RESEARCH ARTICLE

Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling

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Abstract Forests near the Mediterranean coast have been shaped by millennia of human disturbance. Consequently, ecological studies relying on modern observations or historical records may have difficulty assessing natural vegetation dynamics under current and future climate. We combined a sedimentary pollen record from Lago di Massacciucoli, Tuscany, Italy with simulations from the LANDCLIM dynamic vegetation model to determine what vegetation preceded intense human disturbance, how past changes in vegetation relate to fire and browsing, and the potential of an extinct vegetation type under present climate. We simulated vegetation dynamics near Lago di Massaciucoli for the last 7,000 years using a local chironomid-inferred temperature reconstruction with combinations of three fire regimes (small infrequent, large infrequent, small frequent) and three browsing intensities (no browsing, light browsing, and moderate browsing), and compared model output to pollen data. Simulations with low disturbance support pollen-inferred evidence for a mixed forest dominated by *Quercus ilex* (a Mediterranean species) and *Abies alba* (a montane species). Whereas pollen data record the collapse of *A. alba* after 6000 cal yr BP, simulated populations expanded with declining summer temperatures during the late Holocene. Simulations with increased fire and browsing are consistent with evidence for expansion by deciduous species after *A. alba* collapsed. According to our combined paleo-environmental and modeling evidence, mixed *Q. ilex* and *A. alba* forests remain possible with current climate and limited disturbance, and provide a viable management objective for ecosystems near the Mediterranean coast and in regions that are expected to experience a mediterranean-type climate in the future.

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Introduction

Planning for a warmer future requires detailed knowledge about vegetation dynamics under a broad range of climatic conditions. However, in the warmest regions

of Europe, near the Mediterranean coast, millennia of intense land use have strongly altered or even eliminated forest ecosystems (Colombaroli et al. 2007; Carrión and Fernández 2009; Di Rita and Magri 2009; Tinner et al. 2009). In particular, anthropogenic intensification of fire regimes and grazing shaped the landscape by altering vegetation regeneration and succession (Dupouey et al. 2002; Blondel 2006; Colombaroli et al. 2009). Consequently, little is known about the structure and composition of Mediterranean forests that might exist in the absence of human disturbance. In this setting, ecological research based on modern abundances and species-environment relationships may be insufficient to identify desirable management trajectories based on natural vegetation if current forests lack the most disturbance-sensitive species. For example, niche-based models are frequently used to identify potential distributions under current and anticipated climatic conditions (Keenan et al. 2010; Attorre et al. 2011), but may underestimate future potential if the realized niche on the modern landscape is constrained by human disturbance (Guisan and Thuiller 2005; Carrión and Fernández 2009).

Understanding vegetation potential in the Mediterranean region is increasingly important due to ongoing land use and climatic changes. For example, since the 1960s, agricultural abandonment has allowed expansion of shrubby and highly-flammable, early-successional vegetation (Lloret et al. 2002). Furthermore, simulations project northward expansion of the mediterranean climate and vegetation due to greenhouse forcing (Overpeck et al. 2003; Gao and Giorgi 2008). Therefore, accurate information about potential late-successional vegetation types is needed for the development of realistic management strategies that promote natural vegetation with high societal value and low flammability in mediterranean climates (Schröter et al. 2005). Long-term ecological datasets can help fill this need by documenting Mediterranean ecosystems before the onset of intense human disturbance. In particular, paleoecological approaches that predate observations and historical data provide the best means to define natural vegetation potential under a broad range of environmental conditions (Willis and Birks 2006; Carrión et al. 2010).

Pollen data indicate that many areas near the Mediterranean coast that are currently occupied by fire-prone shrublands were previously forested (Colombaroli et al. 2007; Tinner et al. 2009; Calò

et al. 2012). These forests included communities with no modern analogue. In coastal Tuscany, Italy (Fig. 1), *Abies alba* (silver fir) grew near or possibly mixed with evergreen oaks (e.g. *Quercus ilex*), deciduous oaks (e.g. *Quercus pubescens*), and *Pinus* spp. during the middle Holocene (Colombaroli et al. 2007; Mariotti Lippi et al. 2007; Bellini et al. 2009). *A. alba* is generally considered a montane species that is restricted to mesic habitats where fire disturbance is infrequent (Aussenac 2002; Wick and Mohl 2006). Therefore, it is uncertain where in the surrounding landscape the tree may have grown or even if the abundant *A. alba* pollen should be attributed to long-distance transport.

Conflicting interpretations of what caused Mediterranean forests to decline during the Holocene also complicate applying paleoecological records to inform management. For example, forest decline in the Mediterranean region is commonly attributed not only to human impacts, but also to a drying climate (Jalut et al. 2009; Sadori et al. 2011). Under this interpretation, humans contributed to the widespread changes, but declining moisture availability during the middle and late Holocene was the underlying cause. The "aridification hypothesis" implies that many areas that supported closed forests during the middle Holocene are at present too dry to maintain forests or
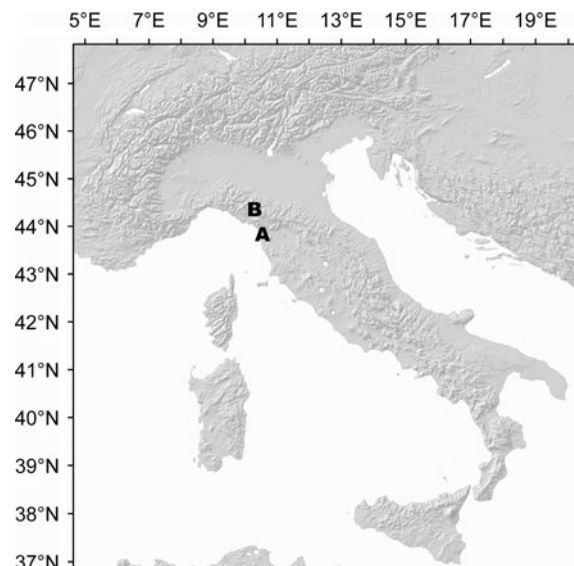

Fig. 1 *Map* showing location of *A* Lago di Massacciucoli in coastal Tuscany, Italy and *B* Lago Verdarolo in the northern Appenine Mountains

to support drought and disturbance-sensitive species such as *A. alba*.

In this paper, we combine paleoecological data with a dynamic landscape vegetation model to investigate the composition and structure of forests that develop under low disturbance near the Mediterranean coast. Specifically, we simulate vegetation dynamics with small, infrequent fires and no browsing pressure in the landscape surrounding Lago di Massacciucoli, Tuscany (Fig. 1) for the last 7,000 years using the LANDCLIM model (Schumacher et al. 2004). We evaluate the plausibility of our simulation by comparison to pollen data from Lago di Massacciucoli (Colombaroli et al. 2007). Land use intensified in the surrounding region during the study period, with human-caused increases in fire frequency and grazing during the Neolithic (i.e. after 8000 cal yr BP; Malone 2003; Vannière et al. 2008). Therefore in a second step, we compare pollen data to vegetation simulated with large, infrequent fires (to simulate a regional increase in fire); small, frequent fires (to simulate a disturbed and fragmented landscape), and use two browsing intensities to simulate the impacts of livestock grazing on regeneration. LANDCLIM simulations provide an independent means to evaluate the pollen-inferred interpretation that *A. alba* grew in a mixed forest with evergreen and deciduous *Quercus* spp. near the Mediterranean coast, and that human disturbance caused their decline. Our combined approach allows us to apply knowledge gained from past ecosystems to the present by exploring whether a non-analogue forest type is possible under existing climatic conditions.

Methods

Ecological setting and current vegetation

We modeled vegetation dynamics within 3 km of Lago di Massacciucoli in coastal Tuscany, Italy (Fig. 1; 43°50′N, 10°20′E). We chose Lago di Massacciucoli for its paleoecological data that suggest the existence of an extinct mixed *Q. ilex–A. alba* forest (Colombaroli et al. 2007; Marchetto et al. 2008). Lago di Massacciucoli is a large shallow lake (ca. 700 ha, 0 m a.s.l., 2 m average depth) situated in a coastal plain 4 km inland from the Tyrrhenian Sea. Wetlands dominated by *Phragmites* and Cyperaceae occupy the peaty soils surrounding the lake. However, much of the low-lying area has been

drained for agriculture. Dunes with sandy soils vegetated by *Pinus pinea* and *P. pinaster* plantations separate Lago di Massacciucoli from the sea. Inland are Mesozoic limestone hills with glacial alluvial fans. Mixed deciduous and evergreen forests (e.g., *Q. pubescens*, *Q. ilex*, *Ostrya carpinifolia*, *Fraxinus ornus*) and Mediterranean shrublands (i.e. macchia) grow in the uplands. Fire is a common disturbance that affects the present vegetation in the surrounding landscape. For example, 2,748 fires burned ca. 23,000 ha between 1985 and 2008 AD in Lucca Province, where Lago di Massacciucoli is located (Data source: European Forest Fire Information System). Lago di Massacciucoli experiences a mediterranean-type climate, with warm, dry summers and mild, humid winters. Mean annual temperature 15 km to the south at Pisa San Giusto Airport (2 m a.s.l.) during the period 1951–2007 AD was 14.6 °C, and mean annual precipitation, 892 mm (Data source: SCIA system).

Holocene vegetation history of Lago di Massacciucoli

The Lago di Massacciucoli pollen record covers the last 7,000 years (Colombaroli et al. 2007). Following a marine transgression, early-successional pine forests established near the lake. These communities were succeeded by unique forests dominated by *A. alba*, evergreen oaks, and deciduous oaks that have no modern analogue. *Abies* began declining after 6000 cal yr BP as fire frequency increased and deciduous species (e.g. *Carpinus betulus*, *Fagus sylvatica*, *O. carpinifolia*, *Corylus avellana*, *Quercus* spp.) expanded. An open landscape with abundant Mediterranean shrubs (e.g. *Phillyrea* spp., *Erica* spp.) formed after about 1500 cal yr BP, as regional fire frequency increased. Chronological constraint is high when *A. alba* is most abundant (i.e. 7 AMS ^{14}C dates between 7000 and 5000 cal yr BP), and is less precise but supported by biostratigraphy for the last 5,000 years. However, this study does not focus on the timing of specific changes. We instead use the data-model comparison to support the reliability of our simulations.

Adaptation of the LANDCLIM model to simulate forest dynamics in the Mediterranean region

We simulated vegetation dynamics in the landscape surrounding Lago di Massacciucoli with the LANDCLIM

model. LANDCLIM is a spatially-explicit, stochastic model that uses competition-driven forest dynamics and landscape-level disturbances to simulate vegetation under changing climate and disturbance intensity (Schumacher et al. 2004; Schumacher and Bugmann 2006). The model is well-suited to comparisons with Holocene pollen records because it operates on spatial scales large enough to contain the dominant source area for pollen, but at a fine enough resolution (i.e. 25 m × 25 m grid cells) to capture variations in soil and topography that create local diversity (Henne et al. 2011). LANDCLIM simulates succession within each grid cell by tracking the establishment, growth, and mortality of species cohorts in 10 year time steps. Seed dispersal, fire, and windthrow are simulated at a landscape scale.

LANDCLIM is well-tested in Central Europe where it was used to evaluate the impacts of soil development, drought stress, temperature change, and fire frequency on Holocene vegetation dynamics (Colombaroli et al. 2010; Henne et al. 2011), but has not previously been applied to Mediterranean ecosystems. Therefore, expanding the species pool to include typical Mediterranean species was necessary. It was not practical to include all possible species in our simulations because of the high species richness of the Italian woody flora. Therefore, we focused on 34 abundant and widely distributed trees and shrubs (Supplemental Table 1).

Expanding the species pool required adding a broadleaved-evergreen biotype with new allometric relationships to estimate biomass and leaf area (Supplemental Materials: Broadleaved-evergreen biotype). For species with distributions extending into Central Europe (e.g. *A. alba*, *Q. pubescens*) we used the species parameters enumerated in previous LANDCLIM studies (Schumacher and Bugmann 2006; Henne et al. 2011). For species that were new to LANDCLIM, we followed previous modeling efforts in the Mediterranean where possible (e.g. Fyllas et al. 2007), and derived new parameters from relevant literature where necessary (Supplemental Table 2; Supplemental Materials: Estimation of life history parameters). LANDCLIM uses a simple soil–water balance model (Bugmann and Cramer 1998) to produce an annual drought index for each cell from monthly precipitation and temperature inputs. Because photosynthesis by broadleaved-evergreen and coniferous species can occur in all months with suitable temperatures (Aussenac 2002; Baldocchi et al. 2010), annual drought

stress for evergreen species is calculated by averaging the drought index from all months with mean temperature >5.5 °C. For all deciduous species, we assumed a 9-month growing season from March to November for our coastal site.

Environmental inputs and settings for LANDCLIM simulations

LANDCLIM uses mean monthly temperature, total monthly precipitation, soil water-holding capacity (i.e. bucket size), topography, and elevation to calculate drought and temperature stress. We developed a climate scenario by combining weather station data, with a new chironomid-inferred Holocene temperature reconstruction from Lago Verdarolo, located 60 km north of Lago di Massacciucoli in the northern Appenine Mountains at 1,394 m a.s.l. (Samartin 2011), following an approach similar to Heiri et al. (2006). The Lago Verdarolo record provides the only quantitative, vegetation-independent, temperature reconstruction for the full Holocene from northern or central Italy and is consistent with qualitative, vegetation-independent temperature reconstructions that show summer temperatures were highest between 9500 and 5500 cal yr BP (Giraudi et al. 2011). Mean July air temperature was reconstructed from 56 chironomid assemblages applied to a transfer function derived from a dataset of 274 lakes in Switzerland and Norway (Heiri et al. 2011). We produced a temperature scenario by combining the most probable reconstructed temperature for each level with weather station data. We first fit mean monthly temperatures from Pisa San Giusto Airport from the period 1951–2007 to a gamma distribution and drew random values to produce an 8000-year simulation period. We then added past temperature changes to the six warmest months by adding the smoothed (5-point moving average) temperature deviation from Lago Verdarolo. We calculated the temperature deviation by subtracting the inferred temperatures for every level from the average of the five youngest inferred temperatures (i.e. 12.9 °C; period 1865–2009 AD). Although winter temperature also limits plant growth near the Mediterranean coast, no quantitative, vegetation-independent, winter temperature records are available. Therefore, we used modern winter temperatures for the coldest 6 months (i.e. November–April) for the entire simulation period. We used modern

precipitation abundances drawn from a gamma distribution for all months.

We separated the landscape surrounding Lago di Massacciucoli into two land types: dunes between the lake and the sea, and uplands east of the lake. Topographical inputs and bucket size for these areas were derived from digital soil maps and a digital elevation model (Data source: Autorità di Bacino del Fiume Serchio). We estimated bucket size as follows:

$$\text{Bucket size (cm)} = \text{AWC} \times D \qquad (1)$$

where AWC is the available water capacity (cm $\times$ cm^{-1}), and D is soil depth (cm). We estimated AWC from a map of soil texture, and calculated the compound topographic index (CTI) of each cell to approximate variations in soil depth using the TauDEM 5.0 extension in ArcGIS 9.3.1. CTI is a quantification of catenary landscape position that is correlated to soil depth and other variables that determine bucket size (e.g. silt and organic matter content) in mediterranean-type ecosystems (Gessler et al. 2000). We used CTI to quantify the gradient in soil depth between shallow soils (40 cm) in landscape positions prone to erosion, and deep soils (150 cm) in zones of colluvial accumulation. CTI is not appropriate for relatively flat landscapes, so we assumed a constant soil depth of 100 cm for the dune land type. Sandy loam soils, typical of the uplands near Lago di Massacciucoli, have an AWC ranging from 0.13 to 0.15 cm $\times$ cm^{-1}, and the sandy soils in the dune land type have an AWC of about 0.07–0.09 cm $\times$ cm^{-1} (USDA 2011). We randomly assigned these AWC ranges to grid cells of both land types, then multiplied AWC and soil depth to estimate bucket size, but used 20 cm as a maximum bucket size, and 6 cm as a minimum bucket size. Our final bucket size map is consistent with soil maps showing sandy soils on ridge tops and soils richer in silt and clay in lower topographic positions, but has a natural gradient between the two.

Simulation scenarios and comparison of model output with pollen data

We simulated vegetation dynamics using the Holocene climatic scenario described above with all combinations of three fire regimes, and three browsing intensities. Although timber exploitation also shaped forest dynamics near Lago di Massaciuccoli during the last 2,000 years, we limited the number of disturbance factors manipulated in order to focus on fire and browsing, two factors that humans have affected since the Neolithic period. Fire is an emergent property in LandClim that depends on an ignition source, fuel availability, and fuel dryness. Ignition frequency is determined by multiplying a user-defined ignition coefficient by the total number of cells in the landscape (Schumacher and Bugmann 2006). We used an ignition coefficient (0.002) that is consistent with low human disturbance and natural ignition sources in south European forests for all simulations (Reineking et al. 2010). LandClim uses a cumulative beta probability density function to relate fuel dryness in each cell to the probability a fire can ignite or spread to the cell (Supplemental Materials: Estimating the probability of fire spread and browsing mortality). We varied the fire regime by altering α (i.e. the shape of the curve), the minimum fire probability, and/or the maximum fire size to attain three fire regimes: (A) small infrequent fires, (B) large infrequent fires, and (C) small frequent fires. We set the maximum size of individual fires in simulations A and C to 10 % of the landscape. However, because we did not limit the total number of fires, more than 10 % of the landscape may burn in any year. Our approach allows us to evaluate the impacts of changing fire size and frequency on vegetation, but does not necessarily mimic historical fire sizes or return intervals.

LandClim simulates the impact of ungulate browsing on regeneration with species-specific browsing tolerances (Supplemental Table 2) and a user-defined browsing intensity (Supplemental Materials: Estimating the probability of fire spread and browsing mortality). We used three levels of browsing: regeneration without browsing (i.e. browsing intensity = 0), low browsing intensity (0.25), and moderate browsing (0.5). Under moderate browsing intensity, species with very low browsing tolerance (e.g. *A. alba*) have a maximum establishment probability <2 %.

We performed simulation experiments that included all combinations of fire and browsing. We initiated our lowest disturbance scenario (i.e. small infrequent fires, no browsing) from bare ground using the full 8000 year climate scenario. However, because pollen data are available only after 7000 cal yr BP, all model/data comparisons follow a 1000-year spin-up period. For all other disturbance combinations, we simulated vegetation dynamics since 7000 cal yr BP using the vegetation simulated after the 1000-year, low-disturbance, spin-up to initiate the model.
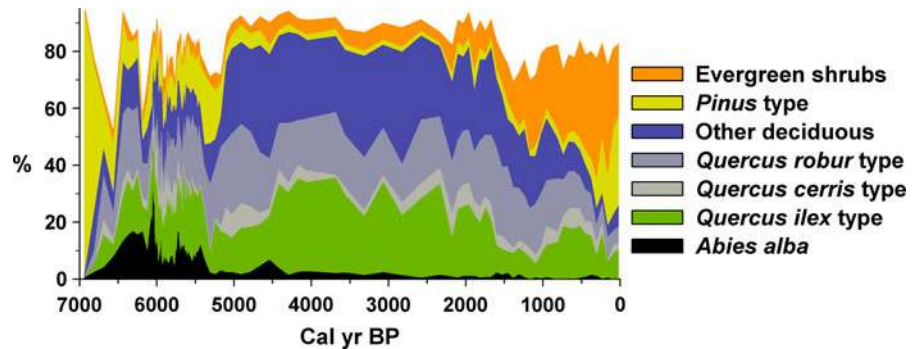
Because LANDCLIM does not simulate wetland vege-
tation, we removed the pollen types of wetland species
at Lago di Massacciucoli (e.g. *Alnus* type) from the
pollen sum for our comparisons (Fig. 2). We chose
two time windows to evaluate spatial variability in the
distribution of dominant species, 6000 cal yr BP when
summer temperatures were ∼1.5 °C above the mod-
ern mean, and the present (0 cal yr BP), with modern
climatic conditions. At each time-window, we mapped
the species or group of species with the highest
biomass for each grid cell in a representative 4 km²
section of the upland land type. We only mapped
vegetation from the upland land type because of the
lesser of variation in topographic and edaphic inputs
for the dune land type.

Results

Simulated forests with low disturbance

LANDCLIM simulates a mixed forest of coniferous,
broadleaved-evergreen, and broadleaved-deciduous
species in the uplands near Lago di Massacciucoli
under low disturbance conditions (Fig. 3a). *Q. ilex* and
A. alba constitute most (77 ± 3 %) of the biomass.
Deciduous oaks, especially *Q. pubescens* and *Q. cerris*
are also abundant, and other deciduous species
including *O. carpinifolia*, *Fagus sylvatica*, *Acer* spp.,
and *Tilia cordata* are consistently present. However,
F. ornus, an early-successional, and relatively fast-
growing species is the most abundant of the other
deciduous species, particularly following fire, when it
occurs with *Pinus halepensis* and shade-intolerant
evergreen shrubs (e.g. *Arbutus unedo*). Other ever-
green shrubs with greater shade tolerance (e.g. *Ilex
aquifolium*, *Phillyrea latifolia*, *Rhamnus alaternus*)

contribute on average <2 % of total biomass.
Although the composition of the forest remains
broadly consistent through the simulation, species
dominance varies with temperature. *A. alba* contrib-
utes the least biomass during the warmest portion of
the simulation when *Q. ilex* is the dominant species
(Fig. 3a). *A. alba* abundance increases as summer
temperature declines, reaching 40 % of simulated
biomass by 4500 cal yr BP, when summer tempera-
tures were similar to the present, and maintaining
>25 % of total biomass for the remainder of the
simulation. Deciduous species also increase with
lower temperatures (Fig. 3a). However, their abun-
dance remains relatively low, contributing about 10 %
of total biomass during the warmest intervals and
15 % when temperature is lower.

Quercus ilex is the dominant species in the dune
land type. *Q. suber* is also common but achieves much
lower abundance (Fig. 4a). Other broadleaved-ever-
green species including *Arbutus unedo*, *Rhamnus
alaternus*, and *Olea europea* contribute 2–3 % of the
total biomass. *Q. pubescens* (4 ± 0.7 %) and *F. ornus*
(2 ± 0.3 %) are the only deciduous species with
notable biomass contributions. Small numbers of
A. alba establish in the understory during cooler inter-
vals, but never attain large size. Temperature change
does not elicit major changes in species composition.

Simulated disturbance impacts

Our simulations with small, infrequent fires have an
average fire return interval (FRI) to each cell that is
roughly double (3,572 years) the FRI of simulations
with large, infrequent fires (1,852 years). With small,
frequent fires, the average FRI is 182 years. In all
simulations, drier sites (e.g. shallow soils, southerly
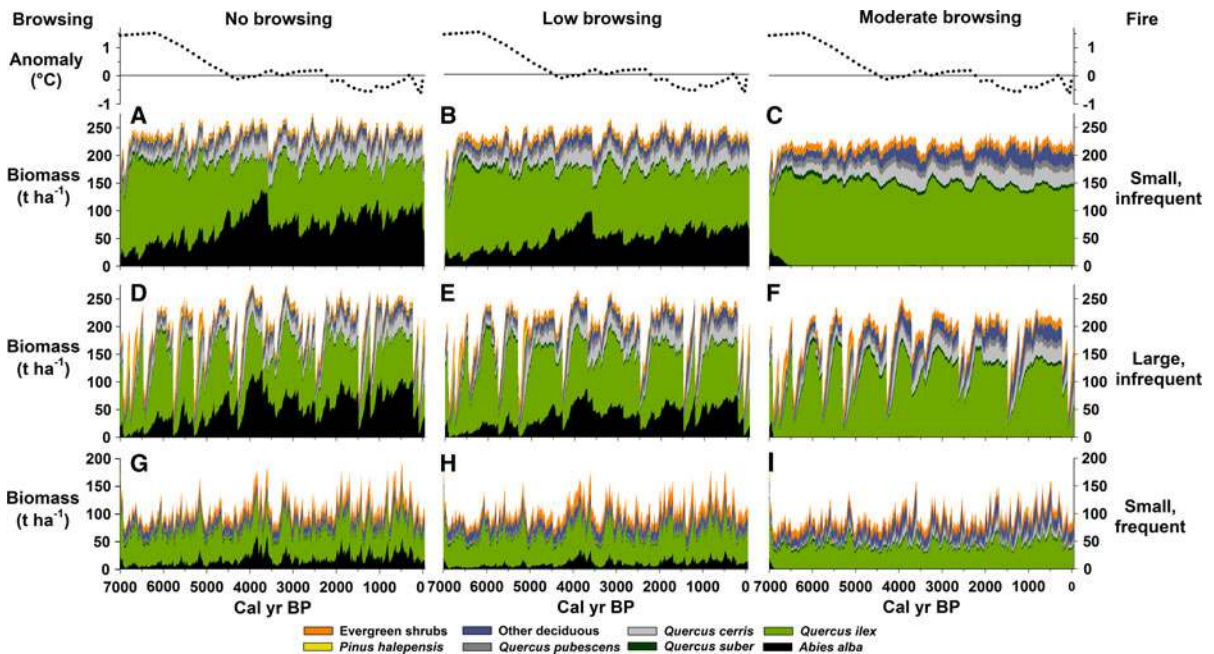aspects) burn more frequently than moister sites (e.g.

Fig. 3 *Top* chironomid-inferred temperature anomaly from Lago Verdarolo (Samartin 2011). *Bottom* vegetation simulated in the upland land type. Browsing intensity increases from *left to right* from no browsing, to low browsing, and moderate browsing. Fire-regime intensity increases from *top to bottom*: small, infrequent fires (**a–c**); large, infrequent fires (**d–f**), and small, frequent fires (**g–i**)
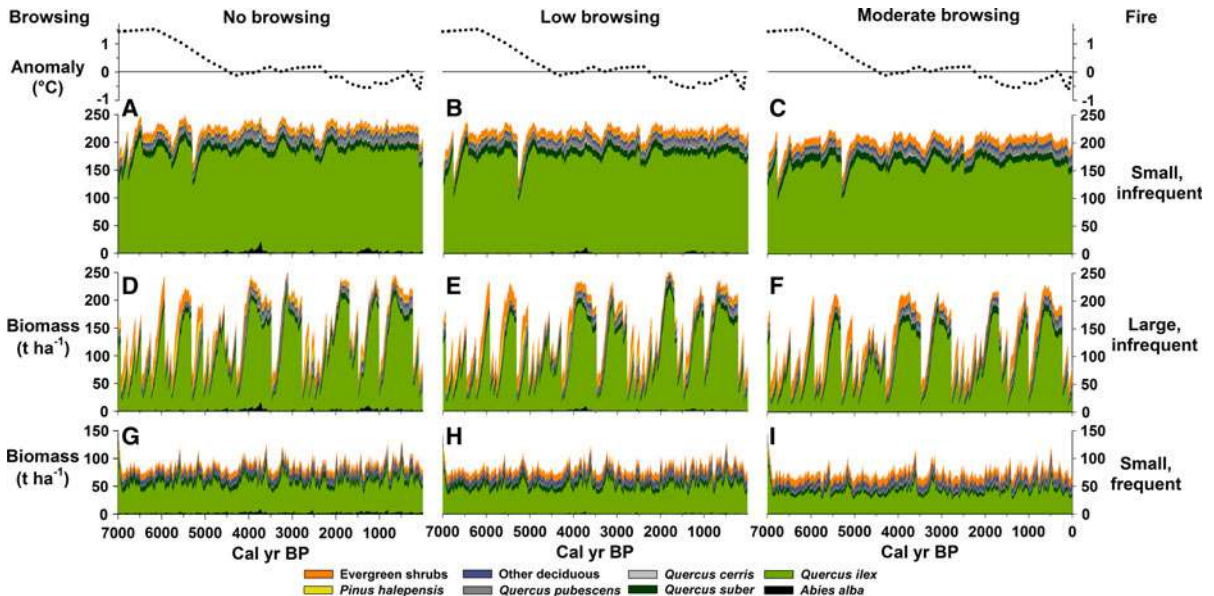

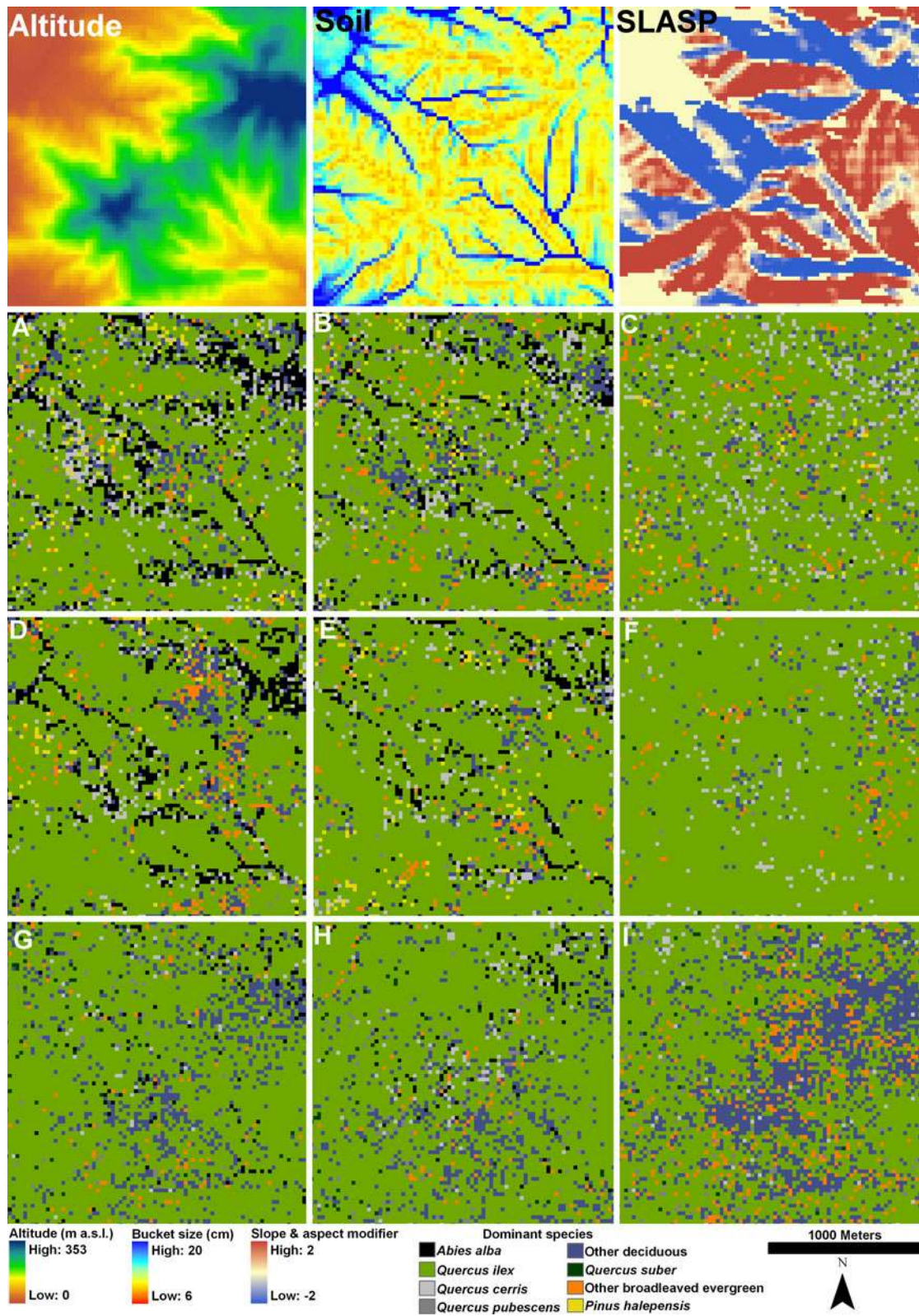**Fig. 4** Vegetation simulated in the dune land type under the fire and browsing regimes described in Fig. 3

deep soils, northerly aspects). Simulated fires are most frequent during intervals with temperature above the Holocene mean. Large, infrequent fires reduce the average biomass and increase its variability in both upland and dune land types (Figs. 3d–f, 4d–f). Simulations with small, frequent fires have less biomass

Altitude (m a.s.l.)
High: 353
Low: 0

Bucket size (cm)
High: 20
Low: 6

Slope & aspect modifier
High: 2
Low: -2

Dominant species
Abies alba
Quercus ilex
Quercus cerris
Quercus pubescens
Other deciduous
Quercus suber
Other broadleaved evergreen
Pinus halepensis

1000 Meters

N

◄ **Fig. 5** *Maps* showing topographic features and the species or groups of species with the highest biomass in each grid cell within a representative 4 km² section of the upland land type at 6000 cal yr ʙᴘ. *Top left* altitude; *center* soil bucket size (see text); *right* slope and aspect modifier (SLASP) used in the soil moisture model to estimate changes in potential evaporation due to topography (Bugmann 1994). *Negative values* decrease evaporative demand and correspond to northerly slopes. *Positive values* increase evaporative demand and correspond to southerly slopes. For the vegetation maps, browsing intensity increases from *left to right*: no browsing (**a**, **d**, **g**), low browsing (**b**, **e**, **h**), and moderate browsing (**c**, **f**, **i**). Fire-regime intensity increases from *top to bottom*: small, infrequent fires (**a–c**); large, infrequent fires (**d–f**); and small, frequent fires (**g–i**)

and lower biomass variability in both land types (Figs. 3g–i, 4g–i).

Interactions between fire and climate affect vegetation dynamics in our simulations. Whereas the abundance of shade-intolerant evergreen shrubs and *P. halepensis* increases after all fires, in simulations with large, infrequent fire, shade-intolerant species are most important on a landscape scale before 5000 cal yr ʙᴘ when high temperatures favor fire ignition and spread (Fig. 3d–f). Although interactions among climate, fire, and vegetation are less pronounced in simulations with small frequent fire, the importance of *A. alba* also increases with the lower summer temperatures after 4000 cal yr ʙᴘ (Fig. 3g–i).

Browsing reduces the total biomass in our simulations, but increases the importance of evergreen oaks and deciduous hardwoods. Low browsing causes only a small decrease in total biomass, and does not eliminate *A. alba* from the upland land type. However, with frequent fire and warmer-than-present summer temperatures, very little *A. alba* biomass is simulated (Fig. 3e, h). Moderate browsing eliminates *A. alba* regeneration (Fig. 3c, f, i). Without late-successional *A. alba*, *Q. ilex* and *Q. suber* are more abundant, as are several deciduous hardwoods, especially *Q. cerris*, *Tilia cordata*, *O. carpinifolia*, and *Fagus sylvatica*. Expansion by deciduous hardwoods is strongest during intervals with declining temperature. Changes due to browsing are less pronounced in the dune land type, although a slight decrease in total biomass is evident, and some expansion by evergreen shrubs occurs (Fig. 4).

Spatial variations in simulated species abundance

Comparison of species dominance at 6000 cal yr ʙᴘ and at present provides two examples of how species abundance varies across the upland land type with soil and topography (Figs. 5, 6). Differences between these periods relate to both the higher average summer temperatures at 6000 cal yr ʙᴘ and to stochastic differences. *A. alba* and *Q. ilex* grow together in the upland land type in individual cells in the low-disturbance scenario. However, *A. alba* is the dominant species only in settings with the highest moisture availability (e.g. colluvial deposits or north-facing slopes; Figs. 5a, 6a). The spatial extent of *A. alba* dominance is smaller at 6000 cal yr ʙᴘ when summer temperatures were higher, than today when drought stress is less severe in the simulations. Much of the expansion by *A. alba* in the simulation during the late Holocene occurs on north-facing slopes. Similarly, deciduous species are mostly restricted to moist landscape settings at 6000 cal yr ʙᴘ, but expand on northerly slopes during the late Holocene (Figs. 5a, 6a).

Disturbance reduces the spatial extent of *A. alba* dominance in the upland land type, mostly to the benefit of *Q. ilex*. However, the impact is larger at 6000 cal yr ʙᴘ than at present. With moderate browsing, *Q. cerris* and other broadleaved-deciduous species replace *A. alba* in the most mesic settings in both time windows (Figs. 5c, 6c). However, the benefit to deciduous species is limited in comparison with *Q. ilex*, especially at 6000 cal yr ʙᴘ. Large, infrequent fires favor *Q. ilex* at all browsing levels at 6000 cal yr ʙᴘ at the expense of *A. alba*, which dominates only the most mesic and least fire-prone settings in valley bottoms (Fig. 5d–f). Under present climate, large, infrequent fires favor *Q. cerris* and *Q. pubescens*, especially in the highest altitudes, and *Pinus halepensis* in the driest settings (Fig. 6d–f). With moderate browsing and large, infrequent fires, other deciduous species, especially *O. carpinifolia* and *Fagus sylvatica*, increase in the highest altitudes, and broadleaved-evergreen shrubs including *Arbutus unedo* and *Phillyrea latifolia* dominate dry settings at lower altitude (Fig. 6f). Topographic and edaphic variations in species abundance are least apparent in simulations with small, frequent fires (Figs. 5j–l, 6j–l). *A. alba* is restricted to mesic sites with frequent fire, and is the most abundant species in little of the landscape. Frequent fire favors expansion by *F. ornus* and other broadleaved-deciduous species, especially with low and moderate browsing. Moderate browsing increases the prevalence of broadleaved-evergreen shrubs.
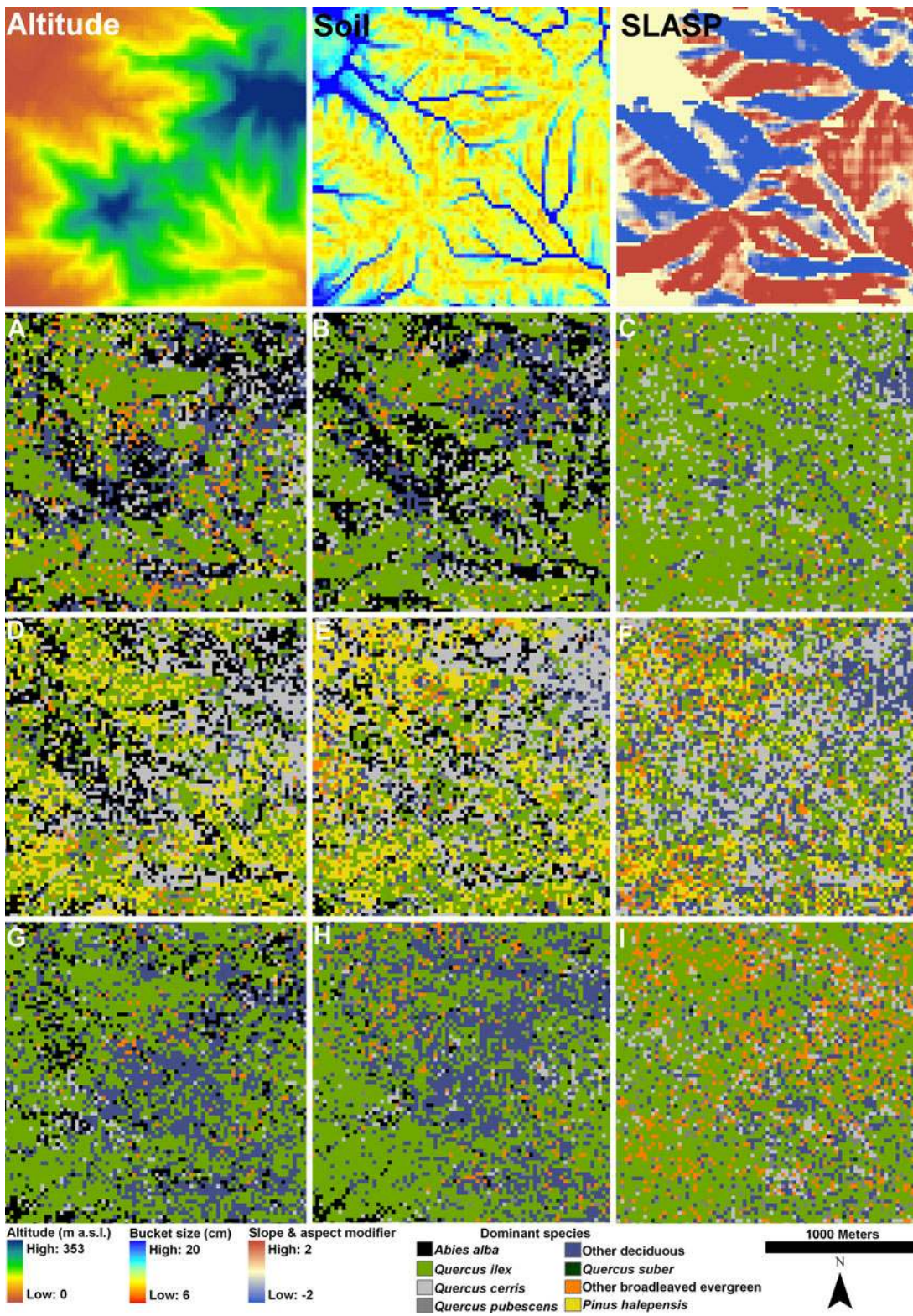
Fig. 6 As in Fig. 5, except dominant vegetation maps of LANDCLIM output for the present

Discussion

Agreement between simulated vegetation dynamics and pollen data

Our simulations provide independent support for paleoecological studies that concluded montane (i.e. *A. alba*), Mediterranean (e.g. *Q. ilex*), and sub-Mediterranean (e.g. *Q. pubescens*, *Q. cerris*) species grew together in mixed forests near the Mediterranean coast during the warmest part of the Holocene (Figs. 2, 3; Colombaroli et al. 2007; Bellini et al. 2009). Thus, we reject the hypothesis that the abundant *A. alba* pollen and wood in lake and wetland sediments at Lago di Massacciucoli result from long-distance fluvial transport. Although similar mixed forests do not exist at present because extant, natural Mediterranean *A. alba* populations are limited to moister and cooler settings above 800 m a.s.l. (Rovelli 1995; Aussenac 2002), our results based on the competitive interactions of individual species indicate climate does not exclude *A. alba* at Lago di Massacciucoli. Instead, the tall-growing and shade-tolerant *A. alba* dominates landscape positions with the highest moisture availability (Figs. 5, 6). This result is consistent with modern observations of regeneration by planted *A. alba* populations at low elevation in mesic settings near Lago di Massaciuccoli (Pedrotti 1967). In favorable settings, and with limited fire and browsing, *A. alba* outcompetes the drought-tolerant, but shorter and slower-growing *Q. ilex* as well as less shade-tolerant competitors. However, as drought stress increases, *Q. ilex* becomes dominant.

Calculation of drought stress in LANDCLIM relies on the assumption that evergreen species can grow in all months with an average temperature >5.5 °C. When winters are mild and moist, this gives *A. alba* an advantage over deciduous species that have a physiologically-limited growing season (e.g. *Fagus sylvatica*, *Q. cerris*). Our assumption of winter growth is justified by observations that *A. alba* photosynthesizes at low temperatures (i.e. above 0 °C) during winter, and that most growth occurs during a short period in spring when moisture availability is typically high at our study site (Aussenac 2002; Robakowski 2005). Furthermore, *A. alba* growth is highest in years that follow a wet autumn (Battipaglia et al. 2009), the season with highest average precipitation at Lago di Massacciucoli. Our results do not mean that *A. alba* is insensitive to climatic change or drought stress. Indeed the lower biomass and restricted distribution during the mid Holocene in comparison to the late Holocene (Figs. 3, 5, 6) demonstrate that *A. alba* responds to changes in summer moisture availability in LANDCLIM.

Although our data indicate *A. alba* and evergreen oak grew together near Lago di Massacciucoli, the entire landscape did not support *A. alba*. For example, *A. alba* was probably never important on the dunes near the lake (Fig. 4). However, it is difficult to evaluate the past importance of the dunes as a pollen source because the extent of dune ecosystems was affected by rising sea level during the middle Holocene, and progradation of the coastal plain with deposition of erosional sediments during the late Holocene (Pranzini 2001; Rossi et al. 2011). In contrast, *A. alba* may have grown near the lake in areas not included in our modeled landscapes. *A. alba* wood is present in cores taken from the lake, as well as wetlands near Lago di Massacciucoli (Colombaroli et al. 2007; Bellini et al. 2009). These areas probably supported upland trees during the early-middle Holocene and contributed pollen to Lago di Massacciucoli, but became wetlands when water levels rose.

Differences between simulated vegetation dynamics and pollen data

The most striking difference between modeled and pollen-inferred vegetation is in *A. alba* abundance during the late Holocene. In contrast to pollen data that show a major decline starting after 6000 cal yr BP, *A. alba* increases in our no- and low-browsing simulations during the mid-late Holocene, especially after 4500 cal yr BP when summer temperatures reached the modern average (Figs. 2, 3). Our results suggest that declining summer temperatures, in the absence of other climatic change, would have favored *A. alba* by decreasing drought stress. However, climatic changes that are not included in our simulations could have caused the difference in *A. alba* importance between pollen-inferred and simulated vegetation. For example, a decline in summer precipitation could have increased drought stress and favored evergreen oaks over *A. alba*. In fact, expansion by evergreen oak in pollen records from the Mediterranean region during the mid-late Holocene has been interpreted as indicating a regional precipitation decline (Jalut et al. 2009; Finsinger et al. 2010;

Sadori et al. 2011). However, rising lake levels at other nearby sites in Tuscany (e.g. Lake Accesa) suggest moisture availability increased during the late Holocene (Magny et al. 2007; Giraudi et al. 2011). Although we cannot completely rule out the possibility that episodic changes in the precipitation regime contributed to the *A. alba* decline after 6000 cal yr BP, our results indicate that recent precipitation abundance and temperatures were favorable for *A. alba*. Thus in agreement with earlier conclusions (Colombaroli et al. 2007), our results do not support the hypothesis that a long-term drying trend caused the collapse of *A. alba* and expansion by drought-tolerant species near the Mediterranean coast.

Other interesting differences exist between our simulations and pollen data. For example, pollen data suggest roughly equal importance of deciduous and evergreen oaks, whereas evergreen species dominate the simulated biomass, especially when disturbance is low (Figs. 2, 3). This difference may partially result from regional pollen inputs. Lago di Massacciucoli is a large lake, with a regional pollen source area. Because the surrounding region is topographically complex with cooler and moister settings than our simulation landscapes, it provides abundant habitat for deciduous species that are prolific pollinators (e.g. deciduous *Quercus* spp., *Corylus avellana*). The increase in deciduous species with altitude is also evident in LANDCLIM (Figs. 5, 6).

Impacts of fire and browsing on forest dynamics

The disappearance of *A. alba* from Mediterranean and sub-Mediterranean ecosystems has been linked to an anthropogenic increase in fire and browsing pressure during the Neolithic, which began ca. 8000 cal yr BP in Central Italy (Tinner et al. 1999; Keller et al. 2002; Wick and Mohl 2006; Colombaroli et al. 2007). Vegetation dynamics simulated under varying fire regimes support this interpretation. Fire reduces *A. alba* biomass in the landscape and favors broad-leaved species capable of resprouting and rapid growth (Fig. 3). Increasing fire in our simulations restricts *A. alba* to the most favorable habitats, especially in valley bottoms (Figs. 5, 6). These sites have the highest soil-moisture availability which favors *A. alba* over more drought-tolerant competitors, and also reduces fire risk. Sites situated at the base of a slope are also less fire prone because fire spreads less

readily downhill (Rothermal 1972). However, landscape positions that are least subject to fires, and most conducive to *A. alba* growth, were probably also most suitable for early land use because they provided deep soils and level terrain that are suitable for agriculture in summer-dry environments. *A. alba* may have been particularly sensitive to fire when summer temperatures were highest. For example, repeated fires during the first 500 years in our simulation with large, infrequent fires nearly eliminated *A. alba* from the landscape. Fire also had the largest impact on *A. alba* abundance in simulations with small, frequent fires when temperature was highest (Fig. 3).

Although previous research demonstrated a link between the *A. alba* collapse and fire, *A. alba* did not re-expand at Lago di Massacciucoli when regional fire activity declined after 5000 cal yr BP (Colombaroli et al. 2007; Vannière et al. 2008). Instead, *Q. ilex* increased and deciduous species remained abundant (Fig. 2). This situation is consistent with simulations with moderate browsing and infrequent fires where *Q. ilex* is the dominant species in a mixed deciduous/evergreen forest with high biomass (Figs. 3, 4). It is plausible that intense browsing related to Neolithic pastoralism limited *A. alba* regeneration, even in the absence of frequent fire. *A. alba* is a preferred browse species for domestic and wild ungulates, and is especially sensitive to browsing pressure because it produces new shoots only at the apex (Ellenberg 1996). Declining *A. alba* regeneration during recent decades has been widely attributed to rising populations of wild ungulates (Motta 1996). However, whereas wild ungulate populations tend to fluctuate through time, providing windows of opportunity for regeneration, livestock grazing is typically persistent and intense with long-term impacts on regeneration and overstory composition (Cierjacks and Hensen 2004; Didion et al. 2009). Neolithic populations in central Italy depended on livestock for sustenance, and browsing pressure was probably substantial, especially near the coasts and large lakes where settlements were concentrated (Malone 2003; Rustioni et al. 2007). Furthermore, archeological evidence documents the use of *A. alba* as animal fodder during the Neolithic (Akeret et al. 1999).

Changes in species composition in our simulations with low and moderate browsing pressure relate not only to the direct impacts of browsing on regeneration, but also to interactions with climate. Moderate

browsing pressure eliminates *A. alba* regeneration which favors *Q. ilex* as well as less shade-tolerant evergreen (e.g. *Phillyrea latifolia*, *Arbutus unedo*) and deciduous (e.g. *Q. cerris*, *F. ornus*, *O. carpinifolia*) competitors that benefit from increased light availability. However, some expansion by deciduous species (e.g. *Q. cerris*) after 5000 cal yr BP is also evident in simulations without browsing pressure (Fig. 3a, d). This result implies that the expansion by deciduous species evident in the pollen record (Fig. 2) resulted from the combined impacts of human disturbance and the contemporaneous shift to cooler and therefore moister summers. Decreased fire activity after 5000 cal yr BP (Colombaroli et al. 2007) may also relate to cooler conditions. Fire impacts on vegetation also declined with summer temperatures in simulations with large, infrequent fires (Figs. 3d–f, 4d–f) due to moister conditions that inhibited fire ignition and spread. In contrast, charcoal evidence demonstrate that fire activity increased during the last 2,000 years when summer temperatures were similar to, or even below, the recent average (Colombaroli et al. 2007). Pollen-inferred vegetation of the last 2,000 years is most similar to our simulations with small, frequent fires that favored low biomass, and a higher importance of evergreen shrubs (Figs. 2, 3, 4). Such changes are consistent with land-use intensification and forest clearance during the Etruscan and Roman periods (Sadori et al. 2010).

Conclusions

Comparison of pollen and simulation data demonstrates that the mixed forests of *A. alba*, *Q. ilex*, and deciduous species that grew near the Mediterranean coast during the warmest part of the Holocene remain possible under present climatic conditions. These forests likely disappeared due to the effects of increasing human land use such as increases in fire activity that eliminated mature trees, and grazing pressure that eliminated regeneration by *A. alba*. Although this extinct forest type remains possible with current climate, the spatial extent of environmental conditions where *A. alba* is competitive declines as temperature increases. Anticipated warming of 4 °C (e.g. Gao and Giorgi 2008) could eliminate the potential for *A. alba* near the Mediterranean coast where urbanization, agriculture, and historic soil degradation also limit the availability of suitable sites for mixed

forests. However, such forests will remain an attractive management goal for areas further north that are expected to develop a mediterranean-type climate in the future. Thus, management strategies that promote long-lived species such as *A. alba* and *Q. ilex* now could provide for long-term security of ecosystem services in a warmer and drier future. Furthermore, even in the absence of *A. alba*, closed forests dominated by *Q. ilex* will remain possible near the Mediterranean coast in a warmer future if fire disturbance is limited. Therefore management strategies that promote succession to evergreen forests could offer long-term ecological benefits such as reduced landscape flammability, protection from erosion, and carbon sequestration, even in a warmer and drier future.

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