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This is the author's manuscript

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1614155> since 2017-05-19T12:41:15Z

Published version:

DOI:10.1016/j.foreco.2016.10.033

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1 **Forest dynamics and disturbance regimes in the Italian Apennines**

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10

11 **Abstract**

12 Forests of the Apennines are characterised by high canopy cover and high tree species diversity (being at
13 the interface between two major climatic zones of Europe), and provide important ecosystem functions
14 to millions of people. They exemplify cutting-edge themes such as forest ecology in warmer climates,
15 consequences of heavy land use, and resilience at the trailing edge of the distribution of many European
16 forest species (Silver fir, Norway spruce, Beech, Black pine, Birch).

17 We introduce the setting under the geological and climatological point of view and review the literature
18 on the interactions between these long-term drivers and the specific, structural, and genetic diversity of
19 these forest communities (e.g., effects of glacial refugia or tectonic/volcanic activity), followed by a
20 brief outline of what little is known about natural disturbance regimes and their range of variability.

21 Anthropogenic disturbances (fire, grazing) and land use changes (abandonment of cropland and pasture)
22 have been by far the main drivers of forest dynamics at least for the last two millennia, determining for
23 examples overageing of coppices, treeline advances, forest encroachment on former agricultural land.

24 We suggest considerations about the interplay between these land use changes and disturbance drivers
25 (e.g. fuel continuity), summarise comparisons between managed and unmanaged forests (e.g., increase
26 in tree size, deadwood, biodiversity indicators), and elaborate on current proposals for climate-adapted

27 management, highlighting specific and genetic diversity as an important source of resilience and
28 adaptive potential.

29

30 **Keywords**

31 Forest dynamics; Italy; Land use change; Mediterranean mountains; Natural disturbances;

32 Palaeoecology

33

34 **Highlights**

- 35 • Forests of the Apennines have been poorly explored in the ecological literature
- 36 • Anthropogenic disturbances and land use changes are the main drivers of forest dynamics
- 37 • Regimes of natural disturbances (avalanches, fires, wind, insects) are masked by human impacts
- 38 • Specific and genetic diversity (e.g., trailing edges) are an important source of resilience and
39 adaptive potential

40

41

42 **1. Introduction**

43 Italy has two main mountain systems: the Alps and the Apennines (Figure 1). The alpine area represents
44 approximately one-quarter of the total Italian land surface (75,000 km²), while the Apennine region
45 accounts for approximately two-fifths (120,000 km²). Together they make up approximately 35% of the
46 total area of the country.

47 The Apennines include a series of mountain ranges (approximately 38-45° N and 8-17° E) bordered by
48 narrow coastlands that form the physical backbone of peninsular Italy. Their total length is
49 approximately 1,400 kilometres, and their width ranges from 40 to 200 km. Mount Corno Grande (2,912
50 m a.s.l.) is the highest point of the Apennines proper on the peninsula, while the stratovolcano Mount
51 Etna (3,323 m) in the island of Sicily is the highest peak, and the highest active volcano in Europe.

52 The Apennines are characterised by high forest cover and high tree species diversity (being at the
53 interface between the temperate and Mediterranean biomes of Europe). Apennine forests provide
54 important ecosystem services for millions of people, e.g., timber and energy wood, non-wood forest
55 products, water, biodiversity, and recreation (Vizzarri et al. 2015). Their functioning is driven by similar
56 macroecological factor as those at work in the Alps (Bebi et al. 2016), but the local peculiarities of
57 geological history, climate, and human influence have shaped a very different situation in terms of forest
58 composition, structure, and landscape mosaic. However, the Apennines have been much less explored
59 than the Alps in the literature in terms of disturbance regimes (both natural and anthropogenic) and their
60 effects on ecosystem processes.

61 The aim of this review is to summarize the main drivers of the composition, cover, structure, and
62 dynamics of Apennine forests, including both macroecological constraints (geology and climate), human
63 influence, and natural disturbance agents. In order to do so, we searched the existing scientific literature
64 (Google Scholar database) using the keywords “Apennine” and “forest”, plus each of the following:
65 “pollen OR charcoal”, “land use change”, “(stand OR forest) structure”, and “disturbances” (all words
66 used in either English or Italian languages). The search produced 9860 unique records. After filtering out

67 irrelevant and inaccessible papers, the total number of reviewed studies was 170 (i.e., 74, 42, 28, and 24
68 papers for each of the last four keywords, respectively) (Appendix 1).

69 Although focused on a specific geographic area, the history and dynamics of forests illustrated herein
70 are similar to those occurred in other heavily anthropized mountain regions of the world, and our
71 conclusions could be relevant in such areas as well.

72

73 **2. Macroecological drivers**

74 **2.1 Geology**

75 The Apennine orogeny began in the middle Miocene (about 20 million years ago, i.e., millions of years
76 later than the Alpine orogeny) (Carminati et al. 2012) as a consequence of the subduction of the African-
77 Adriatic plate below the European plate (Carminati et al. 2003), and still continues today (Devoti et al.
78 2008). At the same time, large faults developed along the western side of the Apennines, connected to a
79 crustal thinning that resulted in the opening of the Tyrrhenian sea (Rosenbaum and Lister 2004).

80 Therefore, these young mountains of Italy are of paradoxical provenience, deriving from both
81 compression (folded systems) and extension (fault-block systems). This is responsible for the great
82 variety of rock types and the rugged appearance of the range today. In the north, sandstones, marls, and
83 greenstones occur. In the central Apennines clay, sandstone, and limestones are common. In the
84 southern Apennines large calcareous rock outcrops are separated by lowland areas of shale and
85 sandstone, and interrupted by extensive argillaceous rock types, which originate frequent erosion of the
86 “badlands” type.

87

88 **2.2 Historical climate**

89 Italy is placed at the boundary between the Mediterranean and the temperate zone of the boreal
90 hemisphere (Blasi et al. 2007). The Mediterranean Sea, which almost surrounds the country, is a
91 reservoir of heat and humidity. The Apennines intercept Atlantic perturbations and, with their rough

92 morphology, experience sharp temperature variations over short distances, frequent rainfalls for
93 adiabatic cooling and *stau* wind currents, and winter fog stagnation inside the several internal closed
94 basins and narrow valleys. The climate is of the mountain variety of the Mediterranean type, with dry
95 summers and rainy (and snowy) winters. Mean temperature ranges from 0 to 11 °C in January and from
96 24 to 28 °C in July. In the upper zone (over 2,000 m) there is snow 180-190 days per year. Annual
97 precipitation ranges from 600 to 4500 mm. Because the Adriatic Sea, rather thin and shallow, exerts a
98 less pronounced effect than the Tyrrhenian Sea, most of the precipitation falls on the western slopes of
99 the mountains (> 3,000 mm per year in Liguria). Precipitation seasonality is another typical trait of
100 Mediterranean climates; summer cyclones bring in torrential rains and may cause severe flooding. The
101 aridity index (ratio between precipitation and ET_0 : Wang et al. 2012) is often < 0.65 (sub-humid),
102 especially in Sicily, Apulia, Sardinia and Basilicata.

103

104 **2.3 Climate change**

105 The Mediterranean basin is very sensitive to climate variation (Lionello et al. 2006). In the last century,
106 Italian temperatures registered a warming (+1°C on average between 1865 and 2003) comparable to
107 Europe-wide trends (Brunetti et al. 2006). Annual precipitation and the number of rainfall days
108 decreased (811 to 723 mm in 1961-2000, and -10% in 1866-1996, respectively), but the intensity of
109 individual events increased (Brunetti et al. 2001). Hot waves increased in frequency and duration (66 to
110 187 hot days in 1951-2000) (Lionello et al. 2010). These trends are expected to worsen in the next
111 decades (Giorgi and Lionello 2008). Conditions simulated by HadCM3 forecast a remarkable increase of
112 maximum July temperatures over the whole country (+7.6 °C and +5.6°C in 2080 under A2 and B2
113 scenarios, respectively). The highest increases are concentrated in the northern Apennines, the lowest in
114 the South. Minimum January temperature is also expected to increase, albeit moderately (+1.8 to +2.8°C
115 in 2080). An overall reduction in annual precipitation is projected for year 2080, more pronounced under
116 the A2 (-18.1%) than the B2 scenario (-5.9%), mainly concentrated along the central Apennines (-22.8%

117 and -9.3% under A2 and B2 scenarios, respectively). The highest reductions are expected in summer (-
118 48.5% and -41.5%) (Dibari et al. 2015). The potential consequences of the northward extension of the
119 Mediterranean subtropical climatic region in Italy include a decline in soil organic carbon, and a
120 reduction in snow cover associated with warming. In turn, a shallower, ephemeral snowpack will
121 promote soil freezing, with important consequences on soil nutrient dynamics (e.g., higher N losses)
122 (Edwards et al. 2007).

123

124 **3. Vegetation history**

125 The flora of the Apennines is the result of several “floristic streams” that have reached Italy since the
126 Tertiary (Valva 1992; Uzunov et al. 2005). Most species migrated from the balkanic-illiric province
127 during the Messinian salinity crisis in the high Miocene – a flow that originated most of the
128 Mediterranean flora (Bocquet et al. 1978) and which explains many disjunct distributions, e.g., *Pinus*
129 *heldreichii* Christ. (Piotti et al. 2014). Another wave of plant migration originated in the Iberian
130 peninsula and northern Africa, again during the Messinian, and enriched the Apennine flora with several
131 drought-tolerant elements (Biondi et al. 2015). During the later cold periods of the Pliocene, some alpine
132 and boreal species migrated from central and northern Europe (Pedrotti and Gafta 2003), while an
133 eastward migration, linked with plate movements, extended the distribution of some Tyrrhenian
134 elements to the southern tip of the peninsula (e.g., *Alnus cordata* (Loisel) Desf. and *Pinus nigra* Arnold
135 in the Calabrian Apennine) (Blasi et al. 2007).

136 After the Pleistocenic glacial (150,000-130,000 years Before Present), at least 24 transitions between
137 glacial (stadial) and warm (interstadial) climate occurred. Several tree species started to expand out of
138 their glacial refugia during each interstadial (e.g., oak in Sicily: Rossignol-Strick and Planchais 1989),
139 only to retreat again when cold and dry conditions returned (Figure 2). However, glacial refugia during
140 this time granted that some of the vegetational complexity that had originated in the Pliocene-

141 Pleistocene period could be maintained in part until the modern era (1800- first half of 1900), especially
142 in the remote areas of the central and southern Apennines.

143 At the Last Glacial Maximum (22,000 to 14,000 years BP) summer temperatures were 6 to 8°C cooler
144 than at present, and sea level 120-140 m lower. Both paleoecological and simulation studies suggest
145 very little closed woody vegetation in the Mediterranean (Ray and Adams 2001; Di Rita et al. 2013),
146 with scattered trees or small pockets of open woodland from about 500 m above [present] sea level in
147 the Apennines and in the other Southern European peninsulas (Tzedakis et al. 1995). Since then, post-
148 glacial migration followed four main routes: (1) northward and upward range expansion, e.g., beech and
149 fir (Bradshaw et al. 2010); (2) continuous persistence with increasing frequencies, e.g., oaks (Petit et al.
150 2002); (3) discontinuous persistence at low frequencies, e.g., birch (Plini and Tondi 1989); (4) failed
151 migration and persistence in localized refugia, e.g., spruce (*Picea abies* (L.) Karst.) (Ravazzi 2002).

152 Following the Younger Dryas cold interval (10,800-10,000 years BP), while beech (*Fagus sylvatica* L.)
153 was gaining dominance over much of temperate Europe (Bradshaw et al. 2010), the Mediterranean
154 region showed moister-than-present conditions. Near the coasts forests might have been dominated by
155 deciduous oaks (Lippi et al. 2007), while mountain areas developed two forest belts– the upper
156 dominated by fir (*Abies alba* Mill.), and the lower with mixed deciduous forests dominated by oak and
157 including maple, ash, linden and elm (Watson 1996).

158 During the Holocene thermal maximum (7,000 to 4,000 years BP), paleoecological records show a rapid
159 and fairly simultaneous decline of elm throughout Europe (Huntley et al. 1989), and a strong increase in
160 beech, which successfully invaded the fir woodland to form a mixed fir-beech complex (Bradshaw et al.
161 2010). Evergreen mediterranean vegetation replaced the deciduous forest on limestone soils (Di Rita and
162 Magri 2009).

163 In the last 4,000 years, climate has been rather stable (except for short-lived fluctuations such as the 550
164 AD and the Little Ice Age cool periods). In the absence of land use by man, forests would dominate the
165 potential vegetation of most of the Apennine region, with an elevational separation between

166 Mediterranean evergreen, deciduous broadleaves, and conifers resulting from differences in cold
167 tolerance of each species (De Philippis 1937). Mountain conifers may descend in the broadleaves belt, as
168 deciduous broadleaves do in the evergreen mediterranean vegetation belt, due to the fact that high
169 temperature extremes produce less distinct zonations (Pignatti 2011). Besides temperature, water
170 availability is a major factor influencing potential forest vegetation: forest cover is generally higher in
171 the regions with temperate climate compared to those with Mediterranean climate, but also in regions
172 with high orographic precipitation (e.g., the Tyrrhenian side of the northern Apennines) with respect to
173 more continental and drier areas (Magri et al. 2015). The superposition of climatic gradients, post-glacial
174 migration routes, and complex orography has produced for most tree species in the Apennines a
175 fragmented distribution, which has promoted reproductive isolation and high genetic diversity (Magri et
176 al. 2006, Leonardi et al. 2012).

177

178 **4. Human history and impacts on vegetation**

179 Anthropogenic land use has had a profound effect on forests of the Apennine region and, in most cases,
180 outweighed by far the effects of macroecological constraints (Brown et al. 2013).
181 Even before the advent of agriculture, the presence of humans has severely influenced the composition
182 and distribution of forests. This is exemplified by the late Holocene dynamics of fir and beech. During
183 the early Holocene (9000–6000 years BP), fir became abundant from the sea level to the mountains
184 (Montanari 1989). After 6,000 years BP, however, its presence declined in many sites (Magri et al.
185 2015), leading to the current reduced distributions. The reasons for such decline, and the relative
186 importance of climate, competition, and anthropogenic impact, are debated. On one hand, fir has
187 retreated into more or less the same areas where it was found at the beginning of the present interglacial
188 (Muller et al. 2007), supporting the hypothesis that its Holocene dynamics are driven by long-term
189 climatic and edaphic patterns (Joannin et al. 2012). On the other hand, multiple palaeoecological
190 evidence shows a synchrony between the reduction of fir at 6,000-3,000 years BP and an increase in

191 human activity, especially from pastoralism and fire (Henne et al. 2013). These dynamics would imply a
192 much wider climatic niche than previously thought for fir, which could have been part of sub-
193 Mediterranean oak forests, as suggested also from Pleistocenic pollen evidence (Tinner et al. 2013).
194 At the same time, beech, which had started expanding into southern and central Italy already 18,000
195 years BP (Joannin et al. 2012), reached its maximum spread between 8,000 and 4,000 years BP (Branch
196 and Marini 2014), i.e. simultaneously to the decline of fir, leading to a mixed *Abies-Fagus* association in
197 the upper belt between from 5,200 yBP and then to a dominance of beech from around 2,900 years BP
198 (Watson 1996). The expansion of beech in the Northern Apennines may have been favored by a
199 decrease in summer insolation (Berger 1978) and a smoothing of seasonal climate extremes (Huntley et
200 al. 1989; Watson 1996), but also facilitated by human activities. Since beech seedlings require moderate
201 light intensity for development (Ellenberg 1986), it is reasonable that clearing of the pre-existing dense
202 fir forest has determined a shift in dominance between the two species (Valsecchi et al. 2008).
203 The transition of the first human communities out of hunting-gathering occurred around the start of the
204 second millennium BC. From this time, semi-nomadic agriculture and herding were accompanied by
205 widespread slash-and-burn deforestation (Watson 1996), a higher hydrogeologic instability (Cremaschi
206 et al. 2008) and an increase in soil erosion, which favored some pioneer tree species, e.g., Calabrian pine
207 (*Pinus nigra* subsp. *laricio*) (Nicolaci et al. 2014). Starting from the 8th century BC, under the Roman
208 influence, Apennine forests were used for timber, fuelwood, and cleared for agriculture and pastures.
209 Forests in the vicinity of the sea or major rivers were harvested and floated to the nearest ports as civil
210 and naval timber (*silva incaedua*); the others were coppiced (*silva caedua*), harvested by hand or
211 animals, and used for tools and small crafts, or as energy wood. This system is believed to be
212 responsible for the degradation of forests along coasts (Calò et al. 2012), and on major river basins
213 (Mercuri and Sadori 2013). However, recent evidence (Sadori et al. 2015) shows that at least beech-fir
214 forests were more widely distributed than today, despite the fact that fir was the most desirable species
215 for ship hulls, construction timber, and furniture (Allevato et al. 2010). Another source of forest

216 degradation was transhumant sheep herding, which was favored in southern Italy by the territorial
217 unification brought about by the Romans, and was practiced up to the beginning of the 20th century. At
218 its apex (5.5 million sheep in year 1604: Venanzoni et al. 1993), the network of seasonal transhumance
219 “highways” had a cumulative length of more than 3000 km. Some Apennine forests still show the legacy
220 of their past use as wooded pastures, e.g., simplified vertical structure (Mancini et al. 2016).

221 The demographic decline that followed the fall of the Roman Empire favored a partial recovery of forest
222 vegetation. In the year 410, emperor Constantine entrusted to the catholic Church all forests that
223 surrounded former sacred temples. Among the general forest abandonment of the early Middle Ages,
224 religious orders (Benedictines, Camaldolese, Carthusians, Vallombrosans) were the only subjects that
225 carried out forest management and conservation (Piccioli 1923), with long-lasting effects on forest
226 structure and composition, e.g., in most present-day pure fir forests of the Apennines (Costantini et al.
227 2010). The population increased again starting from the Late Middle Ages, with the exception of the
228 period 1350-1450 AD (i.e., a period of both climatic, economic, and demographic crisis: Sadori et al.
229 2016, when forests expanded again: Mensing et al. 2013), and clearing was resumed in community
230 forests (Guido et al. 2013), while those belonging to the nobility were restricted to all uses (*foris stare* –
231 “stay outside” edicts may have originated the word *forest*) and preserved as hunting grounds. In
232 response to increasing forest clearing, some states such as the Republic of Venice, the Papal States, and
233 the Granduchy of Tuscany started preserving public forests as a strategic resource for ship and
234 household building (Di Filippo et al. 2007).

235 Around year 1500, most oak high forests had been replaced by chestnut (*Castanea sativa* Mill.)
236 orchards, an important source of food, whose cultivation started during the Roman Age (Di Pasquale et
237 al. 2010) and rapidly spread outside the ecological niche of the species starting from the early Middle
238 Ages (Conedera et al. 2004). The introduction of chestnut coincided with a radical change in local use of
239 land. Fire was no longer used systematically to clear open spaces in forests. Instead, many wooded areas

240 were actively managed as chestnut groves and managed in coppices for pole production (Tinner and
241 Conedera 1995).

242

243 **5. Land use changes in the last 200 years**

244 The decline of forest cover continued in the 17-19th centuries and was finally exacerbated by the needs
245 of the newborn railway network (Zanotti Cavazzoni 1907). The recognition of the link between
246 deforestation and hydrogeologic instability resulted in measures to restore forest cover; between national
247 unification (1861) and 1950, 200,000 hectares of forests were planted (Patrone 1953), and a further
248 560,000 hectares between 1950 and 1980 as a consequence of occupational policies (Romano 1987). At
249 the same time, the abandonment of rural and mountain settlements (Munafò et al. 2015) caused a strong
250 increase in forest cover, ranging from +0.1% and +27% per decade (average: +10.3%) (Fig. 3). The rate
251 of change seems more dependent on local socio-economic changes than on the period, location, or
252 topographic features: forest and shrubland expansion were inversely related to population density
253 (Falcucci et al. 2007; Corona et al. 2008) and occurred mainly at elevations below 1,000 m, on moderate
254 slope gradients (< 40%), and near forest edges and roads (≤ 500 m) (Cimini et al. 2013). In most cases,
255 the process has been related to abandonment of traditional farming or grazing activities (e.g., De Sillo et
256 al. 2012). The period needed for tree canopy closure on former unforested land ranged from 25 to 50
257 years (e.g., Bracchetti et al. 2012). The mode of natural afforestation depended on previous landscape
258 configuration, species composition, and topography. In former agricultural areas, closure of open spaces
259 resulted in homogeneization of the landscape mosaic, while in former pastures complexity increased
260 with incoming forest cover (e.g., Corso et al. 2005; De Sillo et al. 2012). The density and complexity of
261 edges, however, has often increased due to non-homogenous colonization patterns of the incoming
262 forest.

263 Nine studies have addressed treeline shift, a much less researched issue than e.g. on the Alps (Gehrig-
264 Fasel et al. 2007; Leonelli et al. 2011; Bebi et al. 2016). Even though on the Apennines the treeline had

265 been depressed by human activity (fire, grazing) since the Late Holocene (Compostella et al. 2014),
266 recent change was less clearcut. The only reported figures were an increase of 1m per year upwards and
267 3m downwards in dwarf pine (*Pinus mugo* Turra) (Palombo et al. 2013) and an expansion of 1% per
268 year at the beech treeline (van Gils et al. 2008). The relative importance of recent climate warming and
269 land use change was debated, with the first factor playing out at regional level (e.g., simultaneous
270 increases in black pine treeline in the last 30-40 years in the Central Apennines: Piermattei et al. 2016)
271 and the second at local scale (Palombo et al. 2014). Where grazing is still active, it may prevent
272 establishment of shrubs that could subsequently act as nurse sites for beech seedlings (Catorci et al.
273 2012), such that the treeline is actually stable (Pezzi et al. 2007).

274

275 **6. Changes in forest structure**

276 Abandonment of forest management and rural landscapes has also determined a widespread ageing of all
277 Apennine forests (Tellini Florenzano 2004) and an increase of living and dead biomass (Marchetti et al.
278 2010; Motta et al. 2013). Many coppices have been subject to active conversion into high forest, while
279 forest regulations have been issued in many regions imposing a maximum coppice age above which
280 vegetative regeneration was forbidden in order to avoid exhaustion of stumps and fertility declines
281 (usually at 35-40 years, e.g., Regione Toscana 2003). Abandoned coppices of many species transitioned
282 spontaneously to high forest, e.g. in beech (Nocentini et al. 2009), birch (Bagnato et al. 2014), and
283 chestnut stands, which have undergone succession by more shade-tolerant broadleaves such as beech,
284 hop-hornbeam, and downy oak (Pezzi et al. 2011). More intensive silvicultural systems, e.g., uneven-
285 aged coppicing, are all but lost (Coppini and Hermanin 2007). Re-naturalization dynamics and late-seral
286 succession were observed also in former black pine plantations (Tonon et al. 2005).

287 Land abandonment and decrease of forest harvesting has also raised the interest for forests with old-
288 growth characteristics (Marchetti and Blasi 2010; Chirici and Nocentini 2013). These stands, prevalently
289 dominated by beech, house some of the tallest and oldest trees in Europe; they have a significantly

290 higher deadwood volume than ordinarily managed forests with similar composition (Lombardi et al.
291 2013), and a living biomass comparable or higher than central European old-growth forests, in both pure
292 beech (302-1383 m³ ha⁻¹) and mixed beech-fir stands (570-1189) (Calamini et al. 2011). Differences
293 between these old growth stands and managed one are very evident also in terms of genetic diversity
294 (Paffetti et al. 2012), lichen flora (Brunialti et al. 2010), forest dynamics (Travaglini et al. 2012), and
295 structural diversity (Alessandrini et al. 2011). All these factors have a preminent importance as
296 indicators of habitat and biodiversity (Schulz et al. 2014).

297

298 **7. Disturbance regimes**

299 Besides macroecological and anthropic drivers, natural disturbance regimes are one of the main factors
300 shaping the composition, structure, and patterns of forest ecosystems both at the local and at the regional
301 level (Kulakowski et al. 2016). However, the natural disturbance regimes of Southern European forests
302 have been long since masked by human modification to forest cover, composition, structure, and
303 continuity (Bengtsson et al. 2000). Whereas actual disturbance regimes have started to be addressed by
304 ecological research in the Italian Alps (Valese et al. 2014, Vacchiano et al. 2016), data and studies from
305 Apennine forests are conspicuously lacking, so that the properties of disturbance regimes and its
306 historical range of variability (Kulakowski et al. 2016) are still largely unknown.

307 Fire is the most common disturbance agent in peninsular Italy. In the period between 1980 and 2012 the
308 average burned area in Italy was 113,496 ha per year (EC 2013), with a mean yearly frequency of 9,736
309 fires, i.e., 3.2 fires per km² (Spain: 3, Greece: 1.2). With the exception of climatically unfavorable years
310 (e.g., 227,729 ha burned in 2007), the five-year average burned area has decreased steadily (from 46,800
311 ha in 1990-1995 to 36,800 ha in 2005-2010) due to improvements in fire policies and prevention (FAO
312 2010). Long-term data are not available at a regional detail; in year 2015, Apennine regions (i.e.,
313 excluding the Alpine space, Puglia, and islands) included 61% of all forest fires and 70% of total
314 forested burned area of the country (Corpo Forestale dello Stato 2016). The percent of wooded area

315 burned yearly is 1.14% nationally, i.e., the highest in Mediterranean Europe after Portugal (FAO 2010).
316 Mediterranean pine forests have a disproportionately high fire occurrence relative to their area, followed
317 by Mediterranean montane forests and evergreen broadleaves forests (Corona et al. 2014). Most fires are
318 anthropogenic: negligent motives are common, especially agricultural (stubbe burning, land cleaning
319 after harvesting) and pastoral burning (Lovreglio et al. 2010).

320 The National Forest Inventory of 2005 reports the following surfaces for other forest disturbance agents
321 in the Apennine regions: biotic agents 508,803 ha, browsing and grazing 160,965 ha, weather extremes
322 220,223 ha, i.e., respectively 11%, 3%, and 5% of total forest cover (MIPAAF 2007). Abiotic
323 disturbances have been analyzed mostly in relation to the ecology of beech forests; a common feature of
324 such studies is that, contrary to expectations, beech preserves its dominance over competitor species
325 even after low- and medium severity disturbance (van Gils et al. 2010). The high structural complexity
326 of overmature beech forests in the central Apennines has been related to frequent low-severity gap-
327 forming events (Ziaco et al. 2012) (Fig. 4), similarly to central European old-growth beech forests
328 (Westphal et al. 2006). However, recent large stand-replacing windthrows in fir forests (Bottalico et al.
329 2015) suggest that the wind disturbance regime might be composed also by rarer, more intense events.

330 A much common form of disturbance is landslides, which occur in 9% of all Apennine areas (Triglia
331 and Iadanza 2014), with somewhat positive consequences for forest diversity (e.g., exposure of mineral
332 soil) but catastrophic results for society (e.g., the mudflow events in Sarno in 1998 or Genova in 2015).
333 No systematic assessment exists on the extent and severity of biotic disturbances in Apennine forests.
334 Historical evidence (e.g., chestnut blight) and case studies highlight the potential for high-severity
335 events from both native (Puddu et al. 2003; Luchi et al. 2014) and alien pathogens (Vettraino et al. 2005;
336 Luchi et al. 2016). Evidence of insect outbreaks is also limited, mostly to artificial tree plantations
337 (Vignali et al. 2015). However, it has been hypothesized that climate warming might exacerbate tree
338 drought stress, which is already inducing tree decline in sensitive populations (Piovesan et al. 2008; Di

339 Filippo et al. 2010), and hence facilitate the outbreaks of secondary insects and pathogens, especially in
340 southern, low-elevation beech stands (Luchi et al. 2015).

341

342 **8. Management implications**

343 Land use change is currently the dominant driver of forest dynamics in the Apennine, relative to both
344 climate and natural disturbances. If the urbanization trend and the abandonment of marginal lands
345 persist, forests in mountain areas will keep on accumulating live and dead biomass, and the connectivity
346 between old-growth patches will likely increase with ongoing secondary succession in fallow lands.

347 While this might lead to increased provision of some important forest ecosystem services, e.g., timber,
348 carbon stocking, avalanche and rockfall mitigation, or even carnivore habitat (Fabbri et al. 2007, Ciucci
349 and Boitani 2008), some other forest functions are expected decrease, e.g., recreational use, mechanical
350 stability, landscape diversity, and habitat for open-areas plant and animal species (Casanova et al. 2005).

351 Forest planning therefore needs to embrace a comprehensive zonation approach, building on science-
352 based forecasts of forest structure and composition (Vacchiano et al. 2012b), and assigning spatially-
353 explicit priorities to management alternatives needed to maximize each of the desired ecosystem service.

354 We also argue that the ongoing shift from segregation (i.e., each forest accomplishes a single
355 management objectives) to integration (multiple management objectives are sought in the same forest
356 area) should be strengthened, especially for what concerns biodiversity-oriented forest management
357 (Schulz et al. 2014).

358 So far, the pressure posed by climate warming on forest ecosystems has been buffered or even countered
359 by forest expansion following land abandonment. However, while large uncertainties still exist
360 regarding the climate resilience of several important tree species (see below), adaptive management
361 strategies such as intensification of thinning regimes or assisted migration (Temperli et al. 2012) need to
362 be further explored to provide means to counter the negative effects of climate change, e.g. forest
363 decline in drought-prone conifer forests (Vacchiano et al. 2012a). However, the actual outcomes of

364 climate change, and the adaptive management actions needed, will be determined by its interactions with
365 past and future land use, changes in disturbance regimes (e.g., van Gils et al. 2010) and legacies
366 (Vacchiano et al. 2014), endogenous stand dynamics (Long and Vacchiano 2014), resilience drivers
367 (e.g., reproduction dynamics: Ascoli et al. 2015), and novel communities (e.g., Benesperi et al. 2012).
368 In particular, the interplay of climate warming and forest expansion will exacerbate damages by extreme
369 events such as windthrow, forest fires, and insect outbreaks (Seidl et al. 2014). This is particularly
370 troubling where forests play important social functions, such as protection of infrastructure from rockfall
371 or debris flows. Apennine forest seem to have experienced low- to moderate-severity disturbance
372 regimes in the recent past, but managers should be prepared to plan and carry out forest restoration
373 measures on larger scales following the likely increase in frequency of stand-replacing events, as well as
374 measures to increase the resistance and resilience of forest ecosystems to such events.

375 The abundance of coppices due to the prevalent use of small, private forest lots as a source of energy
376 wood, and their subsequent abandonment, raise many question about the best silvicultural practices to
377 preserve the provision of such cultural landscape and its functions, especially soil protection and
378 biodiversity. Current forest regulations forbid clearcutting in overmature coppices; variable retention
379 systems that have recently been proposed for Alpine beech forests could be adopted to foster structural
380 differentiation and avoid vertical and horizontal simplification, which might lead to loss of habitat and
381 productivity (Negro et al. 2015).

382 The reduction of open meadows has also modified the feeding behaviour of wild ungulates, which have
383 increasingly browsed forest regeneration. As repeated and selective browsing threatens the regeneration
384 of forest stands and triggers a loss of ecosystem resilience (Cutini et al. 2011), forest management and
385 wildlife management must be planned together, with an increased communication between stakeholders
386 from the two sectors.

387

388 **9. Directions for research**

389 This review illustrates how cultural factors had a profound effect on forests of the Apennine region and,
390 in most cases, outweighed by far the effects of macroecological constraints. The millennia-long uses of
391 the forest by man, as well as more recent socio-economic changes, seem to play a more important role
392 for current forest structure and dynamics than natural processes driven by geology and climate.
393 Disturbance regimes have also been masked by the pervasive human influence, and their range of
394 variability still represent a large knowledge gap. Finally, the climate plasticity of some important forest
395 species has still to be completely understood (e.g., fir); the high specific and genetic diversity of
396 Apennine forests will have to be leveraged as an important source of resilience and adaptive potential.
397 The future extent, composition and functioning of Apennine forests is therefore dependent on the
398 changes in land use, disturbance regimes, and climate, but only the latter have been subject to rigorous
399 study or simulation. Prediction of future forest will need to incorporate future land use and disturbance
400 scenarios and the complex and spatially-explicit feedbacks between them.

401

402

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404

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764

765 **Figure captions**

766 **Fig. 1** Mountain systems of the Italian peninsula, bounded by the 600 m a.s.l. elevation line

767 **Fig. 2** Simplified pollen diagram (% total pollen) from Lagdei, northern Apennines (modified from
768 Ravazzi 2002; attribution of periods by Bertoldi 1981).

769 **Fig. 3** Forest cover change in the 20th century in the Apennine from selected studies.

770 **Fig. 4** Disturbance chronologies produced for Valle Cervara using the boundary line method for high
771 mountain beech populations in the Apennines. Moderate and major growth releases are those falling
772 within 20–49.9% and 50–100% of the boundary line, respectively. Disturbance event dates (only when
773 ≥ 20 sampled trees) grouped into 5-year intervals (modified from Ziaco et al. 2012)

774

775 **Appendices**

776 Additional supporting information in the online version of this article (see “Supplementary

777 Material”) contains the following: Appendix 1 - List of references reviewed on Apennine forests.

778

779

Appendix 1

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Figure 1
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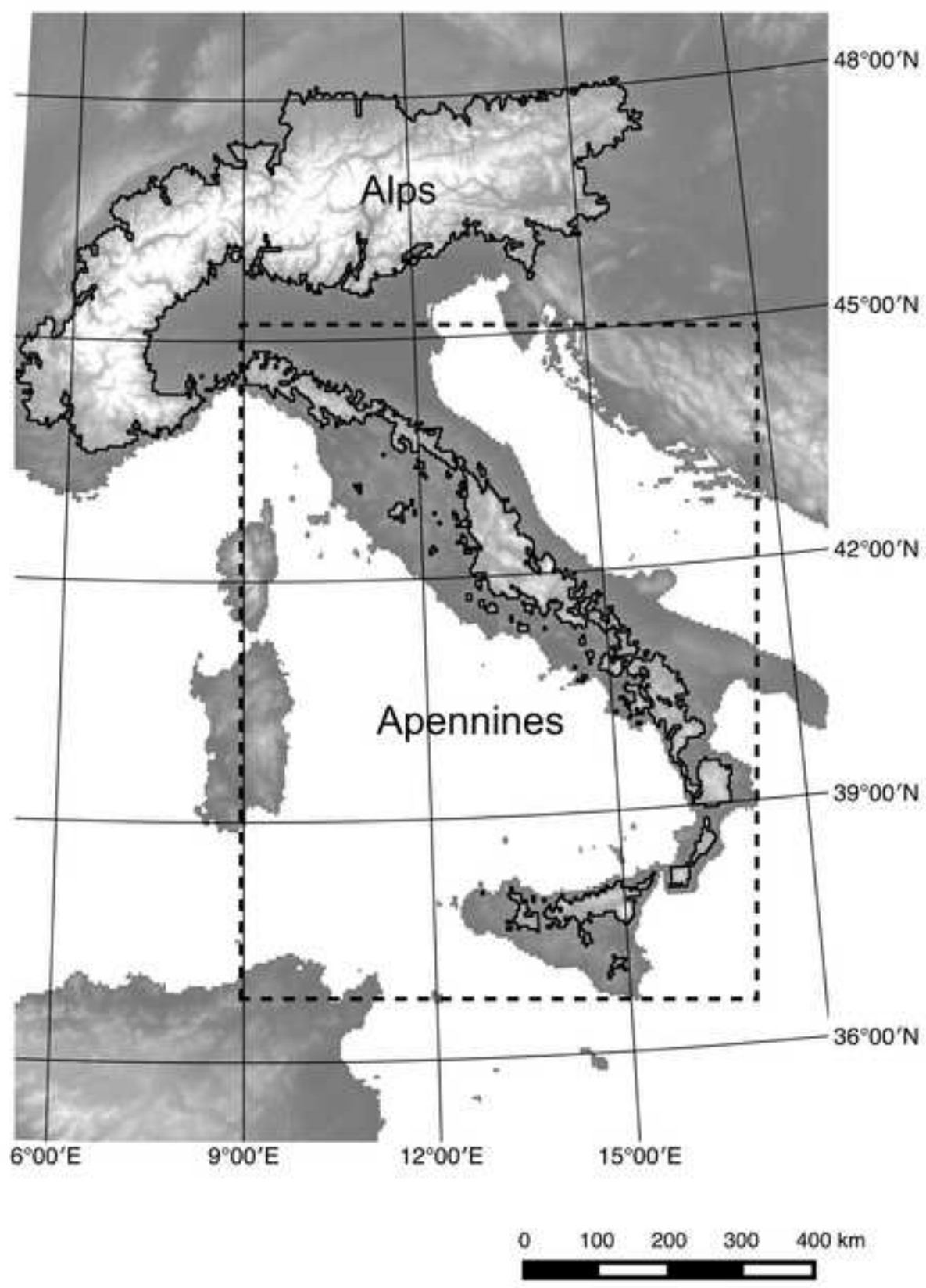


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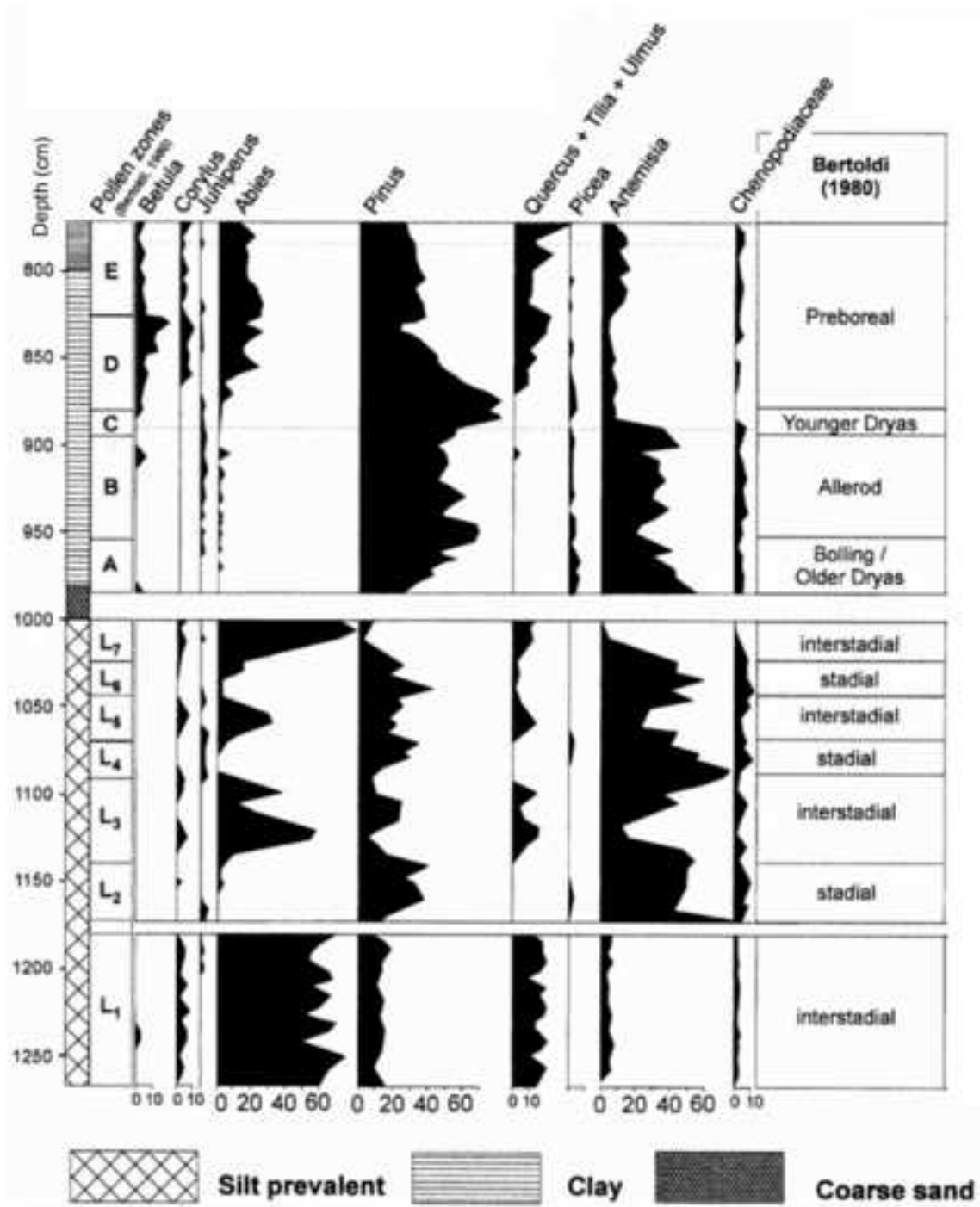


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