

Reviving extinct Mediterranean forest communities may improve ecosystem potential in a warmer future

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The Mediterranean Basin is the region of Europe most vulnerable to negative climate-change impacts, including forest decline, increased wildfire, and biodiversity loss. Because humans have affected Mediterranean ecosystems for millennia, it is unclear whether the region's native ecosystems were more resilient to climate change than current ecosystems, and whether they would provide sustainable management options if restored. We simulated vegetation with the LANDCLIM model, using present-day climate as well as future climate-change scenarios, in three representative areas that encompass a broad range of Mediterranean conditions and vegetation types. Sedimentary pollen records that document now-extinct forests help to validate the simulations. Forests modeled under present climate closely resemble the extinct forests when human disturbance is limited; under future scenarios, characterized by increased temperatures and decreased precipitation, extinct forests are projected to re-emerge. When combined with modeling, paleoecological evidence reveals the potential of native vegetation to re-establish under current and future climate conditions, and provides a template for novel management strategies to maintain forest productivity and biodiversity in a warmer and drier future.

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As the cradle of Western civilization, the Mediterranean region has sustained large human populations for millennia. Nevertheless, the continued provision of ecosystem services in the region is highly uncertain, given that it is a climate-change “hotspot”, where summer warming and drought are likely to intensify during this century. Mediterranean ecosystems may be particularly vulnerable to degradation in a warmer and drier climate. Most vegetation models for the Mediterranean region project declining climatic suitability for economically and ecologically important trees – and concomitant reductions in the ecosystem services they provide – at the warm, dry edges of their current ranges, and increasing risk of catastrophic fire as flammable shrublands replace lowland forests (Schröter *et al.* 2005; Moriondo *et al.* 2006). However, extensive variation in climate sensitivity exists among vegetation models (Cheaib *et al.* 2012). Therefore, individual models require empirical valida-

tion. This is difficult in the Mediterranean region, where millennia of human impacts (eg fire, grazing, logging) have resulted in a mismatch between the distributions and climatic requirements of Mediterranean trees. As a result, models that are calibrated and/or validated with data based on present tree distributions tend to underestimate the potential for native forests to form in warm, dry conditions (Garcia-Valdes *et al.* 2013). New approaches are therefore needed to understand where native forests can develop in the Mediterranean region under current and future climate conditions, and to identify realistic management goals that can maintain biodiversity and productivity in a changing climate.

Combining paleoecological data with process-based models helps to address these needs by testing assumptions about the climatic tolerances of native Mediterranean forests. During the mid-Holocene (approximately 8000 to 5000 years ago), the ranges of important tree species included warmer and drier habitats than those within the species' present ranges. These species formed communities that are absent today (Carrión *et al.* 2010; Tinner *et al.* 2013). Furthermore, closed forests (ie with dense canopies) grew in regions that are now dominated by shrublands. For example, evergreen forests composed of holm oak (*Quercus ilex*) and olive trees (*Olea europaea*) occurred along the southern coast of Sicily, the warmest and driest region of Italy (Tinner *et al.* 2009). Many researchers attribute the widespread decline of Mediterranean forests during the past 7000 years to climatic changes that brought progressively drier conditions to the region (eg Sadori *et al.* 2011).

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Applying the “aridification hypothesis” to current and future landscapes implies that the re-establishment of the former native forest communities of the mid-Holocene (hereafter “extinct” forest communities) is impossible because the present climate is too dry, and that expansion of the Mediterranean climate zone would have marked consequences for the productivity of European forests. Conversely, reconstructions of past climates that rely on multiple indirect environmental indicators or “proxies” linked late-Holocene forest decline (<5000 years ago) – even in the warmest and driest Mediterranean settings – to human impacts rather than climatic change (Colombaroli *et al.* 2007; Tinner *et al.* 2009). Process-based models that use plant physiological traits to simulate competition-driven forest dynamics can test these opposing hypotheses by simulating vegetation under present and future climates. Likewise, paleoecological data may corroborate model output, which is critical if simulated forests do not resemble present-day vegetation.

We combined vegetation simulations from the LANDCLIM dynamic landscape vegetation model (Schumacher *et al.* 2004; Henne *et al.* 2013) with paleoecological records, to demonstrate how extinct native forests provide renewed potential for Mediterranean ecosystems in both present climates and in a warmer and drier future (Figure 1). We modeled vegetation in three representative regions where Holocene pollen records document the species compositions and structure (eg closed canopy versus shrublands) of past “pristine” forests and the effects of the subsequent intensification of human impacts. The warmest and driest conditions are represented by Gorgo Basso, on the Italian island of Sicily (Tinner *et al.* 2009), and are associated with vegetation in the so-called thermo-Mediterranean belt, which extends between ~30–40° N and 15° W–40° E (Lang 1994). At Lago di Origlio, within the Ticino region of southern Switzerland (Tinner *et al.* 1999), sub-Mediterranean vegetation (~43–46° N, 15° W–40° E) grows under a moist and moderately warm climate. Between these sites lies Lago di Massaciuccoli, in

central Italy’s Tuscany region (Colombaroli *et al.* 2007), with average Mediterranean climatic conditions and meso-Mediterranean vegetation (~40–44° N, 15° W–40° E).

Landscape-level simulations are ideal for our research questions. As compared with global dynamic vegetation models, they feature high spatial resolution (eg 25-m × 25-m grid cells) with more realistic landscape properties, including slope, aspect, and soil variability. Moreover, in

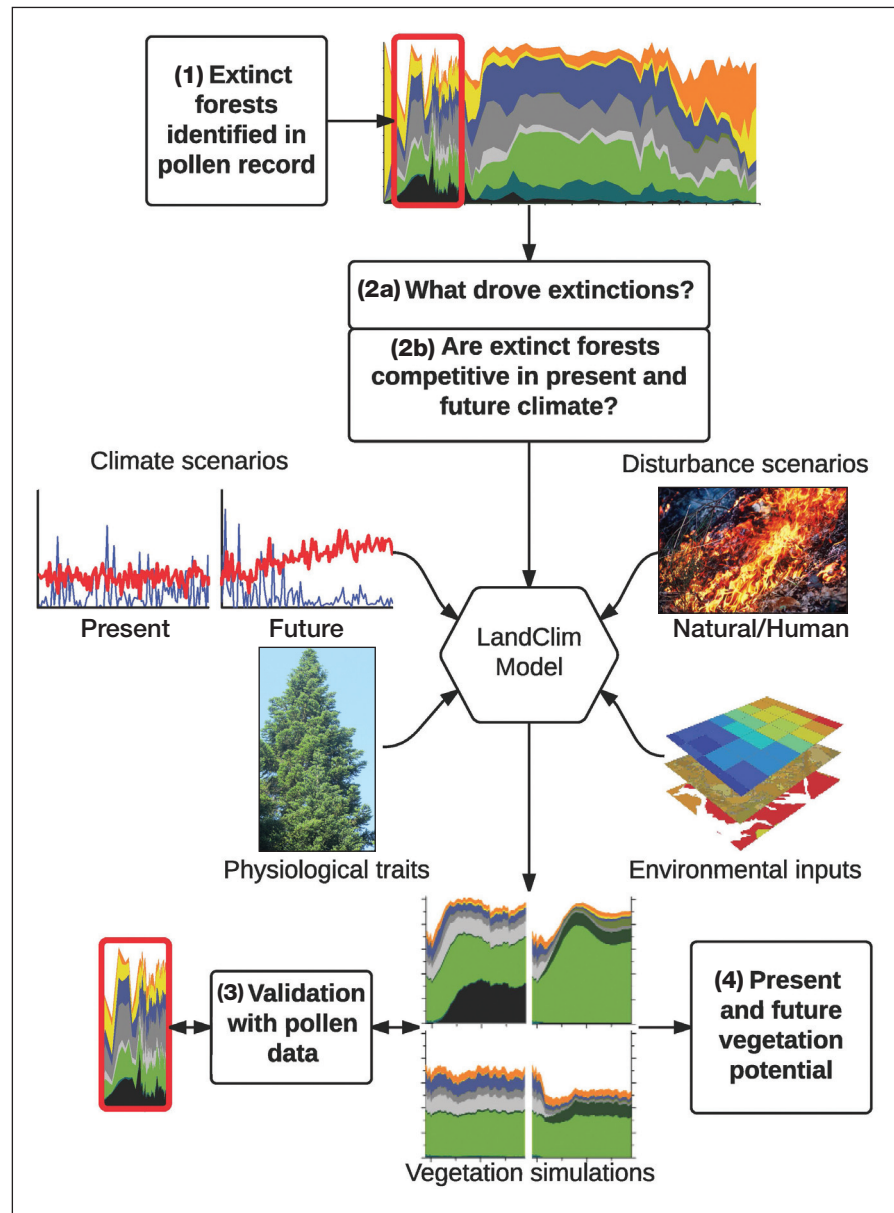


Figure 1. Summary of our research approach using Holocene pollen records and the LANDCLIM dynamic vegetation model to improve understanding of the potential regenerative capacity of native Mediterranean tree and shrub species subjected to present and future environmental conditions. We used separate model scenarios to simulate the impacts of changing climate (present and projected future) and disturbance (separate probabilities for fire ignition and spread, and for the intensity of ungulate browsing). Inputs to LANDCLIM also include tree physiological traits (eg drought, shade, browsing tolerances, and growth rates) and environmental conditions (eg soil depth, elevation, slope, and aspect). Model outputs were validated with local and regional pollen records. Pollen diagram modified from Henne *et al.* (2013).

contrast to species distribution models, dynamic landscape vegetation models simulate interspecific competition and disturbance regimes, which vary with changing climate and land use and are critical determinants of species abundances. We simulated vegetation at each site under present climate using low (pre-human impact) and moderate disturbance scenarios (Henne *et al.* 2013). At each site, we then projected future vegetation under the A1B emissions scenario of the Intergovernmental Panel on Climate Change.

■ Methods

Vegetation dynamics were simulated within 3 km of three lakes – Gorgo Basso, Lago di Massaciuccoli, and Lago di Origlio – with the LANDCLIM model (Schumacher *et al.* 2004). Modeled landscapes included all upland forests, shrublands, and grasslands but omitted regions where upland forests cannot develop (ie wetlands, coastal dunes, and cultivated lands). The LANDCLIM model estimates competitive dynamics among cohorts of trees and shrubs in 625-m² grid cells using monthly temperature and precipitation data and landscape-specific soil conditions and topography (Figure 1). Model cells interact to simulate wildfire over the entire landscape. A cumulative beta probability density function relates a drought index to the probability that a fire will ignite and spread. Browsing by wild and domestic ungulates is simulated by varying the probability of seedling establishment. Without browsing, all species have an equal probability of survival; as browsing intensity increases, trees and shrubs with high sensitivity to browsing have a lower probability of establishment than species that are tolerant of browsing (Henne *et al.* 2013).

We simulated vegetation at each site under low and moderate disturbance using a control scenario with present climate, and future climate scenarios for 2011–3000 AD. Our low disturbance scenario excludes browsing and includes infrequent fire to mimic disturbance regimes that existed before the onset of human impacts on vegetation at the three sites (Tinner *et al.* 1999, 2009; Colombaroli *et al.* 2007). Our moderate-disturbance scenario simulates land-use intensification (Henne *et al.* 2013); simulated browsing limits regeneration of browsing-sensitive species (eg silver fir [*Abies alba*]), and small, frequent fires reduce overall plant biomass (WebPanel 1). To standardize the start of each model run, we initialized all simulations with a 2000-year model “spin-up” period, using a present-day (1951–2000 AD) climate scenario and moderate disturbance. We developed future climate scenarios by combining output from nine regional climate models from the ENSEMBLES project (Van der Linden and Mitchell 2009) for 2011–2100 AD, with local weather station data from 1951–2000 AD (WebPanel 2). We allowed the vegetation to stabilize in our simulations by applying the climate projected for 2075–2100 AD to 2101–3000 AD. We ranked the scenarios based on the

difference between the projected future vegetation and the modern climate control scenario (WebPanel 3); here, we present the future scenario with the median impact on vegetation for each site. LANDCLIM output represents the mean of 10 replicate simulations.

■ Results and discussion

Extinct Mediterranean forests are competitive in the present climate

Forest communities simulated using present-day climate and a low level of disturbance do not resemble today's dominant vegetation. Instead, those communities are consistent with the species compositions of pristine forests that disappeared during the mid to late Holocene. At Gorgo Basso, which is representative of the warmest and driest environments in Europe, *Q ilex* was the dominant tree in closed, broad-leaved evergreen forests that developed after 5000 calibrated years BC (cal BC). These thermo-Mediterranean forests included *O europaea* and evergreen shrubs, predominantly *Pistacia lentiscus*. The present-day landscape, which is dominated by shrubs and grasslands, with few remnant patches of *Q ilex* forest, developed during the past 2000 years as human impacts substantially increased (Tinner *et al.* 2009). LANDCLIM simulates *Q ilex*-dominated forests with large *O europaea* trees contributing 9% of the combined total biomass of trees and shrubs (hereafter “biomass”) under present climate, if disturbance is low (Figure 2). Increasing disturbance reduces the biomass of trees in the model, and increases the abundance of shrubs, especially *Quercus coccifera*, which contributes 23% of biomass. In this scenario, frequent fires prevent *O europaea* from attaining large size, and its average proportion of biomass declines to 5%, which mirrors the present situation in coastal Sicily. Thus, according to the model, management strategies that limit fire occurrence are probably necessary to revive *Q ilex*–*Olea* forests in the present climate.

High potential for the re-establishment of extinct forest types is not limited to Europe's warmest environments. In coastal Tuscany, we project mixed forests of coniferous silver fir (*A alba*), broad-leaved evergreen oaks (*Q ilex*), and deciduous oaks (*Quercus cerris* and *Quercus pubescens*) under present climate and low disturbance (Figure 3). As in the case of the extinct *Q ilex*–*Olea* forests in coastal Sicily, no similar forests exist today. At present, *A alba*, Europe's tallest tree, is restricted to moist, montane ecosystems and does not form coastal forests under meso-Mediterranean conditions (Tinner *et al.* 2013). However, pollen and macrofossil data from Lago di Massaciuccoli and several other sites demonstrate that *A alba* formed forests with *Q ilex* and other Mediterranean species in lowland Tuscany from 4500–3500 cal BC (Tinner *et al.* 2013; Di Pasquale *et al.* 2014), a finding that agrees with our model results. *A alba*

is absent from the region at the onset of our simulations, as a result of moderate disturbance being presumed in the model initialization, but expands to contribute 34% of biomass in the low disturbance scenario. Topography adds another dimension. In our simulations, *A alba* is abundant on relatively moist northerly slopes and in deep soils, but *Q ilex* and other Mediterranean species dominate the driest landscape positions. *A alba* does not expand when subjected to moderate disturbance because fire limits biomass accumulation, and browsing restricts the establishment of this browsing-sensitive species. Instead, simulated forests resemble those that developed after 3500 cal BC, when fire activity increased and deciduous species replaced *A alba*.

Disturbance also limits the species composition of cooler sub-Mediterranean ecosystems today. At Lago di Origlio, *A alba* formed forests with deciduous species between 7000 and 3000 cal BC, but was extirpated by increasing anthropogenic disturbance (Tinner *et al.* 1999). Our simulations also produce forests with *A alba* and deciduous trees under present climate and low disturbance (Figure 4). *A alba* is initially absent due to simulated historical moderate disturbance, but expands to contribute 10% of the biomass and partially replaces deciduous competitors – especially small-leaved lime, *Tilia cordata*, which is an abundant species today. *Fagus sylvatica* and *Quercus petraea* contribute most of the biomass in a species-rich forest that includes *T cordata*, *Carpinus betulus*, and *Ostrya carpinifolia*. Simulations with moderate disturbance and present climate resemble deciduous forests that grow near Lago di Origlio today; *A alba* is absent while *F sylvatica*, *Q petraea*, and *T cordata* are the most abundant species.

Extinct Mediterranean forests provide viable management goals for the future

Future climate change will alter the competitive balance between *Q ilex* and *O europaea* in thermo-Mediterranean ecosystems. The potential for *Q ilex* to form forests in our future climate scenario is greatly reduced at Gorgo Basso. Even when subject to low disturbance, *Q ilex* never grows larger than a shrub and maintains similar abundance as *Q*

coccifera, contributing 8% of total biomass. However, the more drought-tolerant *O europaea* attains large size and contributes 51% of the biomass, and the shrubs *Pistacia lentiscus* and *Phillyrea latifolia* are more abundant than in our present climate scenario. These simulated communities are similar to those that formed under drier conditions in the past. Open woodlands (ie without a closed canopy) dominated by *O europaea* and *P lentiscus* preceded the formation of closed forests with *Q ilex* at Gorgo Basso (Figure 2; Tinner *et al.* 2009), and also grew near the North African coast (Calò *et al.* 2013; Lebreton *et al.* in press). Furthermore, woodlands containing overstory *O europaea* and understory *P lentiscus* form in northwest Africa today when cutting is prohibited and fire is limited, but shrublands form when disturbance is frequent (Deil *et al.* 2005). Including moderate disturbance in our future climate scenario also prevents *O europaea* from forming a canopy and increases the proportion of shrubs.

Quercus ilex forests provide a viable and desirable management goal for a warmer and drier future in meso-Mediterranean ecosystems, especially given that our simulated future climate scenario is too dry for *A alba* to persist at Lago di Massaciuccoli. Instead, with low disturbance, evergreen forests dominated by *Q ilex*, but includ-

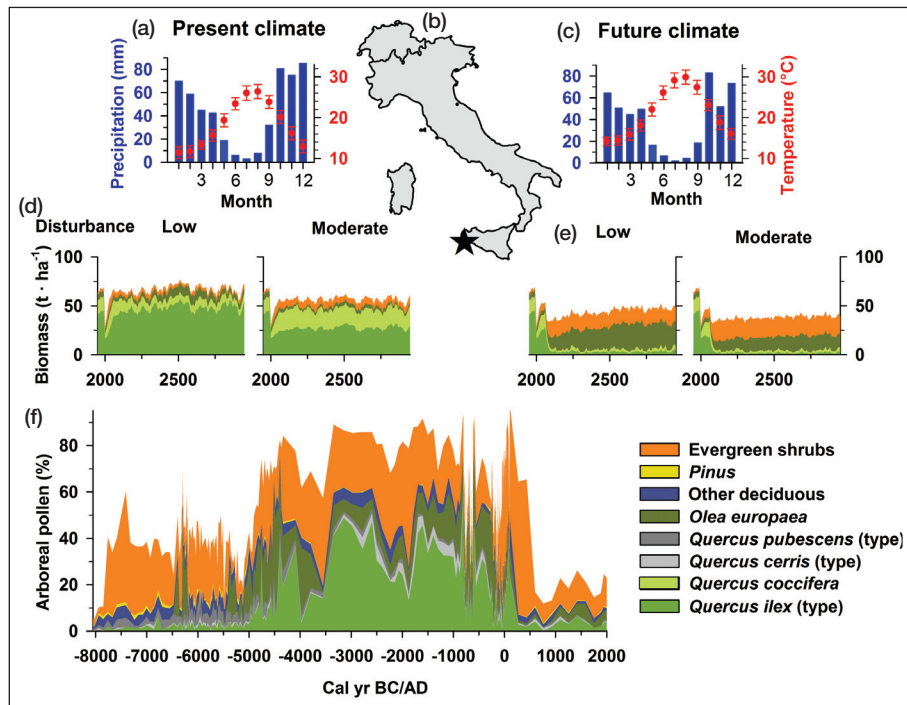


Figure 2. (a) Present-day (1950–2000 AD) mean monthly temperature (± 1 standard deviation) and average total monthly precipitation at Gorgo Basso. (b) Map of Italy and Switzerland, with Gorgo Basso denoted by a star. (c) Future (2071–2100 AD) mean monthly temperature and precipitation, projected by the SMHI regional climate model. (d and e) Vegetation simulated at Gorgo Basso with present climate (d) and with projected future climate (e). All models were initialized with the same present-day climate scenario and moderate disturbance before 2010. (f) Holocene pollen percentages of upland trees and shrubs (Tinner *et al.* 2009). Evergreen shrubs include *Pistacia lentiscus* and *Phillyrea latifolia*. *Quercus cerris*-type pollen includes *Quercus suber*, and *Quercus ilex*-type includes *Quercus coccifera*.

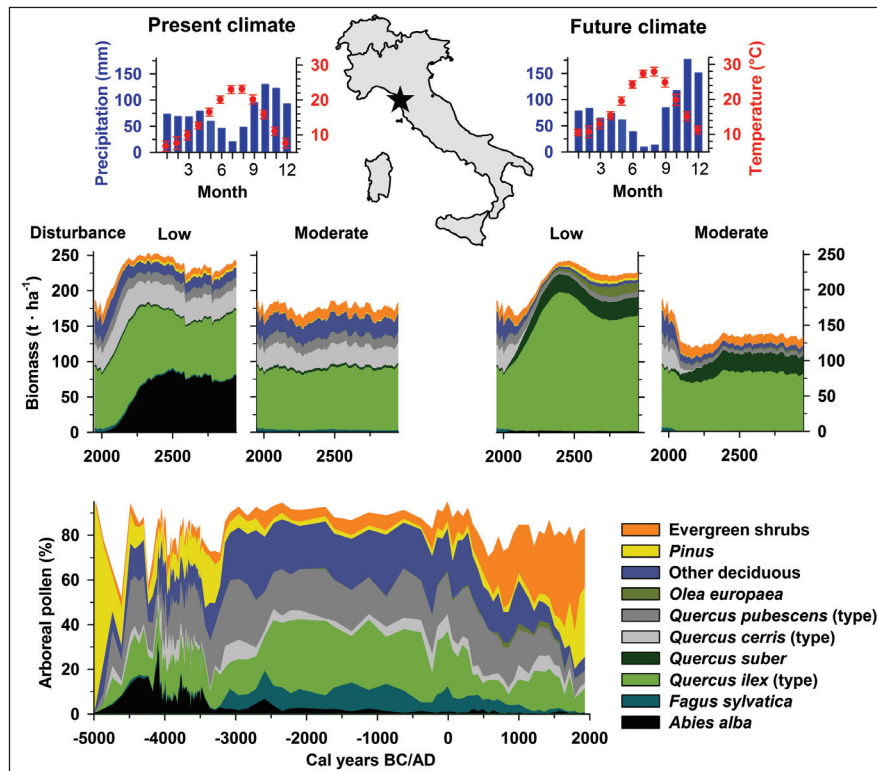


Figure 3. As for Figure 2, except for Lago di Massaciuccoli (Colombaroli *et al.* 2007). The future climate scenario was developed from the ETHZ-CLM regional climate model. Evergreen shrubs include *Phillyrea latifolia*, *Ilex aquifolium*, and *Rhamnus alaternus*. *Pinus* in the simulations is *Pinus halepensis*. Other deciduous species include *Fraxinus ornus*, *Ostrya carpinifolia*, and *Tilia cordata*. Pollen diagram modified from Henne *et al.* (2013).

ing *Quercus suber* and *O. europaea*, replace the mixed deciduous and evergreen communities, with only the drought-tolerant deciduous trees, *Q. pubescens* and *Fraxinus ornus*, contributing >1% of simulated biomass. Although this vegetation does not resemble past local communities, pollen data from Gorgo Basso and elsewhere in thermo-Mediterranean southern Europe (Tinner *et al.* 2009; Carrión *et al.* 2010) demonstrate that *Q. ilex* forests can develop where the climate is even drier than our future scenario for Lago di Massaciuccoli. Furthermore, *Q. ilex* forests burned less frequently than the open communities that replaced them during the Holocene (Tinner *et al.* 2009), and have lower flammability than the evergreen shrublands that are currently expanding in the region's abandoned agricultural lands (Azevedo *et al.* 2013). Therefore, managing to promote late-successional *Q. ilex* forests may help mitigate projected climate-driven increases in wildfire risk in southern Europe (Moriondo *et al.* 2006), and also maintain ecosystem services such as watershed integrity, sustainable timber production, and carbon sequestration. This important implication applies today in the thermo-Mediterranean belt (~30–40° N), and under projected climate change in the meso-Mediterranean belt (~40–44° N).

Including historical pollen data in our analyses reveals

the limitations imposed when only current vegetation is considered in climate-impact research. In the future scenario for Lago di Origlio with low disturbance, *A. alba* becomes the most abundant tree, contributing 67% of biomass and replacing moisture-demanding species (eg *F. sylvatica*; Figure 4). Yet without unambiguous paleobotanical evidence for abundant *A. alba* at sub-Mediterranean and meso-Mediterranean sites (Tinner *et al.* 2013; Di Pasquale *et al.* 2014), projected communities of *A. alba* growing with thermophilous (warmth-loving) trees, which lack a modern analog, would appear highly unrealistic. Furthermore, the paleoecological evidence of extinct *A. alba* populations in regions with mild winters raises questions about the validity of previous approaches that limited *A. alba* populations in process-based models by setting a very low (–2°C) maximum winter temperature for establishment (eg Hickler *et al.* 2012). Our simulations do not constrain *A. alba* with an unrealistic maximum winter temperature threshold, and are supported by observations that deciduous and evergreen oaks, not *A. alba*,

are replacing *F. sylvatica* at the dry edges of its range (Peñuelas *et al.* 2007), when moderate disturbance is included. In our future scenario with moderate disturbance, *F. sylvatica* and *T. cordata* remain important – but they are partially replaced by evergreen and deciduous oaks, with evergreen *Q. ilex* reaching 23% of biomass.

■ Conclusions

Vegetation simulated under low disturbance conditions and present climate captures the dominant species composition of forests that disappeared from the Italian Peninsula and Sicily during the past 5000 years. Forests of *Q. ilex* and *O. europaea* remain well-suited to the present climate of coastal Sicily, the warmest and driest region of Italy. Likewise, *A. alba* competes with thermophilous species in meso- and sub-Mediterranean ecosystems. These findings refute the hypothesis that the establishment of today's open Mediterranean vegetation (ie maquis and garrigue shrublands) was driven by a drying climate. Instead, our simulations support time-series analyses of pollen data that link forest decline and the loss of disturbance-sensitive species to agriculture, silviculture, and other human-mediated impacts (Tinner *et al.* 1999, 2009). Thus, these now-extinct communities provide a template for future management

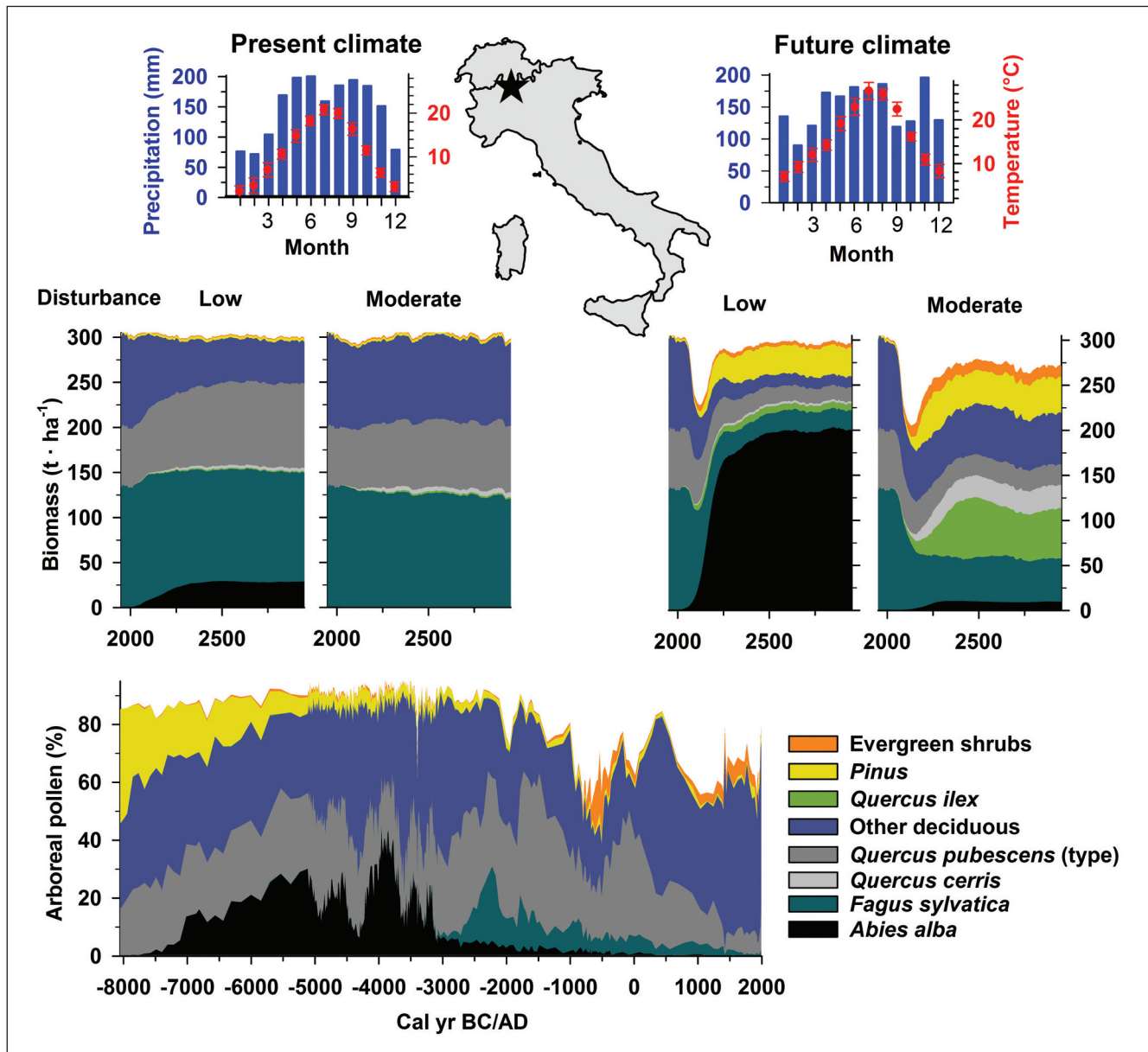


Figure 4. As for Figure 2, except for Lago di Origlio (Tinner et al. 1999). The future climate scenario was developed from the C4IRCA3 regional climate model. Evergreen shrubs are mostly *Ilex aquifolium*. *Pinus* in the simulations is *Pinus sylvestris*. Other deciduous species include *Tilia cordata*, *Ostrya carpinifolia*, and *Carpinus betulus*. *Quercus pubescens*-type pollen includes *Quercus petraea* and *Quercus robur*. We also grouped these species in the model output. However, most of the simulated biomass is *Q. petraea*.

of native forests in the Mediterranean region that is grounded in past evidence. Although future climate may remain suitable for extinct Mediterranean forest communities, their viability will depend on specific disturbance regimes. For instance, fire suppression in highly flammable, early-successional shrublands may be necessary to establish late-successional evergreen forests with lower flammability. Likewise, *A. alba* saplings require protection from ungulate browsing to re-establish in thermophilous forests. Such management strategies may help revive valuable native forests, especially where agricultural abandonment and cessation of forest grazing have allowed forest and shrubland expansion.

Future management strategies to promote native vegetation should be informed by more than data from extant plant communities. Paleoecological evidence can be used not only to test assumptions about the environmental factors that limit species distributions but also to improve and validate models that project vegetation re-establishment in a changing climate. We argue that restoring these native forests would likely provide valuable ecosystem services and increase ecosystem resilience to future climate change. Extreme mitigation approaches, such as replacing native vegetation with plantations of exotic timber species (eg *Eucalyptus*, *Pseudotsuga*), are unnecessary to maintain future productivity and offer a poor sub-

stitute for diverse native forests that are well-adapted to the Mediterranean climate. The advantages of restoring native forests in this region, including the delivery of ecosystem services such as carbon sequestration, should be the subject of future investigations.

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WebPanel 1. Edaphic, topographic, and disturbance inputs to LANDCLIM

LANDCLIM calculates monthly temperature and water availability for each model cell from soil water-holding capacity, topography, mean monthly temperature, and monthly precipitation (Schumacher *et al.* 2004). We estimated soil properties from local soil profiles and maps (data sources: Gorgo Basso [Crescimanno and Garofalo 2005]; Massaciucoli [Autorità di Bacino pilota del fiume Serchio 2006]; Origlio [MWI Schmidt, unpublished soil survey]). LANDCLIM uses a cumulative beta probability density function to relate a drought index to the probability a fire will ignite and spread. The shape of this curve is defined by two parameters, α and β (Henne *et al.* 2013). We used two disturbance scenarios at each site – a low-disturbance, pre-human impact scenario with small, infrequent fires ($\alpha = 2.5$, $\beta = 1.5$; minimum probability = 0.1; maximum probability = 0.8), and no browsing, and a moderate-disturbance scenario with small, frequent fires ($\alpha = 2.0$, $\beta = 1.5$; minimum probability = 0.17; maximum probability = 0.8, maximum fire size = 10% of landscape), and moderate browsing (browsing intensity = 0.5). These disturbance scenarios allow for the investigation of human impacts on extinct forests but may underestimate present disturbance, especially near Gorgo Basso, where fire is used to maintain open land for grazing.

WebPanel 3. Ranking future climate scenarios and comparison to pollen data

We explored the possibility of using the mean climate change projected by the nine regional climate models to drive LANDCLIM. However, when averaged, the seasonal precipitation distributions are inconsistent with every regional climate model, and simulated vegetation is distinct from the individual climate-change scenarios. We therefore considered the median impact on vegetation of the nine regional climate models to be a more useful indicator of potential vegetation outcomes. We identified the median impact scenario by calculating the squared chord distance (SCD) of each future climate scenario from the control (present climate) scenario. SCD reduces two sets of multi-dimensional species abundance data into a single measure of dissimilarity, and moderately increases the importance of rare taxa (Gavin *et al.* 2003). We ranked each scenario using its mean SCD from the control, and indicated the scenario with the median SCD score for each site.

We compared model output to pollen percentages of upland trees and shrubs. Because LANDCLIM does not simulate forest dynamics in wetlands, we removed all species typical of saturated soils (eg *Alnus glutinosa*) from the pollen sums. Upland herbaceous species were included in the pollen sum, but are not shown.

WebPanel 2. Climate scenarios

We initiated LANDCLIM from bare ground with a 2000-year model spin using present-day climatic conditions and the moderate-disturbance scenario. We generated the present climate scenarios for each site by fitting weather station data from the period 1951–2000 AD to a covariance matrix and drawing random monthly temperatures from a normal distribution, and precipitation abundances from a gamma distribution. We obtained weather station data from Mazara del Vallo, 8 km northwest of Gorgo Basso, and Pisa San Giusto Airport, 15 km south of Lago di Massaciucoli. Because complex topography surrounds Lago di Origlio, we used weather station data that were interpolated to a 1-ha grid by the DAYMET model (Thornton *et al.* 1997; Swiss Federal Institute for Forest, Snow, and Landscape Research, WSL). Observed temperature and precipitation data from 1951–2010 AD were used for the final 60 years of the initiation period. Vegetation simulated at 2010 AD was then used as a starting point for all future simulations.

We developed future climate scenarios for each site from the output of nine regional climate models. These models projected climate change in Europe for the period 1951–2100 AD under the IPCC A1B emissions scenario for the ENSEMBLES project (Van der Linden and Mitchell 2009). We compiled monthly climate data from each model for 1951–2100 AD from the 625-km² grid cell that contains each study site. We used 1951–2000 AD as a reference period for the mean and variability in monthly temperatures and precipitation. Deviations from the reference period were calculated for 30-year intervals centered on 2025, 2055, and 2085 AD. We generated climate scenarios by adding the deviations to monthly temperatures and precipitation abundances drawn from weather station data as described above for the present climate scenarios. For 2011–2100 AD, we used linear interpolation between the 30-year intervals to estimate the deviations, and maintained the 2085 deviations for 2101–3000 AD.

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