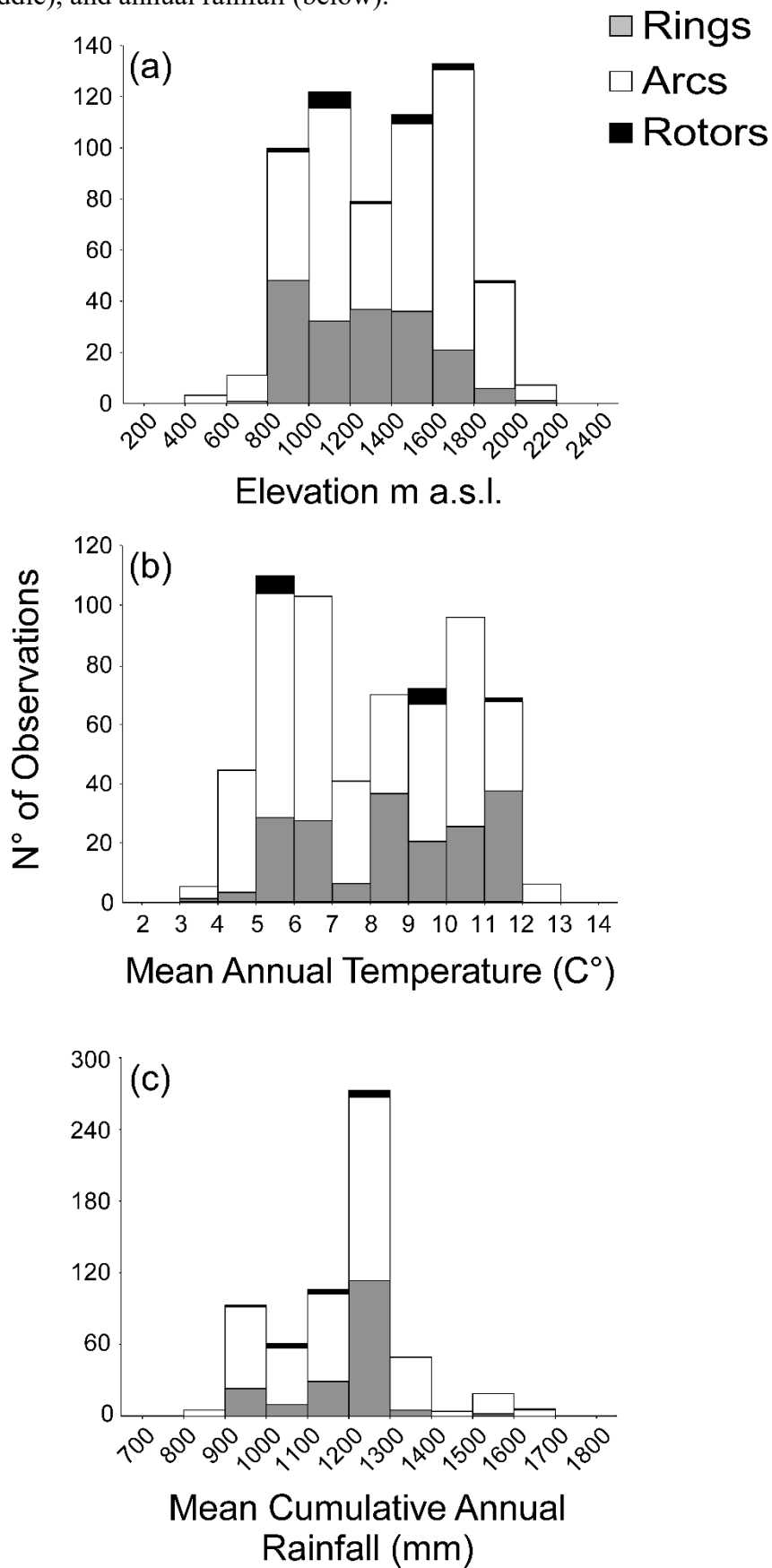
**Figure 3.** Density and relative occurrence of different fungal colony types. Average of fungal colonies per ha across all study sites (a) and in each mountain (b). Relative abundance of the different shapes in either whole data set ( $n=547$ ) (c) or in each site (d).



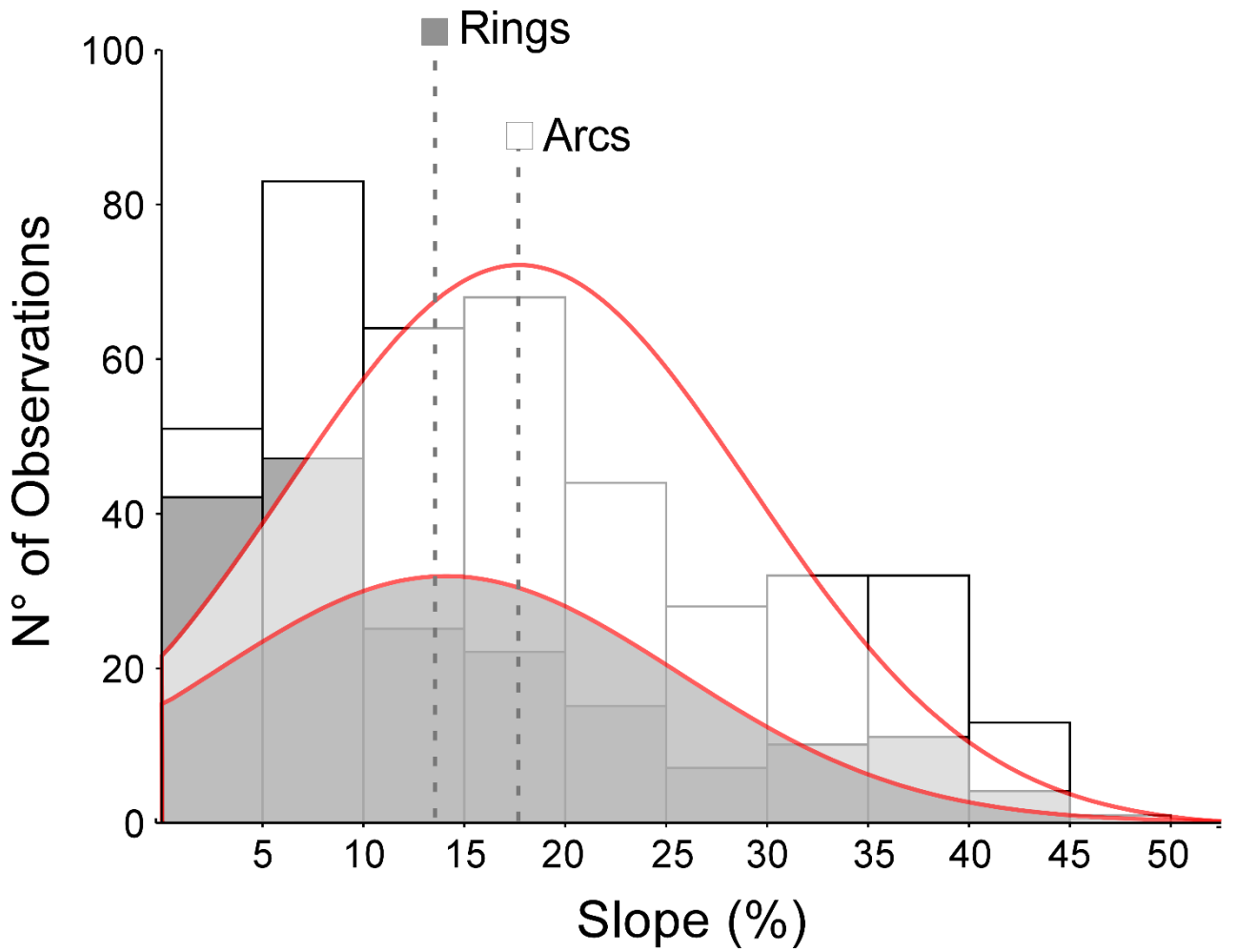
**Figure 4.** Distribution in classes of size (diameter in m) of rings (above), arcs (middle), and rotors (below). All observations for rings ( $n=183$ ), arcs ( $n=416$ ), and rotors ( $n=17$ ) are reported. Red lines represent the best fitting normal distribution. Dashed lines show average values.



**Figure 5.** Distribution of rings, arcs, and rotors in relation to elevation (above), mean annual temperature (middle), and annual rainfall (below).

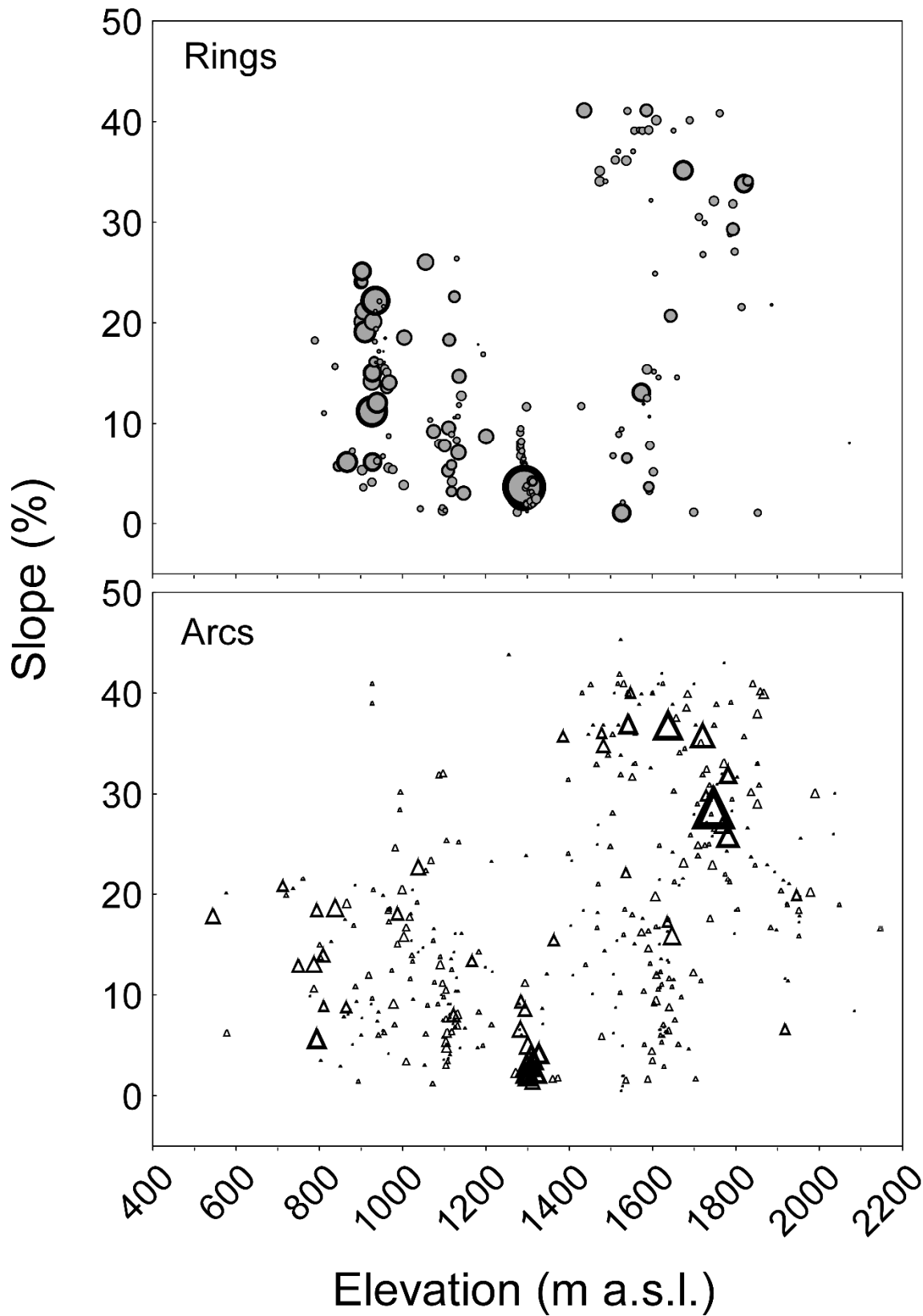


**Figure 6.** Distribution of rings (grey bars and area) and arcs (white bars and area) in relation to slope. Dashed lines refer to mode values. Red contours lines represent best fitting normal distribution.

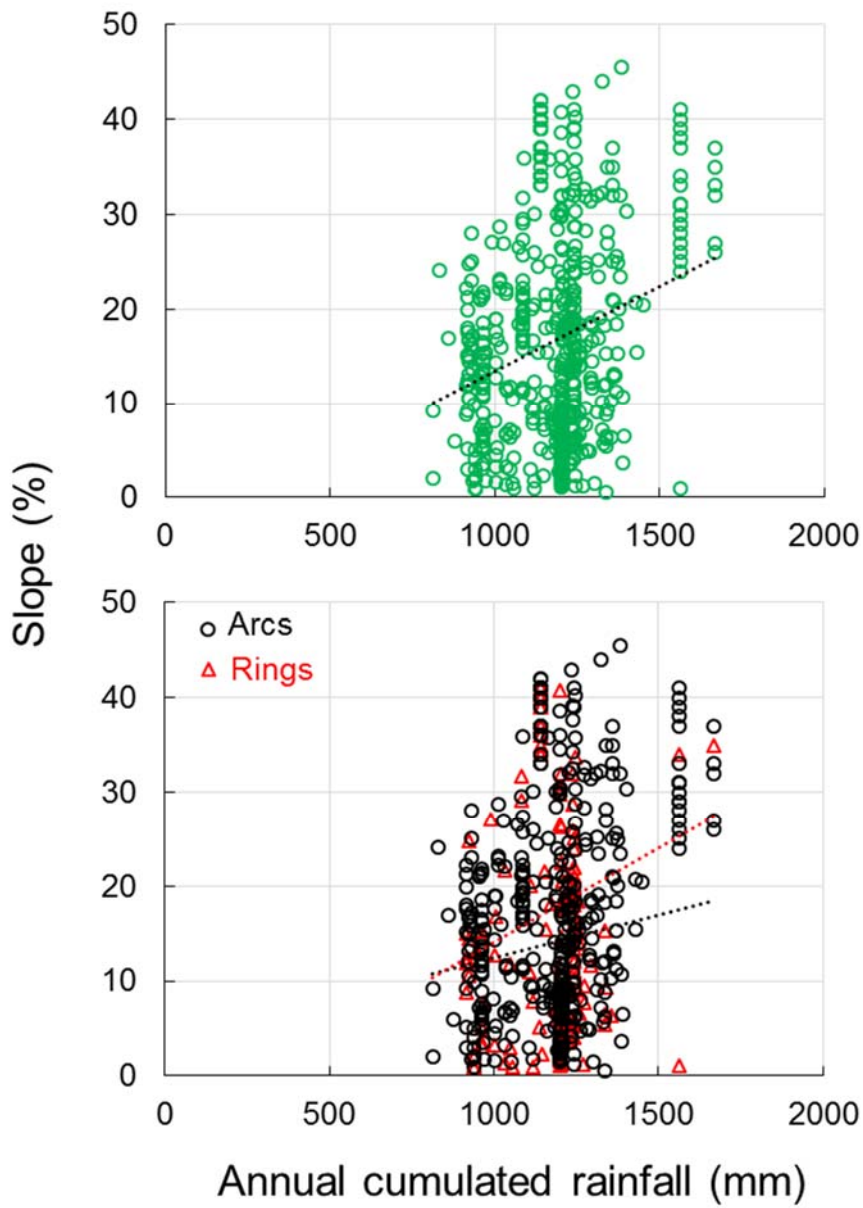




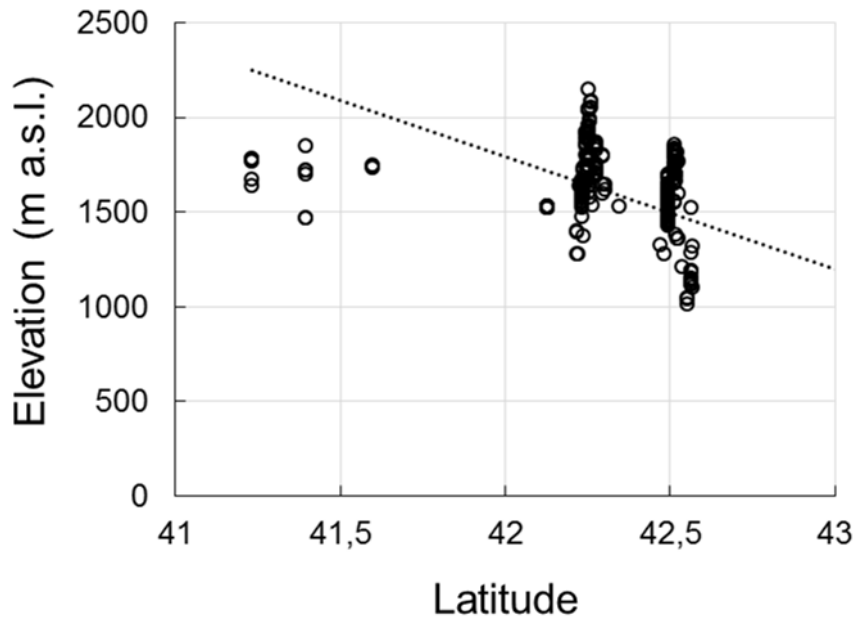
**Figure 7.** Bubble plot showing distribution of rings (up) and arcs (down) in Apennine grasslands in relation to slope and elevation. Label size for rings (circle) and arcs (triangle) is proportional to sample diameters



**Figure 8.** Linear regression between slope and annual rainfall for all FR (above) and separately for arcs and rings (below). Straight lines represent the fitted regressions. **We must add some stat**



**Supplementary Figure S1.** Linear regression between FR altitude and latitude across Apennines. Black circles indicate the position of each FR, straight lines represent the fitted regressions.



**Supplementary Figure S2.** ..... Bars plot distribution with all other temperature variables

**Supplementary Figure S3.** ..... Bars plot distribution with all other rainfall variables

**Supplementary Figure S4.** Selected images of different FR types. A: examples of rings with missing short portion of the fungal front (yellow arrows) at Fiegni site; B: examples of FR coalescence, i.e. the encounter of two fungal fronts (yellow arrows), at Montiego site; C: a population of arcs migrating upslope at the Rogedano site. Bars for scale.

