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Contrasting patterns of tree features, lichen, and plant diversity in managed and abandoned old-growth chestnut orchards of the northern Apennines (Italy)

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(Article begins on next page)

1 **Contrasting patterns of tree features, lichen, and plant diversity in managed and abandoned**
2 **old-growth chestnut orchards of the northern Apennines (Italy)**

3

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18

19 **Abstract**

20 In mountain regions of southern Europe, old-growth chestnut orchards maintained by traditional
21 management were a key component of the economic, cultural, and ecological heritage. Currently,
22 many stands are abandoned due to decreased economic sustainability even though, according to
23 European policies, the loss of traditionally managed old-growth chestnut orchards should be
24 contrasted to prevent biodiversity loss. In this study, we preliminarily mapped the remnants of old-
25 growth chestnut orchards across a region of the northern Apennines (Italy) with a strong tradition of
26 chestnut orchard cultivation. Then, we assessed the effects of management/abandonment in terms of

27 tree features (e.g. size, crown structure, health conditions), occurrence and abundance of target
28 epiphytic lichens, and richness and composition of understory vegetation. Our results revealed
29 contrasting patterns of tree features, lichen, and plant diversity in managed and abandoned old-
30 growth chestnut orchards of the northern Apennines, supporting the view that traditional
31 management is fundamental for the long-term maintenance of healthy veteran trees, the
32 enhancement of epiphytic lichens related to old-growth conditions, and plant diversity. This
33 indicates that 1000 years of ‘chestnut civilization’ represent a cultural heritage that benefits nature
34 conservation, promoting a virtuous interplay between human activities and biodiversity. For this
35 reason, policies aimed at sustaining traditional management in old-growth chestnut orchards are
36 indispensable to avoid the degradation and loss of this habitat and its centuries-old cultural and
37 ecological legacy.

38

39 **Keywords**

40 *Castanea sativa*; Chestnut diseases; Failure risk assessment; Intermediate disturbance hypothesis;

41 *Caliciales*; *Lobaria pulmonaria*

42 **Introduction**

43 In mountain regions of southern Europe, including Italy, *Castanea sativa* Mill. orchards were a key
44 component of the economic, cultural and ecological heritage. Since the early Middle Ages, chestnut
45 orchards provided one of the main staple foods (Pitte, 1986; Conedera et al., 2004; Squatriti, 2013),
46 and influenced the lifestyle of mountain people, leading to a phenomenon called ‘chestnut
47 civilization’ (Gabielli, 1994; Arnaud et al., 1997; Conedera et al., 2004). These anthropogenic
48 woods modelled the landscape and were maintained by traditional management, including mowing,
49 grazing, and tree pruning.

50 Although a first decline coincided with the eighteenth-century Little Ice Age, on Italian mountains
51 the massive abandonment of many chestnut orchards occurred after the mid-20th century. After
52 World War II, strong social-economic changes caused an exodus towards cities, provoking the loss
53 of traditional cultivation and lifestyles (Arnaud et al., 1997; Conedera and Krebs, 2008; Bounous,
54 2014). Besides these social dynamics, pests and pathogens acted as disturbance factors with both
55 direct and indirect effects, i.e. influencing perceptions and attitudes of chestnut growers towards the
56 cultivation (Turchetti et al., 2012). In the middle of the 20th century, the spread of *Cryphonectria*
57 *parasitica* (Murr.) Barr, the agent of chestnut blight, forced the abandonment of many stands, which
58 then started to evolve as mixed woods (Mondino, 1991; Romane et al., 1995; Arnaud et al., 1997;
59 Paci et al., 2000; Conedera et al., 2001). In Italy, since the beginning of the 20th century, chestnut
60 orchards have decreased by about 90%, from more than 608.000 ha (Vigiani, 1908) to 60.000 ha
61 that are currently cultivated (Bounous, 2014).

62 According to the conservation policies of the European Union, the loss of traditionally managed old-
63 growth chestnut orchards should be contrasted to prevent biodiversity loss (Arnaud et al., 1997;
64 Piussi and Pettenella, 2000). Old-growth chestnut orchards with semi-natural undergrowth are
65 included in the list of habitats worthy of conservation according to the Council Directive
66 92/43/EEC. In general, their conservation is likely dependent on moderate, but relatively
67 continuous, traditional management (e.g., Gondard et al., 2001, 2007). In this perspective, they

68 represent a tangible expression of an intangible cultural heritage, and a tight bond between man and
69 forest (see UNESCO Convention) that should be preserved.

70 Traditionally managed old-growth chestnut orchards may host species-rich plant communities
71 (Gondard et al., 2001; Barbati and Marchetti, 2005), including species of conservation concern,
72 such as several orchids or species related to dry grasslands, which may be threatened by
73 abandonment. While management intensification (i.e. frequent mowing) is unlikely to occur due to
74 the scarce economical value of this cultivation, abandonment is expected to drive major changes in
75 plant community composition and richness (Nascimbene et al., 2014, 2016).

76 In old-growth chestnut orchards, the occurrence of veteran trees provides refugia to organisms that
77 depend on this virtually missing habitat across European forests (Krebs et al., 2008). This is the
78 case for epiphytic organisms that require long ecological continuity, in particular the forest lichen
79 *Lobaria pulmonaria* (L.) Hoffm. In Italy, chestnut orchards are among the main habitats for this
80 species, often hosting luxuriant populations (e.g. Matteucci et al., 2012) that were likely originated
81 by propagules from the surrounding beech or oak forests. However, contrary to surrounding forests
82 that may have been intensively exploited, chestnut orchards provide more suitable ecological
83 conditions for this lichen. At the tree level, tree features (e.g. size, age, health conditions) are the
84 main drivers for these species, while at the stand level forest management is the main driver with
85 contrasting effects. Intensive management is usually highly detrimental, while abandonment of
86 management leading to closed canopy stands may also negatively affect this species (Nascimbene et
87 al., 2013a, 2013b, 2016; Brunialti et al., 2015). Besides local factors, also landscape features may
88 influence the occurrence and abundance of this lichen, whose dispersal is mainly related to
89 vegetative propagules over relatively short distances (Löbel et al., 2009). Due to its peculiar
90 ecology and its easy detectability it is considered a valuable indicator of forest sites that host high
91 lichen diversity and species of conservation concern (Nascimbene et al., 2010). Among these,
92 species belonging to the order *Caliciales* are associated with old-growth stands characterized by
93 long ecological continuity (Selva, 1994; Brunialti et al., 2015).

94 In this study, we preliminarily mapped the remnants of old-growth chestnut orchards across a region
95 of the northern Apennines with a strong tradition of chestnut orchard cultivation. Then, we assessed
96 the effects of management/abandonment in terms of tree features (e.g. size, crown structure, health
97 conditions), occurrence and abundance of target epiphytic lichens (*L. pulmonaria*, *Caliciales*), and
98 richness and composition of understory vegetation. Due to the low intensity practices applied in
99 managed orchards, we expect trees to have different and healthier conditions compared to
100 abandoned orchards. Moreover, we expect to find more suitable conditions for *L. pulmonaria* in
101 managed compared to abandoned orchards, and more diverse and richer plant communities that also
102 include species of conservation concern related to semi-open habitats. Finally, we expect that the
103 abundance of *L. pulmonaria* could be a reliable indicator of species related to old-growth stands, as
104 in the case of the lichens belonging to the *Caliciales*.

105

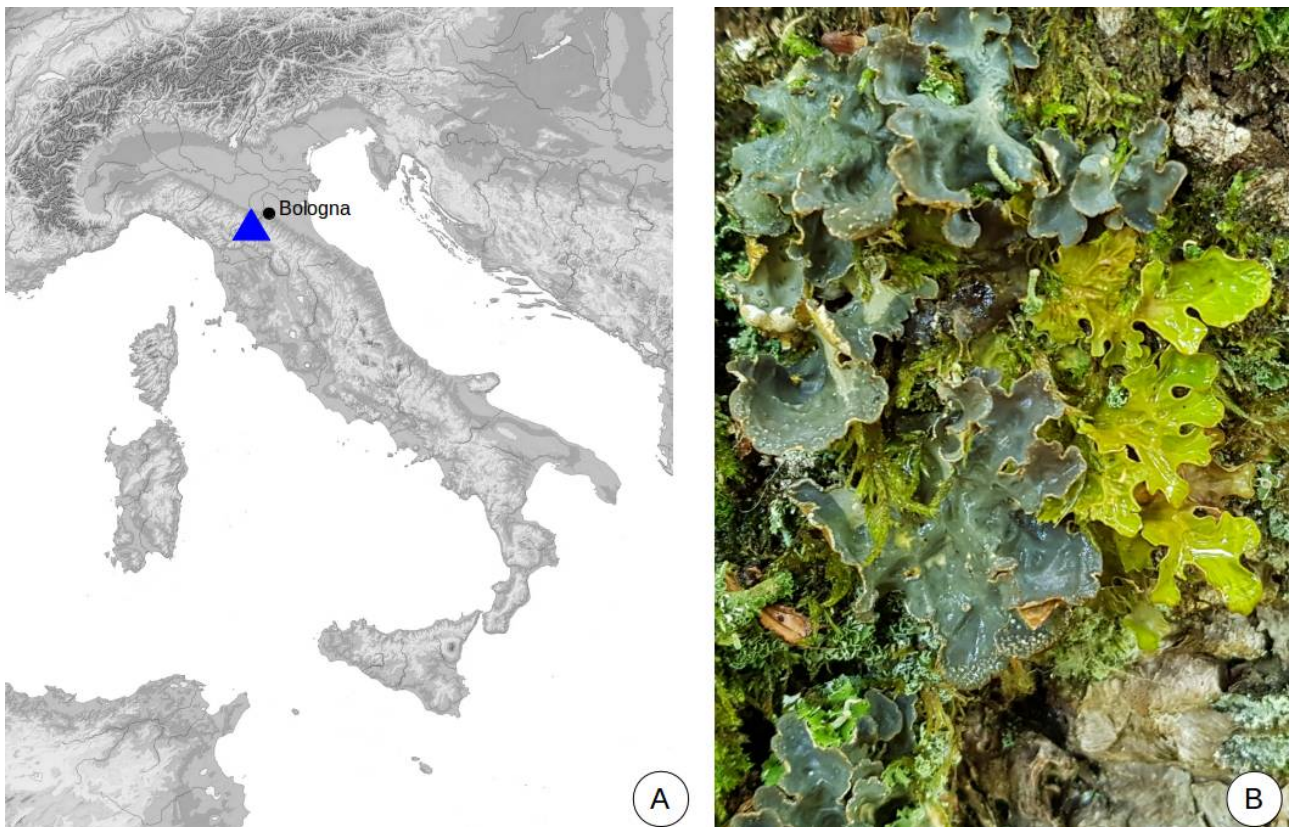
106 **Materials and Methods**

107 *Study area*

108 The study was carried out in a 1935 km² area that includes the chestnut belt of the Apennines
109 between Bologna and Modena (centroid 44.2561645 N, 10.9453453 E; Fig. 1a). Its altitudinal range
110 is about from 300 up to 1000 m a.s.l., from the deciduous *Quercus*-dominated forests to the *Fagus*
111 *sylvatica* belt (Ubaldi et al., 1993). Chestnut orchards cover only 2% of this area and are closely
112 linked to the local tradition and cultural heritage (Pezzi et al., 2019). Traditional management was
113 carried out by regular mowing (twice or thrice a year) and pruning of trees, sometimes topped.
114 Contrary to other Mediterranean areas, fire and *slupatura* (burn inside the trunk cavities and
115 mechanical removal of damaged wood) were rarely used to sanitize decayed trunks (Fenaroli, 1946;
116 Seijo et al., 2017, 2018). Burrs and pruned branches (and even leaves, when they were not used for
117 other purposes) were generally removed, burned in single burning places with localized and
118 controlled fires.

119 Thanks also to specific quality trade-marks and promotion initiatives, only *marroni* (i.e. the top
120 quality fruits) have benefitted from a renewed interest in chestnut cultivation since the 1980s (Pezzi
121 et al., 2017). In these forests, ink disease caused by *Phytophthora cambivora* (Petri) Buism. has
122 been recorded since the last century and initially caused great concern about the survival of chestnut
123 orchards due to the rapid spread of its attacks (Quattrocchi, 1938). Chestnut blight caused by
124 *Cryphonectria parasitica* occurred for the last seventy years but has been controlled by the natural
125 spread of hypovirulence (Turchetti et al., 2008). Asian chestnut gall wasp (*Dryocosmus kuriphilus*
126 Yasumatsu) was first reported in 2007 and its parasitoid *Torymus sinensis* Kamijo was first released
127 in 2010 (Vai et al., 2014).

128



130

131 **Figure 1.** a) Location of the study area (blue triangle) within Italy; b) thalli of *Lobaria pulmonaria*
132 (L.) Hoffm. (grey-green to grey-brown, on the right) and *Lobarina scrobiculata* (Scop.) Nyl. (blue-



133 grey, on the left) on the trunk of a veteran chestnut tree (the thalli are wet); view of an old-growth

134 managed (c) and abandoned (d) chestnut stand. Photographs taken by G. Pezzi, July 2018 (a, b, c),
135 and G. Maresi, July 2018 (d). [2-column fitting image, colour online only]

136

137

138 *Sample selection*

139 As the pattern of old-growth chestnut orchards was largely misunderstood and spatial information
140 was almost lacking, we preliminarily conducted informal interviews to map old-growth stands
141 within the study area (January 2017 to April 2018). We first turned to people in charge of chestnut
142 associations, then to owners/managers and local experts. New contacts were added via snowball
143 sampling (Hislop et al., 2004; Tongco, 2007). We stopped when no additional suitable stands were
144 identified, or when the same stand had been previously mentioned. In total, 48 people were
145 interviewed. These were asked to inform us of chestnut stands at least 0.2 ha wide and with a
146 majority (> 70%) of trees with a diameter at breast height (DBH) at least of 1 m. Despite the lack of
147 a strong correlation between diameter and age for these formations, according to the current
148 literature a chestnut tree with a DBH of about 1 m is centuries old (Krebs et al., 2005; Temel et al.,
149 2009). Preliminary surveys were carried out to check the congruence of the sites with the required
150 standard. Then, each chestnut stand was mapped in QGIS 3.4 (www.qgis.org) by visual
151 interpretation of current digital orthophotographs coupled to a forest map. Overall, 20 old-growth
152 chestnut orchards were mapped. Their surface varied between 0.2 to 4.4 ha (Table 1), mainly with a
153 northern aspect, at an altitude ranging between 600 and 1030 m. Slope was on average 18.3° (\pm
154 12.1°). Canopy cover was on average 82.5% (\pm 18.3%). 12 stands were still traditionally managed
155 (11 through mowing, 1 through grazing) and 8 were abandoned (Fig. 1c,d). Furthermore, 17 were
156 multi-varietal stands, while only 3 were mono-varietal stands (*marroni* stands).

157 The field survey was carried out in June-July 2018 to obtain information on the main tree features,
158 on the occurrence and abundance of target epiphytic lichens (i.e. *L. pulmonaria* and *Caliciales*), and

159 undergrowth vegetation. Each stand was sampled through an 85 m transect, along which 10
 160 chestnut trees were selected and five 5 × 5 m vegetation plots were regularly placed.

161

162

163 **Table 1.** General features of the 20 old-growth chestnut orchards. For each examined stand,
 164 centroid coordinates are given in WGS 84 as reference system.

Stand	Lat. N (°)	Long. E (°)	Extent (ha)	Altitude (m a.s.l.)	Slope (°)	Exposure	Management
ALBE	44.23431569	10.92732514	0.35	820	30	NW	Managed
ALP2	44.13343623	10.88385259	0.40	930	10	NW	
BAL1	44.26506962	11.34018064	0.53	650	20	N	
GAGG	44.24136697	10.99360049	0.56	670	10	NE	
MALA	44.22446988	10.92814309	0.51	900	5	NE	
MART	44.21683909	11.37867011	0.57	730	40	S	
MONT	44.23195568	10.92689686	0.28	800	30	NW	
PIGH	44.22164423	10.93021957	0.20	950	5	W	
SPON	44.13549313	10.89902546	0.35	890	10	NW	
PRIA	44.27244870	11.35271828	0.72	640	20	N	
STAN	44.22920382	10.92679194	0.46	840	10	W	
TRES	44.13208347	10.90276305	0.44	940	30	NW	
ALP1	44.13327507	10.88298493	0.66	890	40	NW	
BAL2	44.26424548	11.33968890	0.40	670	30	N	
BURC	44.10592682	10.92572239	4.06	1030	20	S	
POGG	44.10400122	10.92358048	4.39	1015	25	S	
POR1	44.13296076	11.09445196	0.55	860	0	NW	
POR2	44.13339436	11.09565897	0.57	870	5	NE	
SERR	44.21515106	11.09893862	1.60	670	10	NE	
TORR	44.32923316	11.04493297	1.04	600	15	NW	

165

166 *Assessment of tree features*

167 For each selected tree, DBH, tree height, crown insertion and size were measured (Klamkin, 1971,
 168 1976). A measuring tape was used for diameters, while a Vertex III Haglof hypsometer was adopted
 169 to measure height and crown insertion. The visible crown extension in each of the four cardinal
 170 directions was measured by vertically looking up. Then vitality, presence of diseases, structural
 171 condition and failure risk were evaluated. Vitality was expert-based assessed on crown condition
 172 (Turchetti et al., 2012), adopting the following scale: vigorous plant, slightly suffering, suffering,
 173 declining, dead. The three main diseases of chestnut were considered in the evaluation of healthy

174 status. Chestnut blight was assessed by counting the number of healing, healed, virulent, and
 175 intermediate cankers on the crown and trunk (see Turchetti et al., 2008). Each tree was assigned to
 176 one of the following two levels: predominance of hypovirulent (healing and healed cankers), or
 177 virulent infections. Ink disease was evaluated considering three classes: no symptoms, early
 178 symptoms (rarefied foliage and small and yellowing leaves), dead tree with completely dead crown
 179 and brown flames from collar. We also recorded old and recent attacks. Asian chestnut gall wasp
 180 (hereafter ACGW) was assessed by means of an inspection of the crown. Four levels of parasite
 181 presence were adopted: no galls observed, from 1 to 10 galls, from 11 to 100 galls, more than 100
 182 galls (heavy infestation). When possible, up to 5 galls were collected and opened to assess the
 183 presence of the parasitoid *Torymus sinensis*, whose occurrence was recorded.

184 The state of preservation of the trees was assessed considering the presence of damages and
 185 structural defects (see Table 2) in different parts of the trees (crown, trunk and collar), following the
 186 indications reported by the International society of Arboriculture (Smiley et al., 2017). The level of
 187 damage and related failure risk was assessed by adapting the risk classes reported by Smiley et al.
 188 (2017): low risk (no damage); moderate risk (low level of damages, management needed); high risk
 189 (medium degree of damages, problems for tree stability and need of management); extreme risk
 190 (high degree of damages, tree stability strongly affected and few or no possibilities of management).

191

192 **Table 2.** Summary of structural defects considered in assigning score of damage to the single parts
 193 of the trees (crown, trunk and collar).

Tree part	Defect type
Crown	Asymmetry, dead branches, old or recent pruning wounds, other wounds, decaying wood with rot and/or cavities, fruiting bodies
Trunk	Leaning, wounds, decaying wood with rot and/or cavities (% of diameter), fruiting bodies
Collar and root	Wounds, decaying wood with rot and/or cavities (% of diameter), fruiting bodies, excavation or soil movement in the root area, soil cracking

194

195 *Lichen and plant survey*

196 On each selected tree, the surface covered by *L. pulmonaria* was assessed from the base up to the
197 crown insertion as a proxy for its abundance. The total extent occupied by the species (hereafter
198 abundance) was obtained as a sum of the areas of the thalli occurring on each trunk. The area of
199 each thallus was calculated as the product of the two major axes of the thallus **measured by a ruler**
200 **positioned on a pole** (Benesperi et al., 2018). The occurrence of all the lichen species belonging to
201 *Caliciales* was recorded in a north-exposed 30 × 180 cm plot placed with its shorter side at the base
202 of the trunk. In each of the five 5x5 m plots placed along the transect, the occurrence of all vascular
203 plant species was recorded. Nomenclature of lichens follows Nimis (2016), while for plants it
204 follows Pignatti et al. (2017-2019).

205

206 *Data analysis*

207 We used Canonical Discriminant Analysis (*candisc* package; Friendly and Fox, 2017) to test the
208 effect of management/abandonment on tree features: DBH, crown size, crown insertion, height,
209 vitality, structural defects and failure risk.

210 We tested the effect of management/abandonment, tree DBH (mean value at the stand level), and
211 the landscape composition (500 m and 3000 m spatial extent) on abundance of *L. pulmonaria* at
212 stand level. Multiple linear regression was performed with a stepwise AIC method for the variable
213 selection (*vegan* package; Oksanen et al., 2019). Landscape composition (i.e. amount of beech,
214 chestnut, and oak woods) was evaluated in 500 m and 3000 m radius circular buffers centred on the
215 centroid of each old-growth chestnut orchard. The Forest Map (scale 1: 10000) of the Emilia-
216 Romagna Region (available at [http://ambiente.regione.emilia-romagna.it/it/parchi-](http://ambiente.regione.emilia-romagna.it/it/parchi-natura2000/foreste/le-foreste-dellemilia-romagna/le-foreste-in-emilia-romagna)
217 [natura2000/foreste/le-foreste-dellemilia-romagna/le-foreste-in-emilia-romagna](http://ambiente.regione.emilia-romagna.it/it/parchi-natura2000/foreste/le-foreste-dellemilia-romagna/le-foreste-in-emilia-romagna)) was used as a
218 source of data for landscape analysis. Furthermore, the capability of *L. pulmonaria* abundance to
219 predict the species richness of *Caliciales* at the stand level was tested using the Spearman's
220 correlation coefficient.

221 Finally, we tested the effect of management/abandonment on plant species richness and
222 composition. Differences in species richness between managed and abandoned stands was evaluated
223 by Pearson's test. A Non-Metric Multidimensional Scaling (NMDS) based on Bray–Curtis
224 dissimilarity matrix was used to display the pattern of plant species composition (*vegan* package;
225 Oksanen et al., 2019). An Indicator Species Analysis (*indicspecies* package, ver. 1.7.8; De Cáceres
226 2019) was used to identify species that were overrepresented in managed and in abandoned stands
227 (i.e. indicator species).

228 All the analyses were performed using R 3.6.1 for statistical computing and graphics (R Core Team,
229 2019).

230

231 **Results**

232 *Tree features*

233 Two hundred chestnut trees were sampled. The average DBH was 1.3 m (range: 0.7-3.0 m). The
234 most represented diameter classes ranged between 1.00 and 1.70 m (Fig. 2); classes from 1.90 to
235 3.00 m prevailed in abandoned stands. The average tree height was 9.3 m (range: 4.2-16.7 m),
236 crown insertion 3.3 m (range 1.7-6.0 m) and crown size 221 m² (range: 5-570 m²).

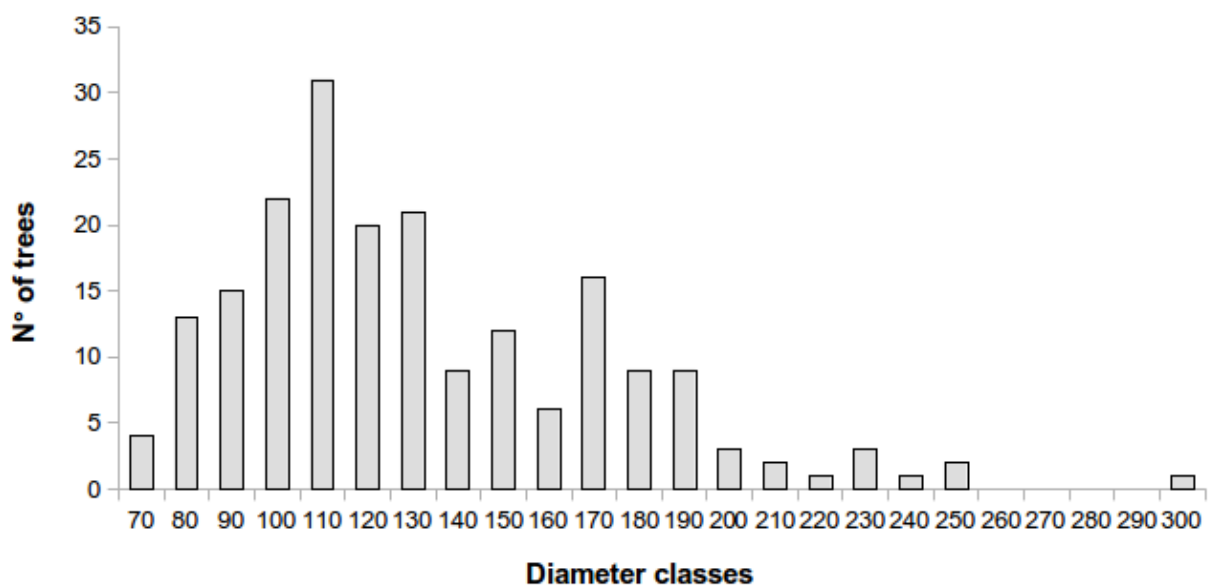
237 In general, vigorous trees prevailed (Fig. 3a); only 13 dead trees were found, 12 of which in
238 abandoned stands. The good vitality conditions were also related to low levels of damage caused by
239 pests and diseases. Chestnut blight was recorded in 98.5% of the trees (Appendix 1), prevalently
240 with hypovirulent infections; only single and sporadic recent virulent infections were found on the
241 crown. Ink disease was only recorded as old attacks in 8 trees (6 of them already dead) clustered in
242 5 stands (3 abandoned, 2 managed). ACGW was recorded on 86 trees, with less than 10 galls per
243 tree. Furthermore, 86% of 120 examined galls contained *T. sinensis* larvae.

244 However, the failure risk ranged from moderate to extreme (Fig. 3b) since all the trees showed
245 some structural problems, mainly related to the presence of wood decay and holes caused by old

246 pruning or other types of wound. Several trees had heavy branches with weak attachment to the
247 trunk.

248 On the whole (Fig. 4), a positive and significant correlation was found between management and
249 tree height ($P = 0.000$) and crown size ($P = 0.014$). In contrast, in abandoned stands trees showed
250 significantly higher values of DBH, defects of the crown, trunk, and collar and failure risk ($P =$
251 0.000), while vitality was lower than in managed sites ($P = 0.001$).

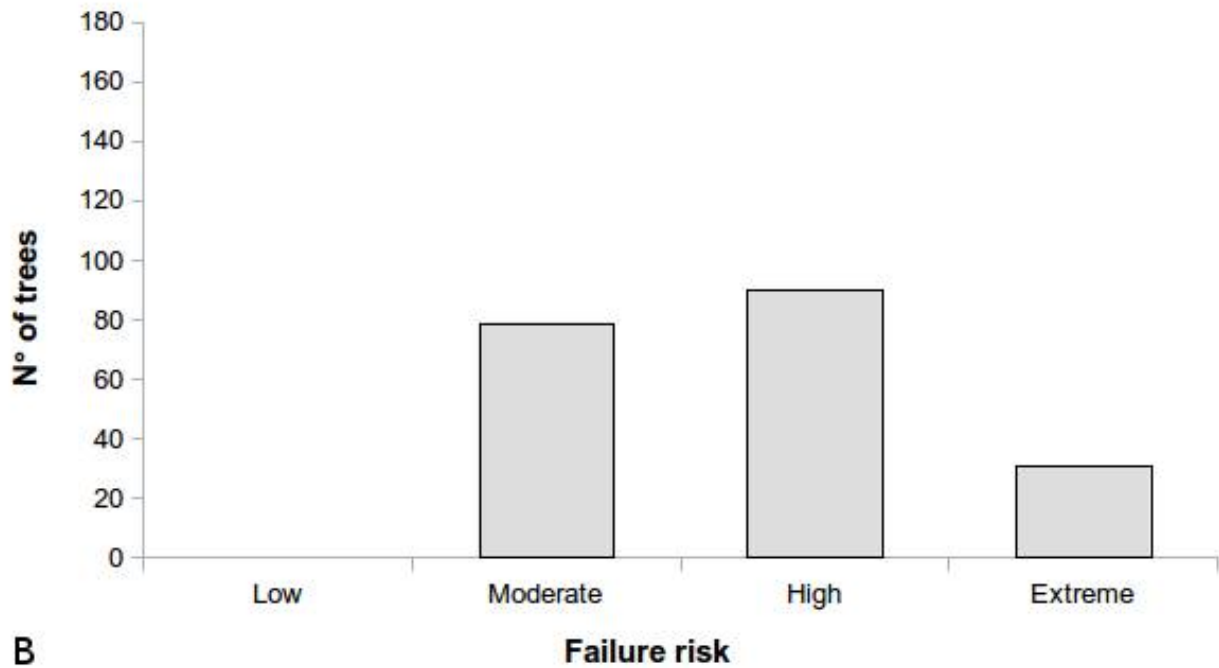
252



254 **Figure 2.** Frequency of the diameter classes of the 200 chestnut trees surveyed. Diameter classes
255 are expressed in cm. [2-column fitting image]

256

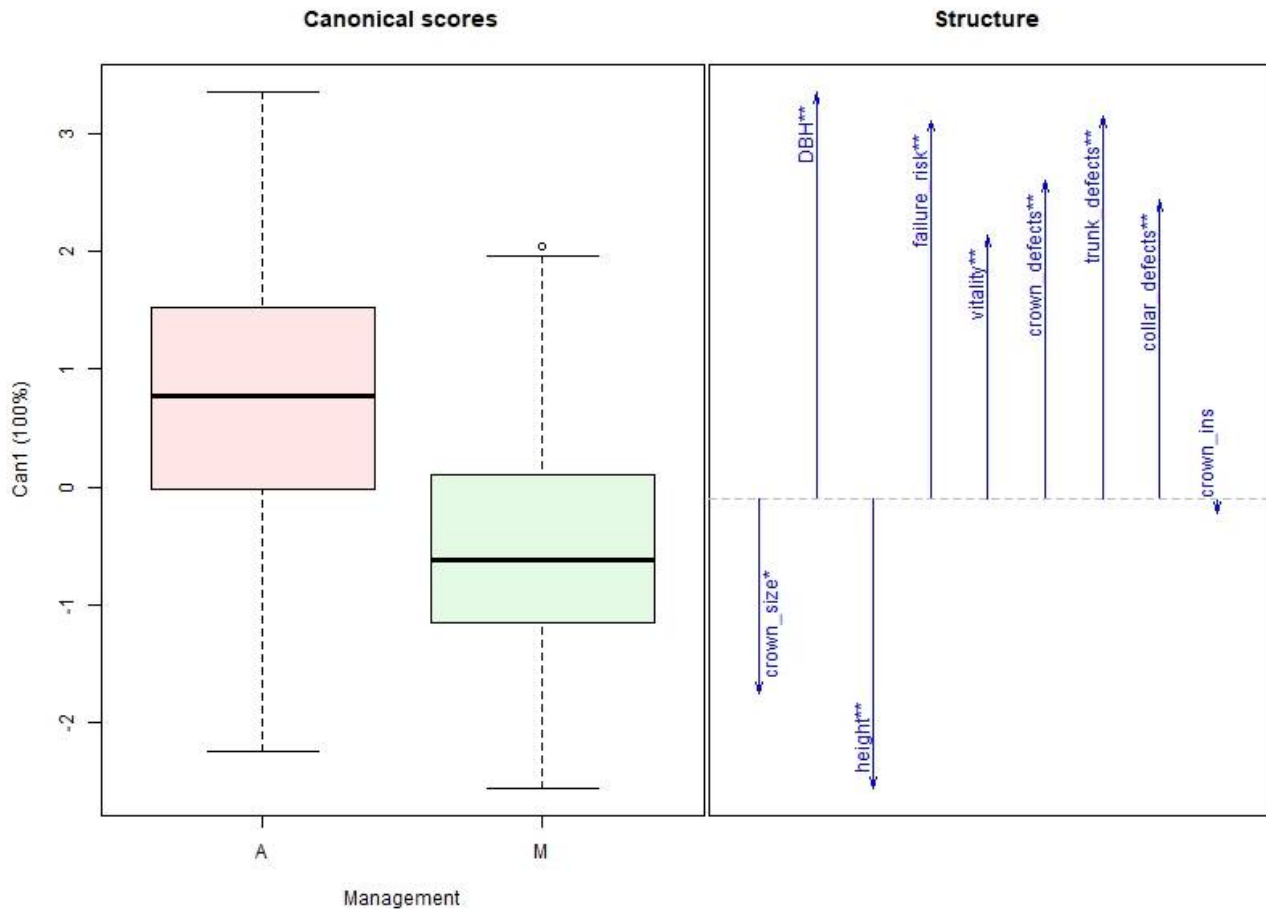
257



259 **Figure 3.** Pattern of vitality (a) and failure risk (b) of the 200 chestnut trees surveyed. [2-column
 260 fitting image]

261

262 **Figure 4.** Results of Canonical Discriminant Analysis of features measured for the sampled trees
 263 stratified under management conditions (M= Managed, A = Abandoned). Levels of significance: *
 264 $P < 0.05$, ** $P < 0.01$. [2-column fitting image; colour online only]



266 *Target epiphytic lichens*

267 *L. pulmonaria* (Fig. 1b) occurred on 38 trees (DBH = 1.32 ± 0.38 m) clustered in 11 old-growth
 268 chestnut orchards (8 managed, see Appendix 2). In two stands the species was found together with
 269 its close relative *Lobarina scrobiculata* (Scop.) Nyl. *L. pulmonaria* abundance ranged from 50 to
 270 3800 cm² at the tree level and from 50 to 14505 cm² at the stand level. The abundance of *L.*
 271 *pulmonaria* was only significantly predicted by increasing beech woods in the landscape (Table 3),
 272 both at 500 m ($P = 0.001$) and at 3000 m ($P = 0.009$) buffers. In the latter model also management
 273 was significant ($P = 0.029$), predicting higher abundance in managed stands.

274 11 *Caliciales* belonging to the genera *Acolium*, *Calicium*, *Chaenotheca*, and *Chaenothecopsis* were
 275 found in 13 stands (Appendix 2). The most common were *Calicium adpersum* (17 records in 10
 276 stands), and *C. salicinum* (12 records in 6 stands). A positive relationship was found between the

277 number of species belonging to *Caliciales* and the abundance of *L. pulmonaria* ($\rho = 0.619$, $P =$
 278 0.0056).

279

280 **Table 3.** Regression models of factors affecting abundance of *L. pulmonaria* at stand level. Model 1
 281 considers habitat amounts at 500 m ring buffer, while Model 2 at 3000 m. M = managed; A =
 282 abandoned.

Model	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-1.046	11.402	-0.092	0.928
1 M/A	24.023	13.450	1.786	0.092
Beech woods (500 m)	11.859	2.812	4.217	0.001
(Intercept)	-97.138	54.789	-1.773	0.095
2 M/A	32.081	13.386	2.397	0.029
Beech woods (3000 m)	3.422	1.162	2.946	0.009

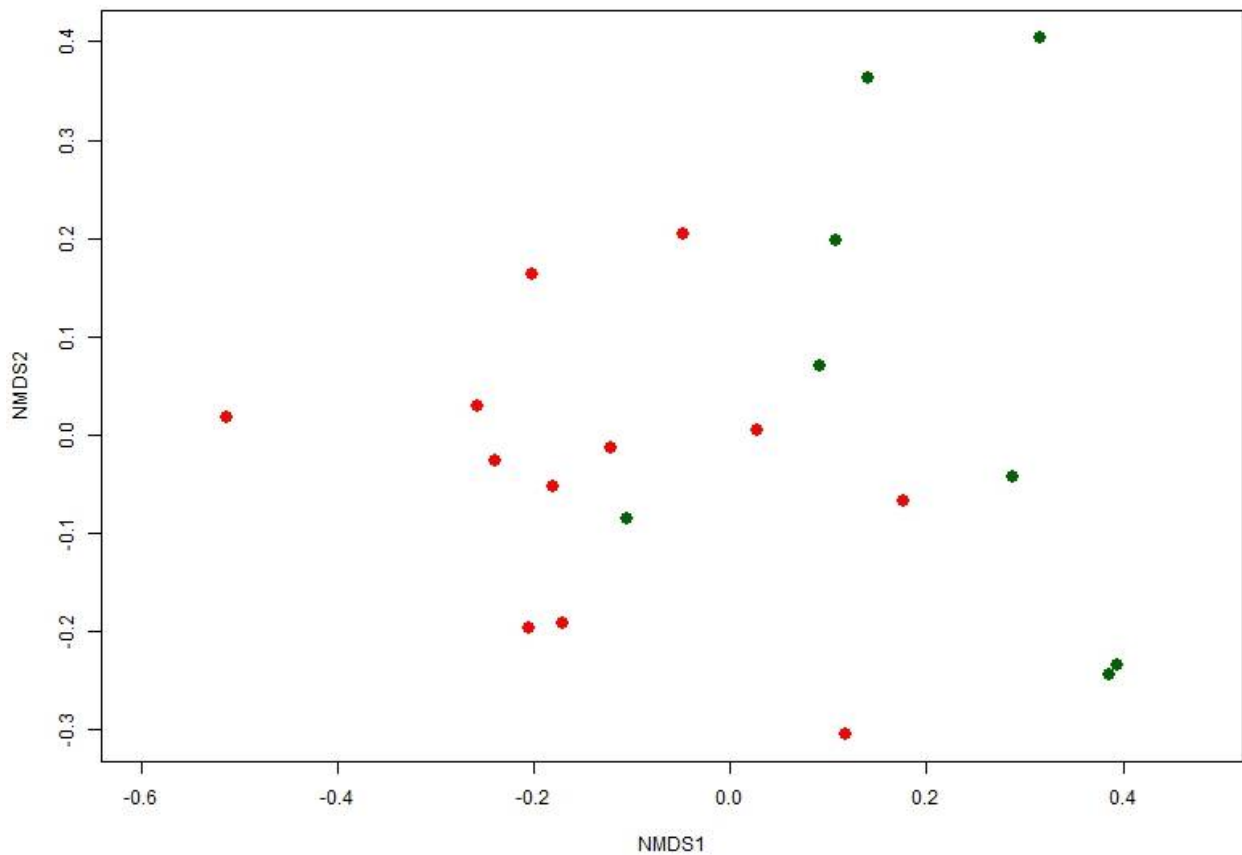
283

284 *Pattern of plant diversity*

285 Overall, 313 plant species were found. Species richness at the stand level ranged from 32 to 106
 286 species. Some species worthy of conservation were found among orchids: *Cephalanthera*
 287 *longifolia*, *C. rubra*, *Epipactis helleborine*, *Listera ovata*, *Neotinea maculata*, *Platanthera bifolia*,
 288 and *P. chlorantha*. Additional species of conservation concern, which are protected at regional level
 289 (Regional Law 24-1-1977, n. 2), were *Dianthus armeria*, *D. balbisii* and *Gentiana asclepiadea*. 40
 290 occurrences of these species were recorded in managed stands and 20 in abandoned stands.

291 Managed stands had a significantly higher species richness than abandoned stands ($P = 0.0014$). In
 292 managed stands, species richness ranged from 72 to 106 species (average: 87.42 ± 3.42), whereas in
 293 abandoned stands it ranged from 32 to 88 species (average: 61.25 ± 6.80). The effect of
 294 management on plant communities was also confirmed by the pattern of species composition, as
 295 indicated by the NMDS plot (stress 0.096, Fig. 5). The Indicator Species Analysis revealed 22
 296 species significantly overrepresented in managed stands and 7 in abandoned stands (Table 4). In
 297 managed stands, grassland species prevailed, whereas in abandoned stands wood and pre-forestry
 298 species prevailed.

299



300 **Figure 5.** NMDS plot of the plant species composition pattern in managed and abandoned stands.

301 Red dots: managed stands; green dots: abandoned stands. Stress = 0.096. [2-column fitting image;

302 colour online only]

303

304 **Table 4.** List of indicator species for managed and abandoned stands. The *p*-value is also given.

Stand type	List of species
Managed	<i>Anthoxanthum odoratum</i> and <i>Lotus corniculatus</i> ($P < 0.01$), <i>Lychnis flos-cuculi</i> , <i>Holcus lanatus</i> , <i>Genista tinctoria</i> , <i>Cynosurus cristatus</i> , <i>Campanula rapunculus</i> , <i>Plantago lanceolata</i> , <i>Achillea collina</i> , <i>Trisetum flavescens</i> , <i>Danthonia decumbens</i> , <i>Polygala vulgaris</i> , <i>Aira elegantissima</i> , <i>Leontodon hispidus</i> , <i>Schedonorus pratensis</i> , <i>Taraxacum</i> gr. <i>officinale</i> , <i>Calluna vulgaris</i> , <i>Leucanthemum</i> gr. <i>vulgare</i> , <i>Trifolium campestre</i> , <i>Helianthemum nummularium</i> , <i>Rhinanthus alectorolophus</i> ($P < 0.05$)
Abandoned	<i>Fraxinus ornus</i> , <i>Rosa canina</i> , <i>Lactuca muralis</i> , <i>Cytisus scoparius</i> , <i>Melica uniflora</i> , <i>Abies alba</i> , <i>Teucrium scorodonia</i> ($P < 0.05$)

305

306 Discussion

307 Our results revealed contrasting patterns of tree features, lichen, and plant diversity in managed and
 308 abandoned old-growth chestnut orchards of the northern Apennines, supporting the view that

309 traditional management is fundamental for the long-term maintenance of healthy veteran trees, the
310 enhancement of epiphytic lichens related to old-growth conditions, and plant diversity.

311 Our old-growth chestnut orchards survived the three main diseases that are currently quite
312 compatible with tree health. For example, blight damages are low, usually involving only single
313 desiccated branches, and hypovirulence predominated as in other Italian chestnut areas (Turchetti et
314 al., 2008). Also ink disease rarely occurs in the investigated stands, even if the disease remains as a
315 potential risk. ACGW is present only with few galls always parasitized by *Torymus sinensis*, thus
316 confirming the effectiveness of the biological control (Vai et al., 2014). However, in abandoned
317 orchards these reduced damages likely accumulate over the years, producing the spectral aspect of
318 these stands (Turchetti and Maresi, 2008). Moreover, in abandoned stands crown size, and height
319 are lower possibly due to competition with invading trees, while crown, trunk and collar defects due
320 to wood decay are higher. [Light reduction, competition and decay are worsened by the age of the
321 plants, producing the failure or the death of the old trees, whose main trunk is often replaced by
322 clones of the same tree \(when some roots survive\) as if it were coppice.](#) Consistently, our results
323 indicate that in abandoned stands failure risk is significantly higher than in managed stands and
324 overall tree vitality is lower.

325 In managed orchards the occurrence of veteran trees arranged in an open forest structure [and the
326 absence of shoots that cover the trunks](#) may explain the higher abundance of the forest lichen *L.*
327 *pulmonaria* (Nascimbene et al., 2013) as compared to abandoned stands, where increasing canopy
328 closure [and the decay of the more ancient trees coupled with re-sprouting of new shoots around
329 remnant trunks](#) may reduce [habitat suitability](#) for this large lichen. In these anthropogenic habitats,
330 the maintenance of the most valuable species is thus related to low intensity, traditional
331 management (Nascimbene et al., 2014). The exclusive occurrence of the declining and red-listed
332 lichen *Lobarina scrobiculata* (Nascimbene et al., 2013c, 2016) and the higher occurrence of
333 *Caliciales* (whose species richness is predicted by the abundance of *L. pulmonaria*) in managed
334 orchards clearly corroborate the importance of these anthropogenic habitats for epiphyte

335 conservation. However, our results also stress the role of landscape composition around the old-
336 growth chestnut orchards, indicating that the abundance of *L. pulmonaria* is maximized in stands
337 embedded in a beech forest-dominated landscape. The huge historical herbarium records, available
338 since the first half of 19th century, suggest a long lasting persistence and a higher commonness of
339 both *L. pulmonaria* and *Lobarina scrobiculata* in our study area (Bertoloni, 1867; Saccardo and
340 Fiori, 1894; Zanfognini, 1902; see also Appendix 3), where they established luxuriant populations
341 in both beech and chestnut stands (Bertoloni, 1867). In this historical scenario, **old-growth** beech
342 forests may be considered the primary habitat for these lichens, while anthropogenic chestnut stands
343 likely provided a suitable secondary habitat **that allowed their survival when most beech stands**
344 **were converted to coppice**. Frequent disturbance in **coppice** stands **coupled with the absence of old**
345 **trees and the muffling of the trunks by the excess of shoots** may have caused the rarefaction of these
346 lichens in **beech stands**, while the more stable ecological conditions **and the occurrence of veteran**
347 **trees** in old-growth chestnut orchards provided a **valuable** refuge. In this perspective, the effect of
348 the landscape found in our study may reflect a historical condition in which the **old-growth** beech
349 forest originally supplied propagules for the establishment of the species in old-growth chestnut
350 orchards that currently are likely the main propagule hot-spots in the mountain forest landscape of
351 the Northern Apennines (Matteucci et al., 2012).

352 The role of managed old-growth chestnut orchards for biodiversity is also confirmed for plant
353 communities (e.g. Gondard et al., 2001, 2007; Nascimbene et al., 2014), with significantly higher
354 species richness than in abandoned stands. Moreover, our results indicate that the abandonment of
355 management practices (i.e. mowing and/or grazing) triggers compositional shifts that may cause the
356 loss of several species of conservation concern, as in the case of many orchids. In general, plant
357 communities of the managed stands host species related to open habitats (*Molino-Arrhenatheretea*
358 Tüxen 1937 or *Festuco valesiacaе-Brometea erecti* Br.-Bl. & Tüxen ex Br.-Bl. 1949), while in
359 abandoned stands pre-forestry and woody species tend to prevail (*Laburno-Ostryion* Ubaldi 1980
360 and/or *Fagetalia sylvaticae* Pawłowski in Pawłowski, Sokołowski & Wallisch 1928; Ubaldi et al.,

361 1993; Pezzi et al., 2011). Historical records (Bertoloni, 1867) corroborate the view that the floristic
362 composition of managed stands remained almost unchanged for decades, further underlining the
363 role of traditional management for maintaining stable ecological conditions (Tomaselli, 1989).

364

365 **Conclusions**

366 Our study supports the view that old-growth chestnut orchards are a perturbation-dependent system
367 (Vogl, 1980; Gondard et al., 2001) whose effectiveness for biodiversity conservation depends on the
368 maintenance of low-intensity management. In this perspective, mowing and pruning are still the
369 most effective practices for preserving the old-growth chestnut orchard habitat and its associated
370 biodiversity. However, pruning needs to be light and not frequent, aiming to restore a suitable
371 architectural structure, cutting only dangerous branches and saving biodiversity niches (Zapponi et
372 al., 2017). Topping and heavier pruning used in the past are likely the main causes of the current
373 precarious status of the surviving trees. Moreover, also sporadic fire as a sanitation method or to
374 burn mowed and pruned material should be avoided, since it may negatively impact on long-term
375 soil conservation. Our results indicate that 1000 years of *chestnut civilization* represent a cultural
376 heritage that benefits nature conservation, promoting a virtuous interplay between human activities
377 and biodiversity. For this reason, policies aimed at sustaining traditional and even more sustainable
378 management in old-growth chestnut orchards are indispensable to avoid the degradation and loss of
379 this habitat and its centuries-old cultural and ecological legacy.

380

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397

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564

565 **CR CRediT author statement**

566

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