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Giorgio Vacchiano[*a], Matteo Garbarino[b], Emanuele Lingua[c], Renzo Motta[d]

[a] Università degli Studi di Torino, DISAFA. Largo Braccini 2, 10095 Grugliasco (TO) Italy. giorgio.vacchiano@unito.it

[b] Università Politecnica delle Marche, D3A. Via Brecce Bianche, 60131 AN Italy. matteo.garbarino@univpm.it

[c] Università degli Studi di Padova, TESAF. Viale dell'Università 16, 35020 Legnaro (PD) Italy. emanuele.lingua@unipd.it

[d] Università degli Studi di Torino, DISAFA. Largo Braccini 2, 10095 Grugliasco (TO) Italy. renzo.motta@unito.it

* corresponding author: giorgio.vacchiano@unito.it

Abstract

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

We introduce the setting under the geological and climatological point of view and review the literature on the interactions between these long-term drivers and the specific, structural, and genetic diversity of these forest communities (e.g., effects of glacial refugia or tectonic/volcanic activity), followed by a brief outline of what little is known about natural disturbance regimes and their range of variability. Anthropogenic disturbances (fire, grazing) and land use changes (abandonment of cropland and pasture) have been by far the main drivers of forest dynamics at least for the last two millennia, determining for examples overageing of coppices, treeline advances, forest encroachment on former agricultural land. We suggest considerations about the interplay between these land use changes and disturbance drivers (e.g. fuel continuity), summarise comparisons between managed and unmanaged forests (e.g., increase in tree size, deadwood, biodiversity indicators), and elaborate on current proposals for climate-adapted

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

Keywords

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

Highlights

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

1. Introduction

Italy has two main mountain systems: the Alps and the Apennines (Figure 1). The alpine area represents approximately one-quarter of the total Italian land surface (75,000 km^2), while the Apennine region accounts for approximately two-fifths (120,000 km^2). Together they make up approximately 35% of the total area of the country.

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

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

The aim of this review is to summarize the main drivers of the composition, cover, structure, and dynamics of Apennine forests, including both macroecological constraints (geology and climate), human influence, and natural disturbance agents. In order to do so, we searched the existing scientific literature (Google Scholar database) using the keywords “Apennine” and “forest”, plus each of the following: “pollen OR charcoal”, “land use change”, “(stand OR forest) structure”, and “disturbances” (all words used in either English or Italian languages). The search produced 9860 unique records. After filtering out irrelevant and inaccessible papers, the total number of reviewed studies was 170 (i.e., 74, 42, 28, and 24 papers for each of the last four keywords, respectively) (Appendix 1).

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

2. Macroecological drivers

2.1 Geology

The Apennine orogeny began in the middle Miocene (about 20 million years ago, i.e., millions of years later than the Alpine orogeny) (Carminati et al. 2012) as a consequence of the subduction of the African-Adriatic plate below the European plate (Carminati et al. 2003), and still continues today (Devoti et al. 2008). At the same time, large faults developed along the western side of the Apennines, connected to a crustal thinning that resulted in the opening of the Tyrrhenian sea (Rosenbaum and Lister 2004). Therefore, these young mountains of Italy are of paradoxical provenience, deriving from both compression (folded systems) and extension (fault-block systems). This is responsible for the great variety of rock types and the rugged appearance of the range today. In the north, sandstones, marls, and greenstones occur. In the central Apennines clay, sandstone, and limestones are common. In the southern Apennines large calcareous rock outcrops are separated by lowland areas of shale and sandstone, and interrupted by extensive argillaceous rock types, which originate frequent erosion of the "badlands" type.

2.2 Historical climate

Italy is placed at the boundary between the Mediterranean and the temperate zone of the boreal hemisphere (Blasi et al. 2007). The Mediterranean Sea, which almost surrounds the country, is a reservoir of heat and humidity. The Apennines intercept Atlantic perturbations and, with their rough morphology, experience sharp temperature variations over short distances, frequent rainfalls for adiabatic cooling and *stau* wind currents, and winter fog stagnation inside the several internal closed basins and narrow valleys. The climate is of the mountain variety of the Mediterranean type, with dry summers and rainy (and snowy) winters. Mean temperature ranges from 0 to 11 °C in January and from 24 to 28 °C in July. In the upper zone (over 2,000 m) there is snow 180-190 days per year. Annual precipitation ranges from 600 to 4500 mm. Because the Adriatic Sea, rather thin and shallow, exerts a less pronounced effect than the Tyrrhenian Sea, most of the precipitation falls on the western slopes of the mountains (> 3,000 mm per year in Liguria). Precipitation seasonality is another typical trait of Mediterranean climates; summer cyclones bring in torrential rains and may cause severe flooding. The aridity index (ratio between precipitation and ET_0: Wang et al. 2012) is often < 0.65 (sub-humid), especially in Sicily, Apulia, Sardinia and Basilicata.

2.3 Climate change

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

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

3. Vegetation history

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

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

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

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

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

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

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

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

4. Human history and impacts on vegetation

Anthropogenic land use has had a profound effect on forests of the Apennine region and, in most cases, outweighted by far the effects of macroecological constraints (Brown et al. 2013).

Even before the advent of agriculture, the presence of humans has severely influenced the composition and distribution of forests. This is exemplified by the late Holocene dynamics of fir and beech. During the early Holocene (9000–6000 years BP), fir became abundant from the sea level to the mountains (Montanari 1989). After 6,000 years BP, however, its presence declined in many sites (Magri et al. 2015), leading to the current reduced distributions. The reasons for such decline, and the reltive importance of climate, competition, and anthropogenic impact, are debated. On one hand, fir has retreated into more or less the same areas where it was found at the beginning of the present interglacial (Muller et al. 2007), supporting the hypothesis that its Holocene dynamics are driven by long-term climatic and edaphic patterns (Joannin et al. 2012). On the other hand, multiple palaeoecological evidence shows a synchrony between the reduction of fir at 6,000-3,000 years BP and an increase in human activity, especially from pastoralism and fire (Henne et al. 2013). These dynamics would imply a much wider climatic niche than previously thought for fir, which could have been part of sub-Mediterranean oak forests, as suggested also from Pleistocenic pollen evidence (Tinner et al. 2013). At the same time, beech, which had started expanding into southern and central Italy already 18,000 years BP (Joannin et al. 2012), reached its maximum spread between 8,000 and 4,000 years BP (Branch and Marini 2014), i.e. simultaneously to the decline of fir, leading to a mixed *Abies-Fagus* association in the upper belt between from 5,200 yBP and then to a dominance of beech from around 2,900 years BP (Watson 1996). The expansion of beech in the Northern Apennines may have been favored by a decrease in summer insolation (Berger 1978) and a smoothing of seasonal climate extremes (Huntley et al. 1989; Watson 1996), but also facilitated by human activities. Since beech seedlings require moderate light intensity for development (Ellenberg 1986), it is reasonable that clearing of the pre-existing dense fir forest has determined a shift in dominance between the two species (Valsecchi et al. 2008). The transition of the first human communities out of hunting-gathering occurred around the start of the second millennium BC. From this time, semi-nomadic agriculture and herding were accompanied by widespread slash-and-burn deforestation (Watson 1996), a higher hydrogeologic instability (Cremaschi et al. 2008) and an increase in soil erosion, which favored some pioneer tree species, e.g., Calabrian pine (*Pinus nigra* subsp. *laricio*) (Nicolaci et al. 2014). Starting from the 8th century BC, under the Roman influence, Apennine forests were used for timber, fuelwood, and cleared for agriculture and pastures. Forests in the vicinity of the sea or major rivers were harvested and floated to the nearest ports as civil and naval timber (*silva incaedua*); the others were coppiced (*silva caedua*), harvested by hand or animals, and used for tools and small crafts, or as energy wood. This system is believed to be responsible for the degradation of forests along coasts (Calò et al. 2012), and on major river basins (Mercuri and Sadori 2013). However, recent evidence (Sadori et al. 2015) shows that at least beech-fir forests were more widely distributed than today, despite the fact that fir was the most desirable species for ship hulls, construction timber, and furniture (Allevato et al. 2010). Another source of forest degradation was transhumant sheep herding, which was favored in southern Italy by the territorial unification brought about by the Romans, and was practiced up to the beginning of the 20th century. At its apex (5.5 million sheep in year 1604: Venanzoni et al. 1993), the newtwork of seasonal transhumance "highways" had a cumulative length of more than 3000 km. Some Apennine forests still show the legacy of their past use as wooded pastures, e.g., simplified vertical structure (Mancini et al. 2016).

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

Around year 1500, most oak high forests had been replaced by chestnut (*Castanea sativa* Mill.) orchards, an important source of food, whose cultivation started during the Roman Age (Di Pasquale et al. 2010) and rapidly spread outside the ecological niche of the species starting from the early Middle Ages (Conedera et al. 2004). The introduction of chestnut coincided with a radical change in local use of land. Fire was no longer used systematically to clear open spaces in forests. Instead, many wooded areas were actively managed as chestnut groves and managed in coppices for pole production (Tinner and Conedera 1995).

5. Land use changes in the last 200 years

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

Nine studies have addressed treeline shift, a much less researched issue than e.g. on the Alps (Gehrig-Fasel et al. 2007; Leonelli et al. 2011; Bebi et al. 2016). Even though on the Apennines the treeline had been depressed by human activity (fire, grazing) since the Late Holocene (Compostella et al. 2014), recent change was less clearcut. The only reported figures were an increase of 1m per year upwards and 3m downwards in dwarf pine (*Pinus mugo* Turra) (Palombo et al. 2013) and an expansion of 1% per year at the beech treeline (van Gils et al. 2008). The relative importance of recent climate warming and land use change was debated, with the first factor playing out at regional level (e.g., simultaneous increases in black pine treeline in the last 30-40 years in the Central Apennines: Piermattei et al. 2016) and the second at local scale (Palombo et al. 2014). Where grazing is still active, it may prevent establishment of shrubs that could subsequently act as nurse sites for beech seedlings (Catorci et al. 2012), such that the treeline is actually stable (Pezzi et al. 2007).

6. Changes in forest structure

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

Land abandonment and decrease of forest harvesting has also raised the interest for forests with old-growth characteristics (Marchetti and Blasi 2010; Chirici and Nocentini 2013). These stands, prevalently dominated by beech, house some of the tallest and oldest trees in Europe; they have a significantly higher deadwood volume than ordinarily managed forests with similar composition (Lombardi et al. 2013), and a living biomass comparable or higher than central European old-growth forests, in both pure beech (302-1383 m^3 ha^{-1}) and mixed beech-fir stands (570-1189) (Calamini et al. 2011). Differences between these old growth stands and managed one are very evident also in terms of genetic diversity (Paffetti et al. 2012), lichen flora (Brunialti et al. 2010), forest dynamics (Travaglini et al. 2012), and structural diversity (Alessandrini et al. 2011). All these factors have a preminent importance as indicators of habitat and biodiversity (Schulz et al. 2014).

7. Disturbance regimes

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

Fire is the most common disturbance agent in peninsular Italy. In the period between 1980 and 2012 the average burned area in Italy was 113,496 ha per year (EC 2013), with a mean yearly frequency of 9,736 fires, i.e., 3.2 fires per km^2 (Spain: 3, Greece: 1.2). With the exception of climatically unfavorable years (e.g., 227,729 ha burned in 2007), the five-year average burned area has decreased steadily (from 46,800 ha in 1990-1995 to 36,800 ha in 2005-2010) due to improvements in fire policies and prevention (FAO 2010). Long-term data are not available at a regional detail; in year 2015, Apennine regions (i.e., excluding the Alpine space, Puglia, and islands) included 61% of all forest fires and 70% of total forested burned area of the country (Corpo Forestale dello Stato 2016). The percent of wooded area burned yearly is 1.14% nationally, i.e., the highest in Mediterranean Europe after Portugal (FAO 2010). Mediterranean pine forests have a disproportionately high fire occurrence relative to their area, followed by Mediterranean montane forests and evergreen broadleaves forests (Corona et al. 2014). Most fires are anthropogenic: negligent motives are common, especially agricultural (stubbe burning, land cleaning after harvesting) and pastoral burning (Lovreglio et al. 2010).

The National Forest Inventory of 2005 reports the following surfaces for other forest disturbance agents in the Apennine regions: biotic agents 508,803 ha, browsing and grazing 160,965 ha, weather extremes 220,223 ha, i.e., respectively 11%, 3%, and 5% of total forest cover (MIPAAF 2007). Abiotic disturbances have been analyzed mostly in relation to the ecology of beech forests; a common feature of such studies is that, contrary to expectations, beech preserves its dominance over competitor species even after low- and medium severity disturbance (van Gils et al. 2010). The high structural complexity of overmature beech forests in the central Apennines has been related to frequent low-severity gap-forming events (Ziaco et al. 2012) (Fig. 4), similarly to central European old-growth beech forests (Westphal et al. 2006). However, recent large stand-replacing windthrows in fir forests (Bottalico et al. 2015) suggest that the wind disturbance regime might be composed also by rarer, more intense events. A much common form of disturbance is landslides, which occur in 9% of all Apennine areas (Triglia and Iadanza 2014), with somewhat positive consequences for forest diversity (e.g., exposure of mineral soil) but catastrophic results for society (e.g., the mudflow events in Sarno in 1998 or Genova in 2015). No systematic assessment exists on the extent and severity of biotic disturbances in Apennine forests. Historical evidence (e.g., chestnut blight) and case studies highlight the potential for high-severity events from both native (Puddu et al. 2003; Luchi et al. 2014) and alien pathogens (Vettraino et al. 2005; Luchi et al. 2016). Evidence of insect outbreaks is also limited, mostly to artificial tree plantations (Vignali et al. 2015). However, it has been hypothesized that climate warming might exacerbate tree drought stress, which is already inducing tree decline in sensitive populations (Piovesan et al. 2008; Di

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

8. Management implications

Land use change is currently the dominant driver of forest dynamics in the Apennine, relative to both climate and natural disturbances. If the urbanization trend and the abandonment of marginal lands persist, forests in mountain areas will keep on accumulating live and dead biomass, and the connectivity between old-growth patches will likely increase with ongoing secondary succession in fallow lands. While this might lead to increased provision of some important forest ecosystem services, e.g., timber, carbon stocking, avalanche and rockfall mitigation, or even carnivore habitat (Fabbri et al. 2007, Ciucci and Boitani 2008), some other forest functions are expected decrease, e.g., recreational use, mechanical stability, landscape diversity, and habitat for open-areas plant and animal species (Casanova et al. 2005). Forest planning therefore needs to embrace a comprehensive zonation approach, building on science-based forecasts of forest structure and composition (Vacchiano et al. 2012b), and assigning spatially-explicit priorities to management alternatives needed to maximize each of the desired ecosystem service. We also argue that the ongoing shift from segregation (i.e., each forest accomplishes a single management objectives) to integration (multiple management objectives are sought in the same forest area) should be strengthened, especially for what concerns biodiversity-oriented forest management (Schulz et al. 2014).

So far, the pressure posed by climate warming on forest ecosystems has been buffered or even countered by forest expansion following land abandonment. However, while large uncertainties still exist regarding the climate resilience of several important tree species (see below), adaptive management strategies such as intensification of thinning regimes or assisted migration (Temperli et al. 2012) need to be further explored to provide means to counter the negative effects of climate change, e.g. forest decline in drought-prone conifer forests (Vacchiano et al. 2012a). However, the actual outcomes of climate change, and the adaptive management actions needed, will be determined by its interactions with past and future land use, changes in disturbance regimes (e.g., van Gils et al. 2010) and legacies (Vacchiano et al. 2014), endogenous stand dynamics (Long and Vacchiano 2014), resilience drivers (e.g., reproduction dynamics: Ascoli et al. 2015), and novel communities (e.g., Benesperi et al. 2012). In particular, the interplay of climate warming and forest expansion will exacerbate damages by extreme events such as windthrow, forest fires, and insect outbreaks (Seidl et al. 2014). This is particularly troubling where forests play important social functions, such as protection of infrastructure from rockfall or debris flows. Apennine forest seem to have experienced low- to moderate-severity disturbance regimes in the recent past, but managers should be prepared to plan and carry out forest restoration measures on larger scales following the likely increase in frequency of stand-replacing events, as well as measures to increase the resistance and resilience of forest ecosystems to such events.

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

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

9. Directions for research

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

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Figure captions

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

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

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

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

Appendices

Additional supporting information in the online version of this article (see "Supplementary Material") contains the following: Appendix 1 - List of references reviewed on Apennine forests.

Appendix 1

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Figure 1
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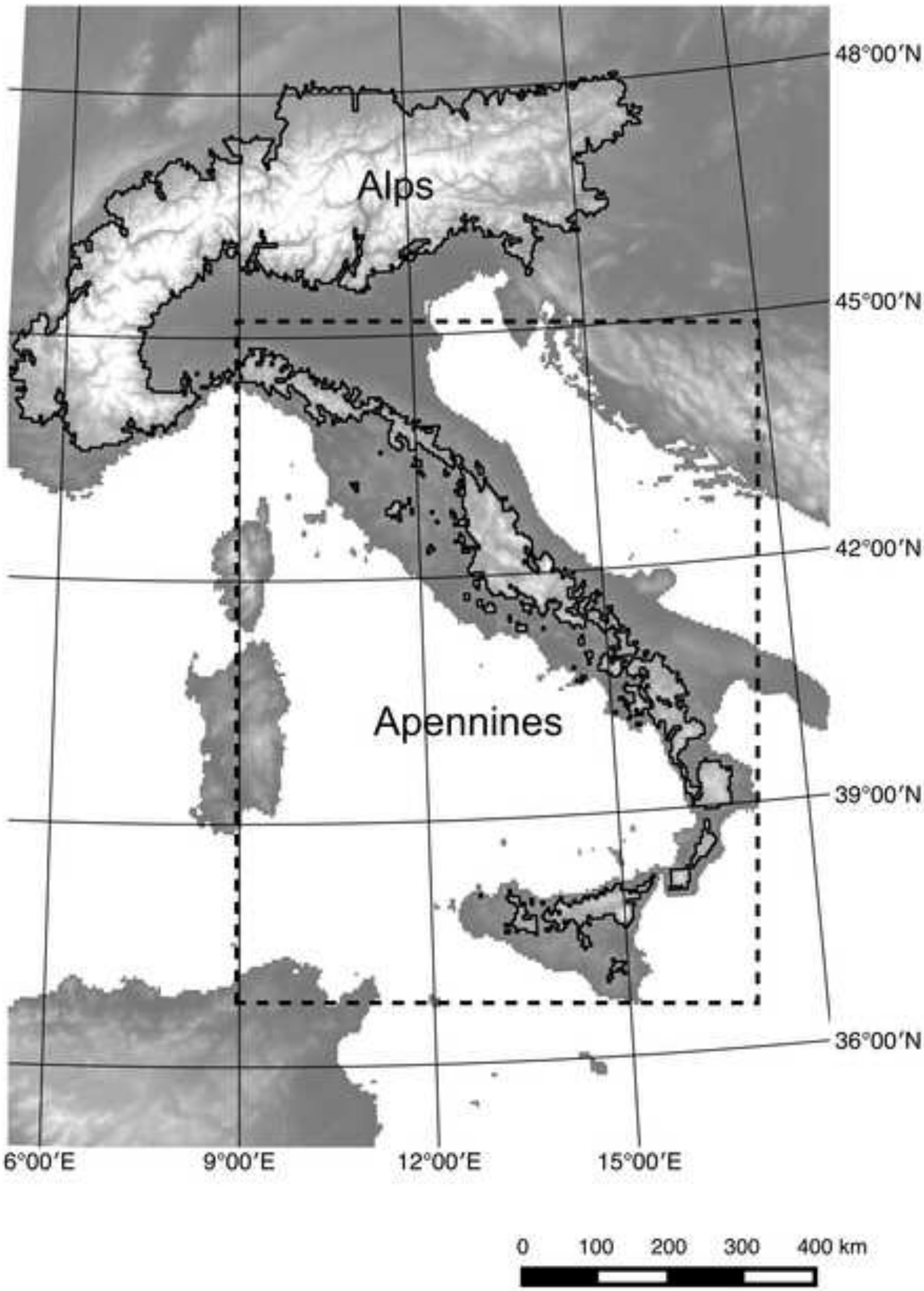

Figure 2
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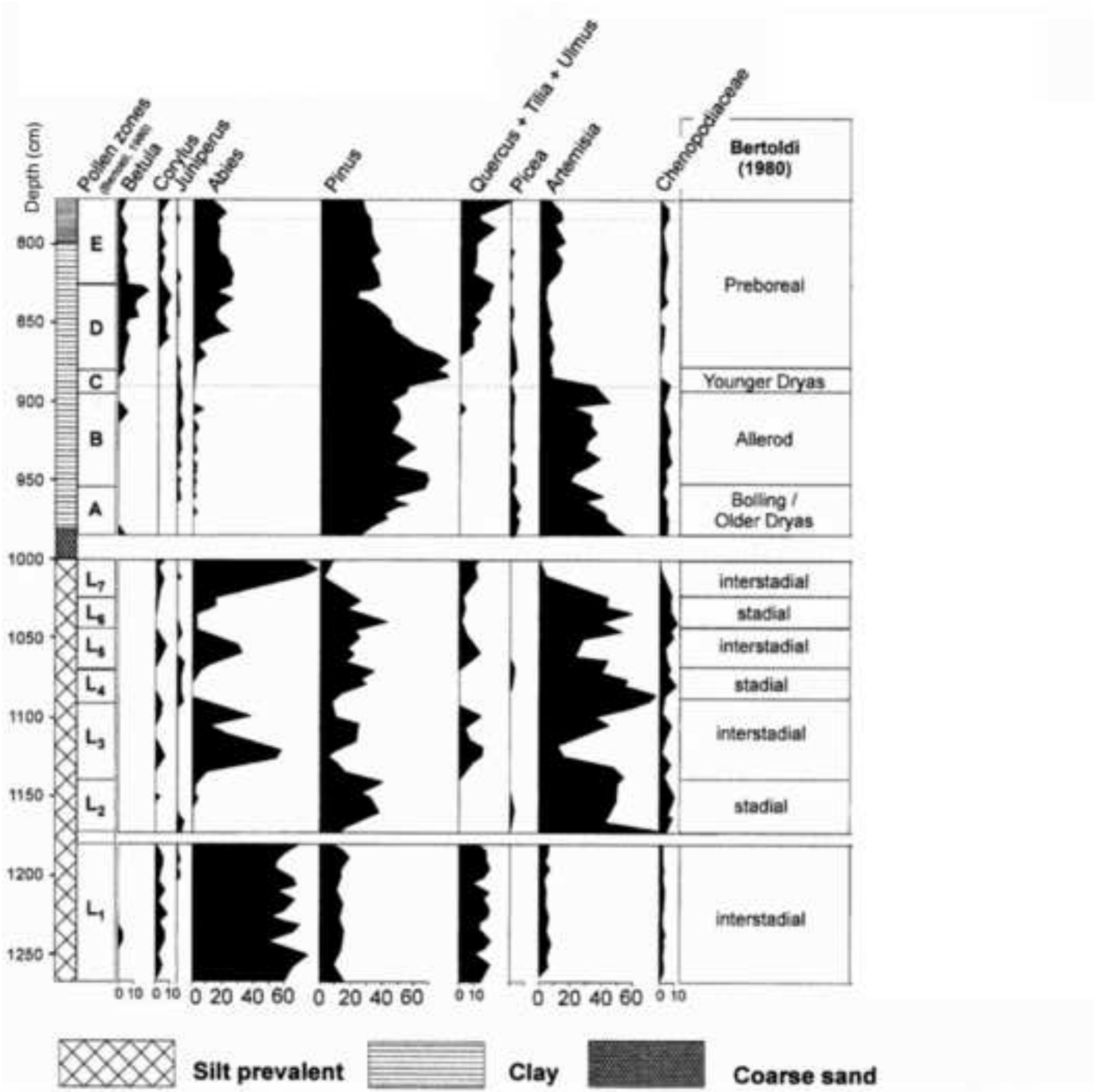

Figure 3
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Figure 4

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