Drivers of Holocene Land Cover Change in Europe

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PAR

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Lausanne, 19 February, 2013 *Pamela M. Collins*

Abstract

The modern vegetation of Europe is a product of its history. Climate change, plant migration, and human activity have all been important drivers of Holocene (11,500 years ago to the present) vegetation dynamics, but it is difficult to disentangle the relative importance of the three processes. This thesis uses a vegetation model and land cover reconstructions based on pollen data to explore the drivers of European vegetation change. I conclude that human activity has likely been an important driver for many millennia, both through disturbing the vegetated landscape and possibly also through causing soil erosion in drought-sensitive areas, but that post-glacial migration is likely also an important factor. In the face of future climate change and intensifying human land use, it will be necessary to incorporate these results into landscape management and conservation planning.

Keywords. Biodiversity, biogeography, biomes, climate, erosion, Europe, Holocene, human impact, land cover, landscape openness, Mediterranean, phytogeography, plant functional types, pollen, ruined landscape hypothesis, soil, vegetation dynamics, vegetation history

Résumé

La végétation moderne de l'Europe est un produit de son histoire. Le changement climatique, la migration de la flore et l'activité humaine ont tous été d'importants agents des dynamiques de la végétation de l'Holocène (depuis 11 500 ans à nos jours), mais il est difficile de démêler l'importance relative de chacun de ces trois processus. Cette thèse utilise un modèle de végétation et des reconstitutions de la couverture terrestre basées sur des données polliniques afin d'explorer les moteurs du changement de végétation européen. Je conclure que l'activité humaine a probablement été un agent important durant des millénaires, à la fois à travers la perturbation du paysage végétalisé et peut-être aussi en causant de l'érosion des sols dans des zones sensibles aux sécheresses, mais que la migration post-glaciale est aussi probablement un facteur important. En regard du changement climatique à venir et de l'intensification de l'utilisation humaine des terres, il sera nécessaire d'incorporer ces résultats à la gestion de l'aménagement du territoire et de la conservation de la nature.

Mots clés. Biodiversité, biogéographie, biomes, climat, couverture du sol, dynamique de la végétation, érosion, Europe, Holocène, hypothèse de la ruine du paysage, histoire de la végétation, impact des activités humaines, Méditerranée, ouverture du paysage, phytogéographie, pollen, sol, types fonctionnels de plantes

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1 Introduction

1.1
Background

This thesis is about Holocene land cover change in Europe. Using vegetation modelling and pollen data, I explore some of the ways in which various aspects of European vegetation changed over the past 11,500 years, and I examine the potential roles of climate, migration, soil, and human activity in influencing these changes (Fig. 1.1).

The present-day vegetation cover of Europe has been shaped by glacial-interglacial cycles. Glacial periods caused the southward expansion of tundra and steppe vegetation (Prentice *et al.* 2000), with boreal, temperate, and subtropical taxa seeking refuge along the Mediterranean coast (Bennett *et al.* 1991; Hewitt 1999; Médail & Diadema 2009) or in small pockets of favourable climate scattered around the rest of Europe (Kullman 2008; Svenning *et al*. 2008), while interglacial periods reversed these trends (Prentice *et al*. 2000). Vegetation migration between glacial and interglacial periods has had consequences for genetic diversity (Petit *et al.* 2002; Magri *et al*. 2006) and even the survival (or extinction) of species (Petit *et al*. 2008). Comparative studies across continents suggest that such glacially-driven floristic impoverishment did not occur in places of similar latitude/climate that did not experience glaciation (Adams & Woodward 1989).

The present interglacial period, known as the Holocene, began roughly 11,500 years ago. Though Holocene climatic and vegetation conditions are relatively stable compared to glacial/interglacial transitions, change did still occur throughout the Holocene (COHMAP 1988; Wanner et al 2008); however, the orbital forcing parameters, ice sheets, sea levels, and atmospheric circulation had all settled into more or less the conditions we experience today by around 6,000 years ago (COHMAP 1988).

Neither was European vegeation stable throughout the Holocene. Rather, taxa moved independently around the continent throughout the Holocene, causing continuous change to community composition (Huntley & Birks 1983; Huntley 1990; Huntley 1990[a]). Pollen data has been used to study the spatial and temporal dynamics of individual tree taxa as they moved around Europe (Giesecke & Bennett 2004; Tinner & Lotter 2006; Giesecke *et al*. 2007; Magri 2008; Seppa *et al.* 2009). Much attention has also been devoted to reconstructing the vegetation of the mid-Holocene (6,000 years ago) for comparison against climate model output (Guiot *et al*. 1996; Prentice *et al*. 1996; Prentice *et al*. 2000; Gachet *et al*. 2003; Gritti *et al*. 2004), as that time period was selected as a focus of the Palaeoclimate Modelling Intercomparison Project (Braconnot *et al.* 2007).

Thus, it is clear that climate is recognized to be an important driver shaping the Holocene vegetation of Europe, and it is already well understood that vegetation has changed continuously throughout the present interglacial.

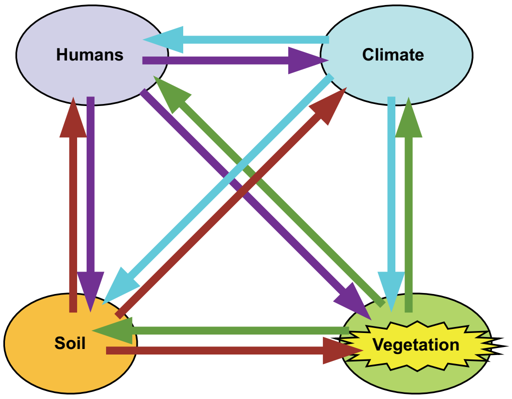


Figure 1.1. Vegetation, climate, soils, and humans all interact with one another.

1.2
Open questions

It is less clear, however, to what extent human activity influenced vegetation change over the Holocene, or to what extent vegetation change was in equilibrium with, or lagging, changing climate. These ideas can be captured by the question "What is natural?" The concept of "potential natural vegetation" is often invoked in the contexts of vegetation ecology and conservation planning; if human activity or plant migration were important drivers of European vegetation development for a significant part of the Holocene, what would be the consequences for the potential natural vegetation concept? Through modelling and reconstructing various aspects of the Holocene vegetation of Europe, this thesis seeks to explore the relative importance of climate, soil, migration, and human activity in shaping the European vegetation.

1.3
Materials and methods

1.3.1
Global-to-continental scale vegetation modelling

Early examples of "modelling" vegetation cover at the continental or global scale include the classic work of Köppen (1936) and Holdridge (1967), who formally describe relationships between vegetation cover and climate parameters such as temperature, precipitation, and evapotranspiration. More recent and sophisticated approaches involve computational modelling, incorporating parameters and processes such as nutrient cycling, soil hydrology, or competition within and between species and cohorts. Models such as BIOME1 (Prentice *et al*. 1992) and BIOME4 (Kaplan 2001) predict equilibrium vegetation using static input data, while more complex dynamic global vegetation models (DGVMs) such as LPJ (Sitch *et al*. 2003) and ORCHIDEE (Krinner *et al*. 2005) incorporate processes such as population dynamics, litter turnover, and disturbance by fire. Choice of model design and complexity is determined by the research question and spatial/temporal scales of interest; one might select a different tool to explore biogeochemical cycling (uptake/sequestration of C or N, for example), vegetation biogeography, or calculation of parameters directly relevant to climate modelling (e.g. surface roughness or albedo).

To perform a preliminary assessment of the importance of soil quality to vegetation cover, I used the comparatively simple BIOME1 equilibrium vegetation model in conjunction with the soil module from the ARVE-DGVM (under development). In addition to being computationally efficient, BIOME1 is simple to modify at the code level, making it particularly appropriate for performing exploratory analyses.

1.3.2
Pollen data

While vegetation models estimate what kind of vegetation *ought* to occur in a given area, working with pollen data makes it possible to approximate the *actual* vegetation cover. Lakes and bogs act as pollen "traps", capturing and storing airborne pollen from the surrounding vegetation. Coring of the peat or lake sediments, and subsequent classification and counting of the pollen present at different depths, yield a record of regional vegetation history (Fig. 1.2). Radiocarbon and/or stratigraphic dating of core material are used to determine the relationship between core depth and pollen age, where deeper usually corresponds to older.

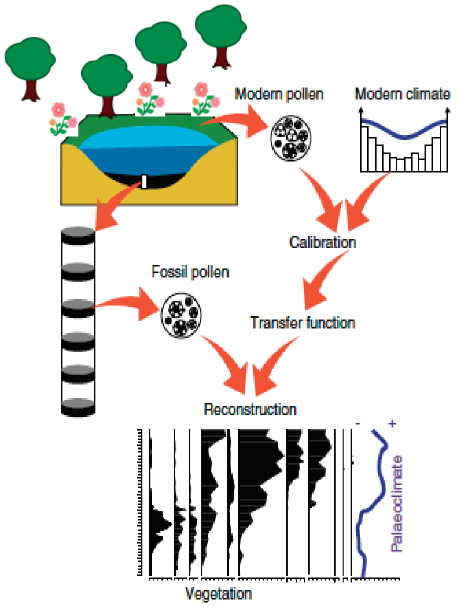
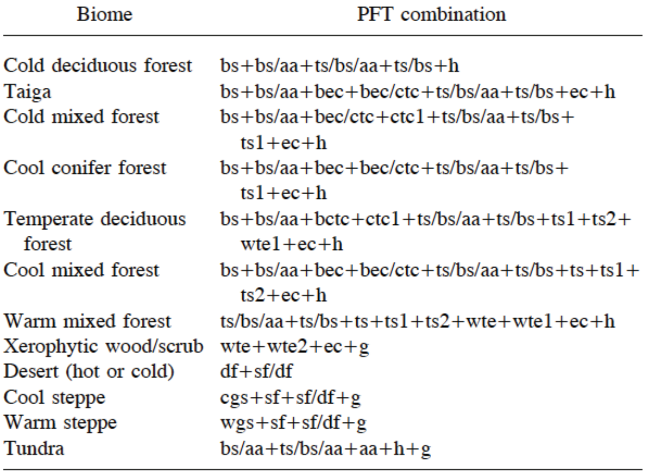


Figure 1.2. Lakes trap pollen from surrounding vegetation. Pollen is recovered from sediment cores (deeper = older) and used to reconstruct vegetation (or climate). Adapted from Brewer *et al*. 2007.

Pollen data offer an approximation rather than an exact reconstruction of vegetation due to certain limitations. For example, pollen productivity and atmospheric transport vary both within and between species (depending on location, season, weather, etc.) (e.g. Broström *et al*. 2008; Gaillard *et al*. 2010). Also, the number of pollen grains counted per sample, as well as the taxonomic resolution to which the grains are identified (species, genus, or family) vary depending on the skills and research goals of the pollen analyst.

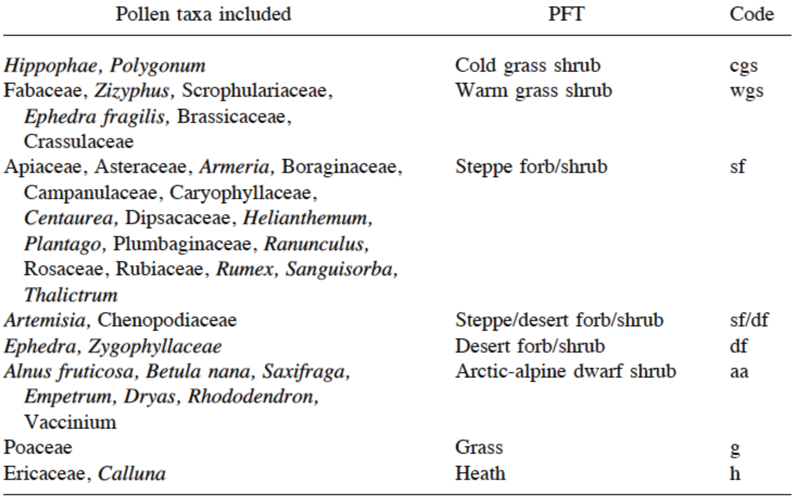
Nevertheless, analysis of pollen data remains the most commonly used approach to reconstructing past vegetation (sometimes in conjunction with macrofossil [e.g. Jolly *et al*. 1998] or phytolith [e.g. Delhon *et al*. 2003] data), due to the abundance of data available and the excellent spatial and temporal coverage of the European Pollen Database (EPD; Fyfe *et al*. 2009). Choosing to use only data with reliable age-depth models, as well as working with the pollen data at meta-taxonomic resolutions (plant functional types or biomes, rather than taxa) both offer ways to mitigate some of the limitations associated with working with pollen data. Additionally, working with PFTs and biomes makes it possible to use pollen-based vegetation reconstructions to evaluate the performance of vegetation models (Prentice & Webb 1998) while still addressing questions of ecological significance (Díaz & Cabido 2001).

Definitions of plant functional types (PFTs) and biomes vary by study system and research question (Prentice *et al*. 1996; Smith *et al*. 1997; Peyron *et al*. 1998; Tarasov *et al*. 1998; Williams *et al*. 1998). In this study I use the method described by Peyron *et al*. (1998) because it is designed for Europe and incorporates herbaceous as well as arboreal vegetation. Taxa are categorized into PFTs, and PFTs into biomes, as outlined in Tables 1.1, 1.2, and 1.3.



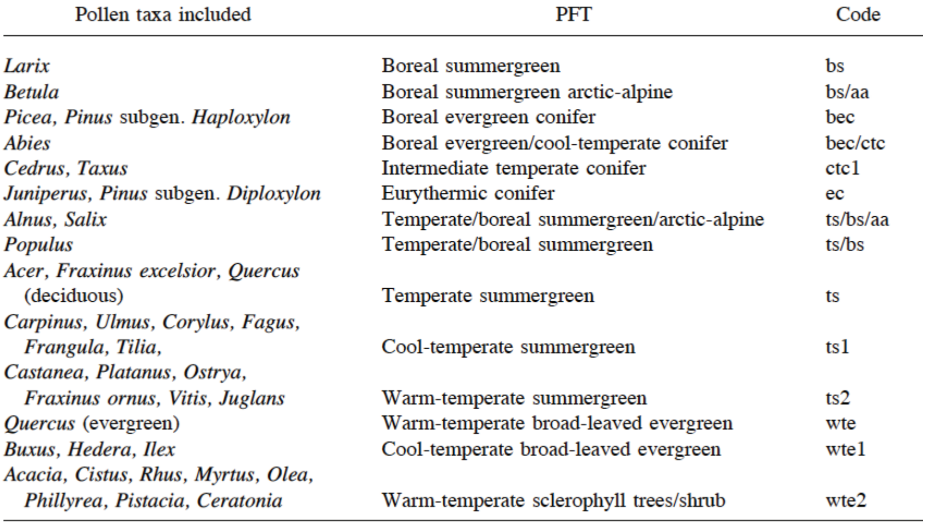
Biome	PFT combination
Cold deciduous forest	bs+bs/aa+ts/bs/aa+ts/bs+h
Taiga	bs+bs/aa+bec+bec/ctc+ts/bs/aa+ts/bs+ec+h
Cold mixed forest	bs+bs/aa+bec/ctc+ctc1+ts/bs/aa+ts/bs+ts1+ec+h
Cool conifer forest	bs+bs/aa+bec+bec/ctc+ts/bs/aa+ts/bs+ts1+ec+h
Temperate deciduous forest	bs+bs/aa+bctc+ctc1+ts/bs/aa+ts/bs+ts1+ts2+wte1+ec+h
Cool mixed forest	bs+bs/aa+bec+bec/ctc+ts/bs/aa+ts/bs+ts+ts1+ts2+ec+h
Warm mixed forest	ts/bs/aa+ts/bs+ts+ts1+ts2+wte+wte1+ec+h
Xerophytic wood/scrub	wte+wte2+ec+g
Desert (hot or cold)	df+sf/df
Cool steppe	cgs+sf+sf/df+g
Warm steppe	wgs+sf+sf/df+g
Tundra	bs/aa+ts/bs/aa+aa+h+g

Table 1.1. Classification of plant functional types into biomes. Adapted from Peyron *et al.* 1998.



Pollen taxa included	PFT	Code
Hippophae, *Polygonum*	Cold grass shrub	cgs
Fabaceae, *Zizyphus*, Scrophulariaceae, *Ephedra fragilis*, Brassicaceae, Crassulaceae	Warm grass shrub	wgs
Apiaceae, Asteraceae, *Armeria*, Boraginaceae, Campanulaceae, Caryophyllaceae, *Centaurea*, Dipsacaceae, *Helianthemum*, *Plantago*, Plumbaginaceae, *Ranunculus*, Rosaceae, Rubiaceae, *Rumex*, *Sanguisorba*, *Thalictrum*	Steppe forb/shrub	sf
Artemisia, Chenopodiaceae	Steppe/desert forb/shrub	sf/df
Ephedra, *Zygophyllaceae*	Desert forb/shrub	df
Alnus fruticosa, *Betula nana*, *Saxifraga*, *Empetrum*, *Dryas*, *Rhododendron*, Vaccinium	Arctic-alpine dwarf shrub	aa
Poaceae	Grass	g
Ericaceae, *Calluna*	Heath	h

Table 1.2. Classification of non-arboreal pollen taxa into plant functional types. Adapted from Peyron *et al.* 1998.



Pollen taxa included	PFT	Code
Larix	Boreal summergreen	bs
Betula	Boreal summergreen arctic-alpine	bs/aa
Picea, *Pinus* subgen. *Haploxylon*	Boreal evergreen conifer	bec
Abies	Boreal evergreen/cool-temperate conifer	bec/ctc
Cedrus, *Taxus*	Intermediate temperate conifer	ctc1
Juniperus, *Pinus* subgen. *Diploxylon*	Eurythermic conifer	ec
Alnus, *Salix*	Temperate/boreal summergreen/arctic-alpine	ts/bs/aa
Populus	Temperate/boreal summergreen	ts/bs
Acer, *Fraxinus excelsior*, *Quercus* (deciduous)	Temperate summergreen	ts
Carpinus, *Ulmus*, *Corylus*, *Fagus*, *Frangula*, *Tilia*,	Cool-temperate summergreen	ts1
Castanea, *Platanus*, *Ostrya*, *Fraxinus ornus*, *Vitis*, *Juglans*	Warm-temperate summergreen	ts2
Quercus (evergreen)	Warm-temperate broad-leaved evergreen	wte
Buxus, *Hedera*, *Ilex*	Cool-temperate broad-leaved evergreen	wte1
Acacia, *Cistus*, *Rhus*, *Myrtus*, *Olea*, *Phillyrea*, *Pistacia*, *Ceratonia*	Warm-temperate sclerophyll trees/shrub	wte2

Table 1.3. Classification of arboreal pollen taxa into plant functional types. Adapted from Peyron *et al.* 1998.

1.4
Overview of projects presented in this thesis

In this thesis, I used the BIOME1 equilibrium vegetation model and data from the EPD (supplemented by additional published pollen data not included in the EPD) to explore the drivers and dynamics of European land cover over the Holocene. The first two studies focus on the Mediterranean region of southern Europe, examining the importance of soil quality to vegetation type and assessing shifts in the northern extent of the mesic/xeric boundary at the mid-Holocene as compared to the present. The second two studies reconstruct multiple aspects of European vegetation history from pollen data to examine the relative importance of climate and human activity in shaping the Holocene vegetation of Europe, to address various questions in palaeoecology, and to offer insight into how vegetation might respond to future changes in climate and human land use.

1.4.1
Vegetation modelling, soil hydrology, and episodic precipitation

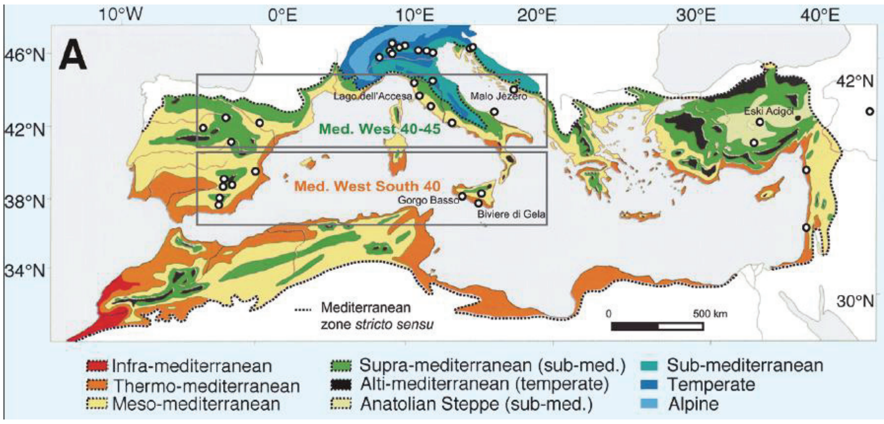


Figure 1.3. Distribution of modern Mediterranean life zones, adapted from Vannière *et al*. 2010.

Chapter 2 uses the BIOME1 equilibrium vegetation model in conjunction with a set of pedotransfer functions (converting soil physical properties into plant-available water holding capacity) to assess the importance of soil depth and texture to the Mediterranean landscape's ability to support drought-tolerant vs. drought-intolerant vegetation types. Contrary to my expectations, the results of the study suggested that soil properties had little impact on modeled vegetation at the biome scale, except for places where environmental conditions existed on the threshold between two biomes. This work was published as Collins *et al*. (2010).

Considering the drought-limited nature of the Mediterranean climate and the potential importance of good soils as moisture reservoirs, I considered the results presented in Chapter 2 surprising. A closer examination of the hydrology component of the BIOME1 vegetation model revealed a potential explanation: precipitation input data were represented as monthly mean values equally distributed over all days of the month.

However, summer precipitation in the Mediterranean region takes the form of brief, intense thunderstorms separated by days or weeks of very hot days with lots of sunshine and no precipitation. This discrepancy between the model's representation of hydrology and the actual behavior of the Mediterranean climate has important implications for the plant-available water in the model, especially under conditions of low soil water-holding capacity.

If the total monthly precipitation falls in small amounts every day, then it is likely that most of this moisture enters the soil and becomes available for plant uptake, even under conditions of very low soil water-holding capacity. However, if the total monthly precipitation is concentrated into one or two intense rainfall events per month, one of two things could happen. If the soil has a large water-holding capacity (e.g. it is deep and has a loamy texture), then perhaps most of this water is still captured in the soil and becomes available to the plant. If, however, the soil has a small water-holding capacity (e.g. it is shallow and stony, as is frequently the case for modern Mediterranean soils), then much of the moisture is lost to the system through runoff, and only a small fraction of the total monthly precipitation actually becomes available to the plant through storage in the soil.

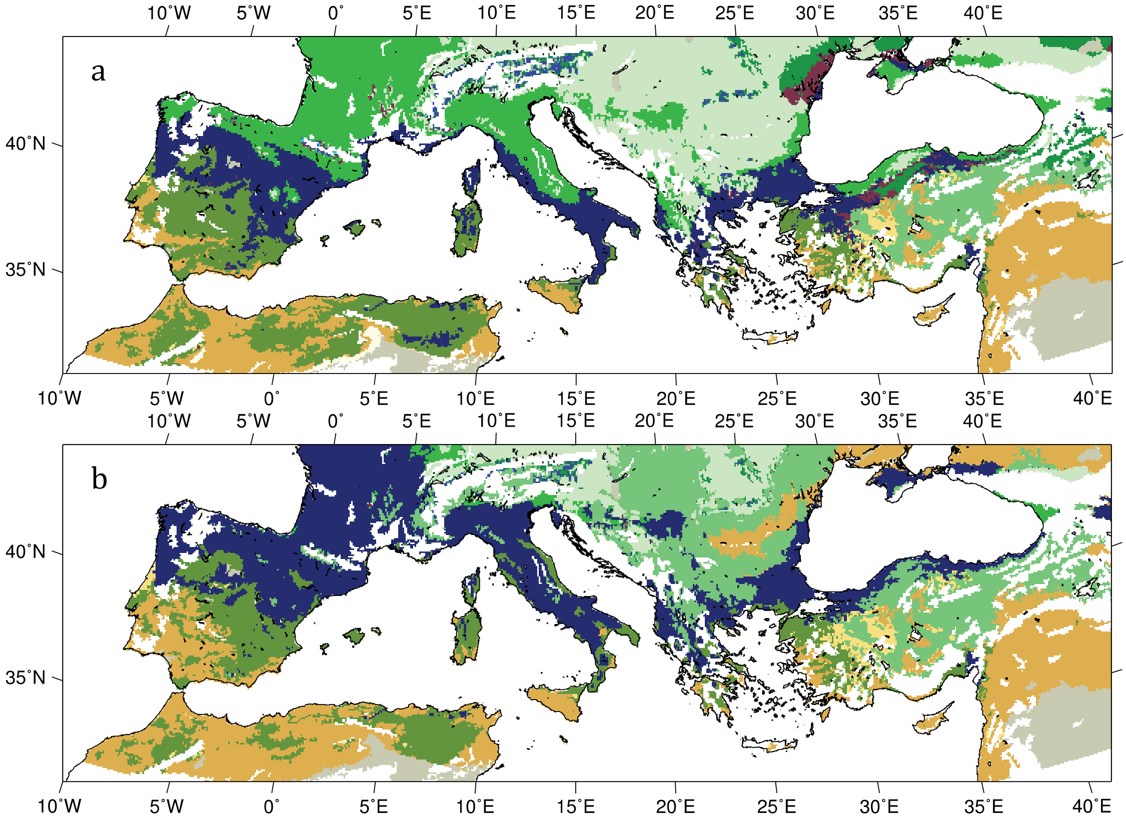


Figure 1.4. When real soil data are used, the BIOME1 equilibrium vegetation model predicts different biome distributions in southern Europe depending on whether precipitation is evenly distributed (a) over all days of the summer months June, July, August or grouped into three days per month (b).

To test the hypothesis that distribution of monthly precipitation data equally across all days of the month could have caused the insensitivity of the vegetation to soil degradation observed in Chapter 2 of this thesis, I designed and incorporated an additional module into the BIOME1 equilibrium vegetation model. In this module, the monthly precipitation of the summer months (June, July, August) was equally distributed across three days of each month, equally spaced in time, and the remaining days of each month were assigned no precipitation. This regime approximates the rhythm of intense but rare summer thunderstorms separated by periods of drought. The remaining months of the year retained the original model formulation of distributing the monthly precipitation evenly across all days of the month, to emulate the cooler, wetter patterns of Mediterranean winters. Then, I ran BIOME1 with the original hydrological scheme and with my episodic precipitation module, using actual soil data to determine available water capacity (Fig. 1.4). Next, I artificially prescribed three soil scenarios for the whole of the Mediterranean study area: low, medium, and high soil water-holding capacity, and mapped the resulting biome distributions with the episodic precipitation module activated (Fig. 1.5).

My results showed that, under normal soil conditions, distribution of precipitation evenly over all days of the summer months produced different biome distributions than did grouping each month's precipitation into three isolated rainfall events (Fig. 1.4). Next, the results demonstrate that this effect is increasingly severe as soil water-holding capacity decreases (Fig. 1.5).

These results suggest that the traditional approach of distributing monthly mean climatology evenly across all days of the month in vegetation modeling might be inappropriate, at least in the case of precipitation data in drought-limited areas with poor soils. As such areas often support significant human populations and are considered to be especially sensitive to land degradation and climate change (e.g. Mediterranean region, Sahel), improvements in the model representation of present and future vegetation dynamics will be necessary to informing adaptation and mitigation strategies.

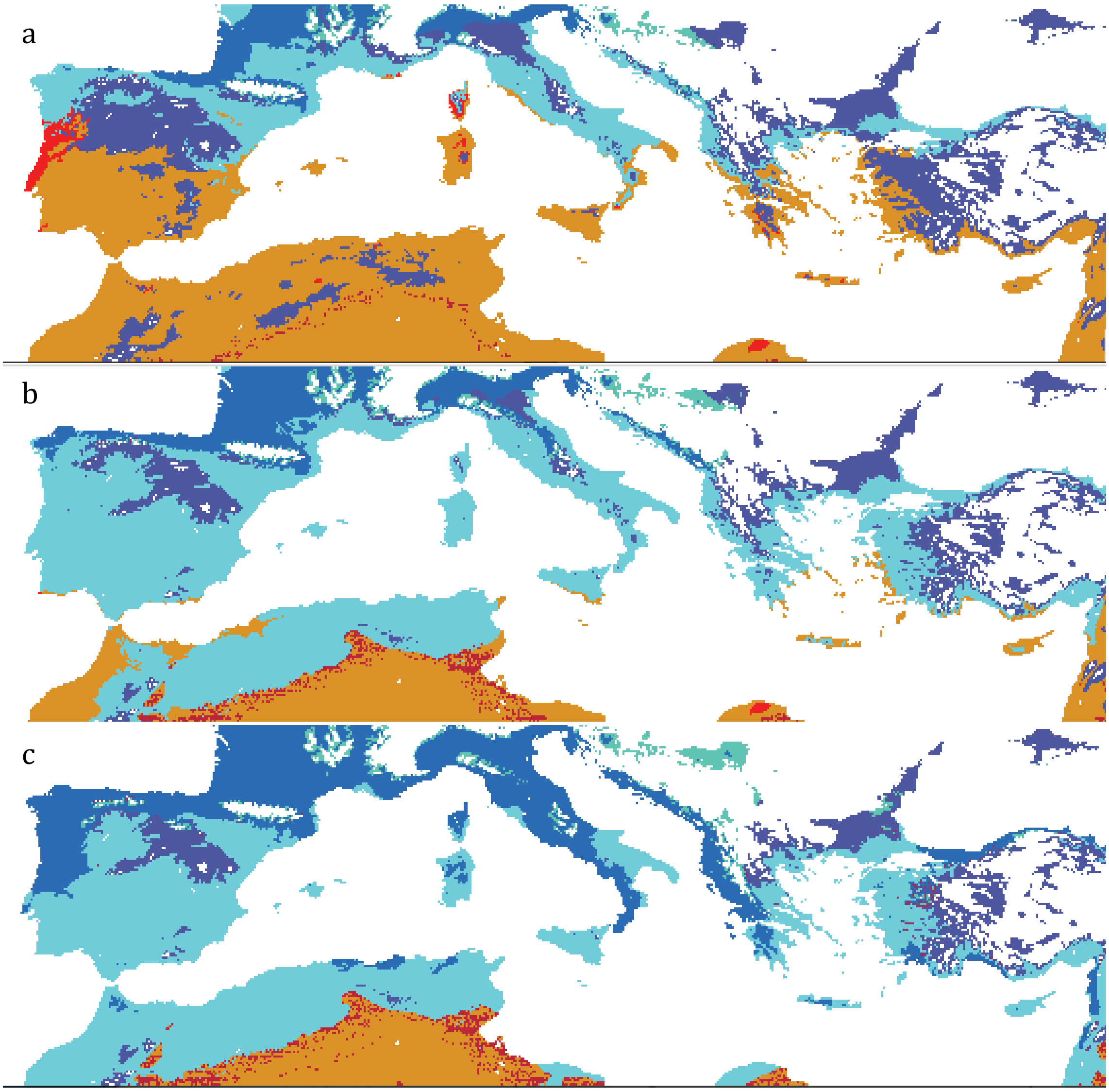


Figure 1.5. When mean monthly precipitation is grouped into three rainfall events per month in June, July, and August and soil available water capacity (awc) is artificially prescribed, the BIOME1 equilibrium vegetation model predicts different biome distributions in southern Europe depending on the value of awc. (a) 5 mm water/m soil; (b) 50 mm/m; (c) 650 mm/m. Tan = warm grass steppe; bright red = cool grass steppe; dark red = xerophytic wood/scrub; purple = cool conifer forest; turquoise = temperate evergreen/warm mixed forest; blue = temperate deciduous

1.4.2
Vegetation reconstructions from pollen data

1.4.2.1
Taxa, biomes, landscape openness, and the age of the modern vegetation cover

Chapter 3 presents the results of a pilot study in which I compared the landscape of the Mediterranean region at the mid-Holocene (6,000 cal yr BP) to that of the present day. I did this by using pollen data to reconstruct biomes at individual pollen sites, along with the interpolated distribution and abundance of woody vegetation cover and 11 key Mediterranean taxa. I found that temperate deciduous forest did extend farther south into the Mediterranean region at the mid-Holocene than it does in modern times, yet drought-tolerant vegetation remained widespread. The results of this work have been published as Collins *et al.* (2012).

Next, I extended my temporal and spatial ranges of study to incorporate the whole of Europe for the entire Holocene (11,500 cal yr BP to present). This time, I assessed the age of the modern European landscape, along with changes in biome cover and landscape openness throughout the Holocene. All my calculations were based on interpolated plant functional type (PFT) scores derived from point pollen data. These results are presented here in Chapter 4, and a journal manuscript is nearly ready for first submission (Collins *et al.* in prep[a]).

In addition to these two studies, I also pursued two smaller projects focused on human interaction with specific taxa.

1.4.2.2
Cereals and the spread of Neolithic civilizations in Europe

Though Chapters 3 and 4 of this thesis used pollen data to reconstruct various aspects of the “natural” Holocene vegetation of Europe, much can also be learned from studying the distribution and abundance of weedy or agricultural plants, or “anthropogenic indicators”, as they present a possible way of tracing human activity across Europe over the Holocene using the pollen record. In this project, I wanted to assess the value of using cereals (a primary Neolithic crop, and distinguishable on the palynological level from native grasses) as an anthropogenic indicator.

To do so, I compared the spread of Neolithic civilizations through Europe as documented in the archaeological record (Turney & Brown 2007) against the spread of cereals as documented in the pollen record (Fig. 1.6). I found that the spread of Neolithic civilizations through Europe pre-dated the significant presence of cereals in the pollen record by many millennia. This suggests that the absence of cereals in the pollen record does not automatically imply the absence of Neolithic settlements nearby. Indeed, recent work by Ravazzi *et al.* (2013) in the Po Valley of Italy illustrates this point. It presents a sediment core collected immediately adjacent to an Etruscan settlement that nevertheless contained little to no cereal pollen until much later in the sequence.

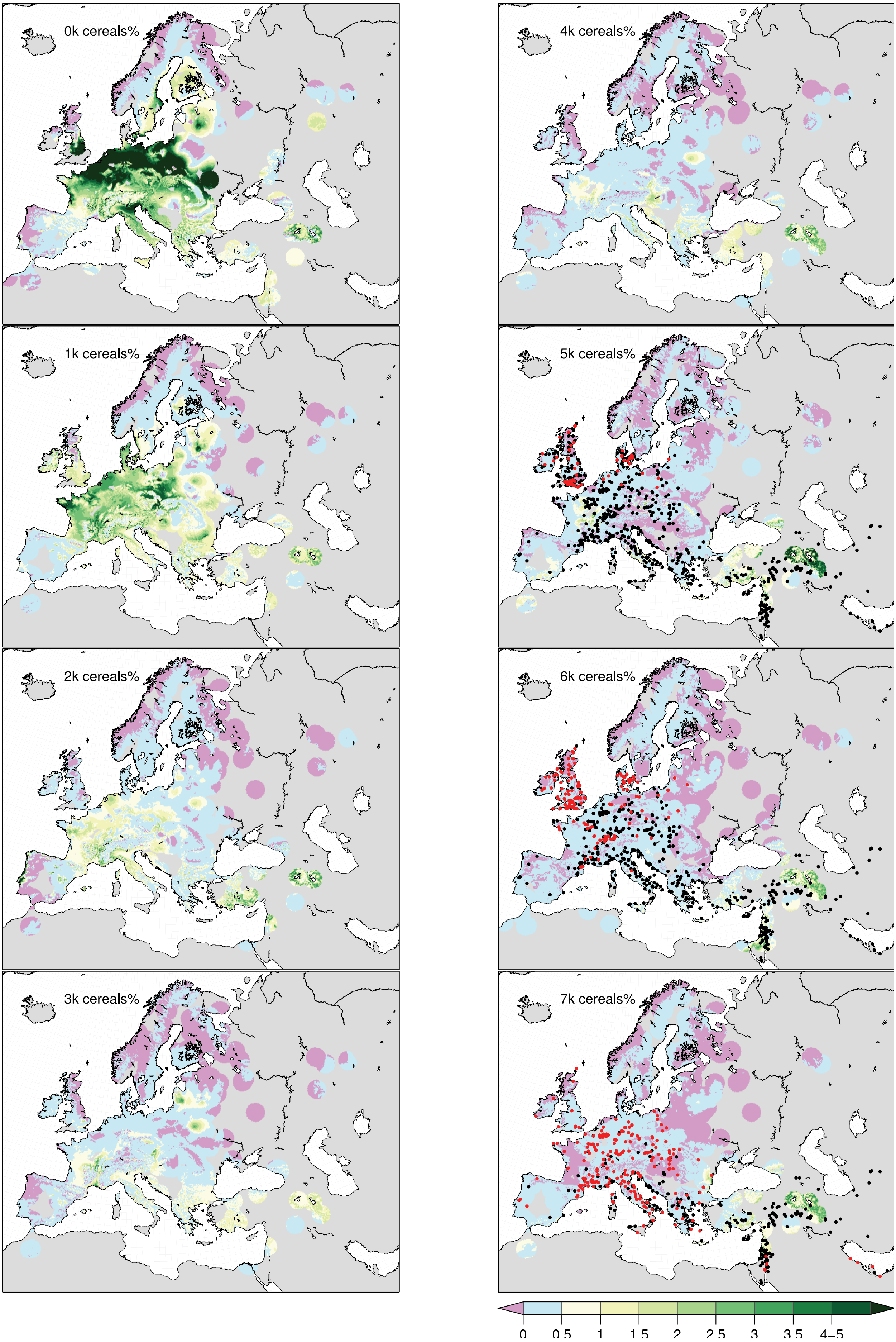

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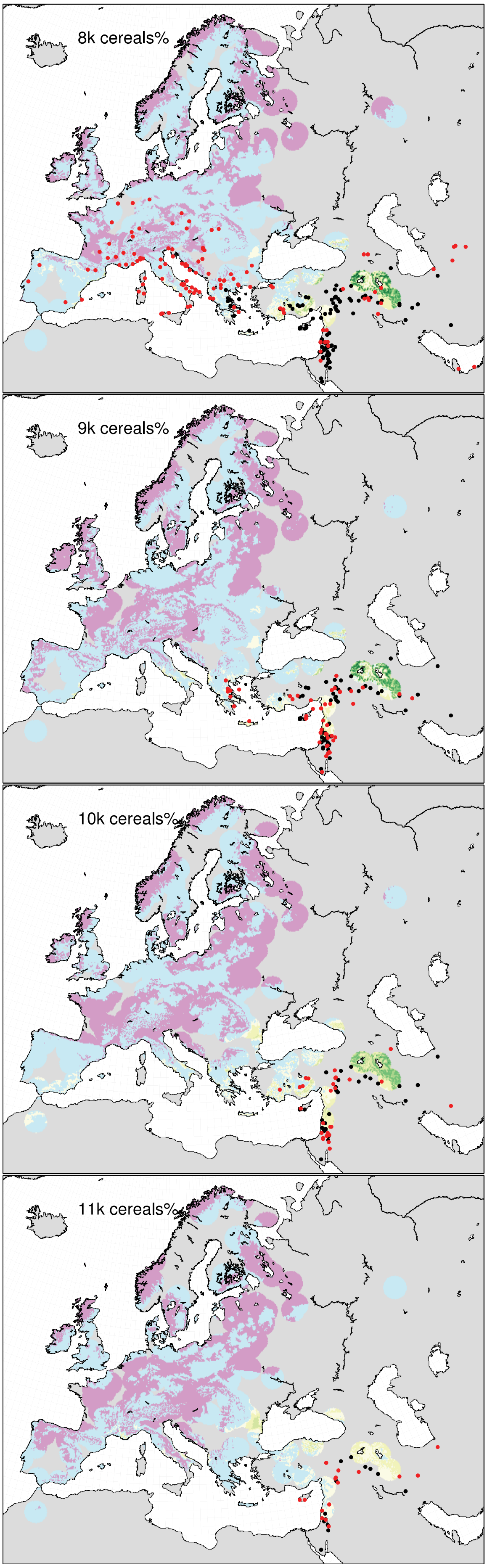
Figure 1.6.



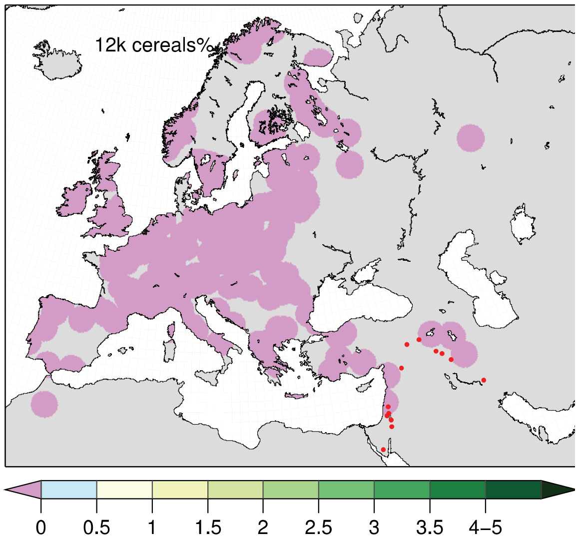


Figure 1.6 continued. Percent abundance of cereals in the pollen record at thousand-year intervals throughout the Holocene. Pollen sum calculated as percentage of total terrestrial pollen. Red dots = first evidence of Neolithic settlement occurred at that time slice. Black dots = Neolithic settlements already present at previous time slices (Turney & Brown 2007). Neolithic settlements dataset ends at 5,000 years before present, when Neolithic transition in Europe was

1.4.2.3
The rise and fall of *Abies alba* in central Europe north of the Alps

During the acid-rain-induced forest dieback of the 1970s in Europe, *Abies alba* was observed to suffer disproportionately more than other tree species. This observation prompted Dr. Ulf Büntgen of the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) to examine Holocene trends in the distribution and abundance of *Abies alba* through tree-ring and pollen-based reconstructions, to better understand when and why *Abies alba* prospered or suffered in the past.

I contributed to his study by using pollen data to reconstruct the distribution and abundance of *Abies alba* in central Europe north of the Alps throughout the Holocene, in order to explore whether the modern dieback of *Abies* was anomalous or had palaeoecological precedents. I observed that *Abies alba* reached maximum relative abundance between about 1000 BC and AD 1000, after which its abundance decreased consistently throughout its range until modern times. This suggests that, although the recent dieback was severe, it did fit with the longer-term trend of late-Holocene *Abies* decline. The combined results of the pollen and tree ring reconstructions indicate that *Abies alba* is especially sensitive to a wide range of human activities (from felling to grazing to pollution) and suggest that the observed Holocene decline is largely anthropogenic in nature.

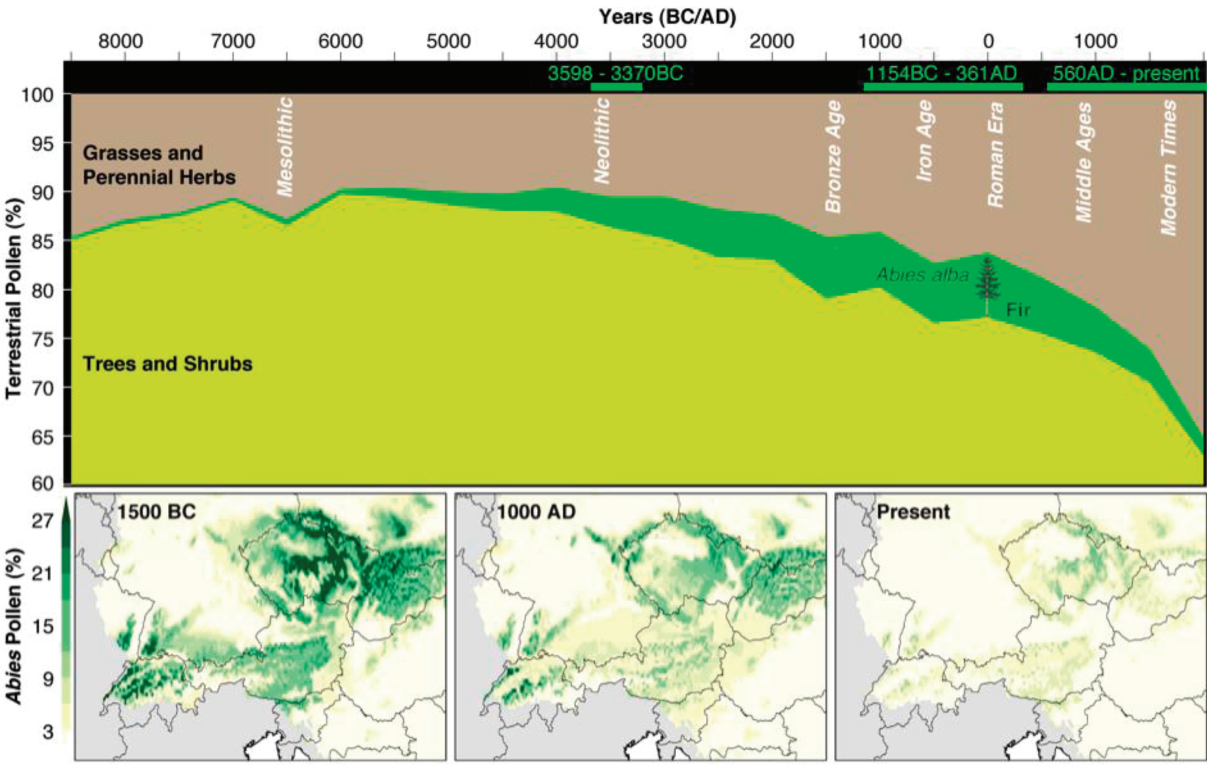


Figure 1.7. *Abies alba* reached maximum relative abundance in the Holocene pollen rain of central Europe north of the Alps between 1,000 BC and AD 1,000, after which it declined through to modern times (top). Interpolation of pollen data showing spatial distribution of decline. Image created by J.O. Kaplan and P.M. Collins for Büntgen *et al.* (in prep).

1.4.3
PFT diversity

The interpolated PFT scores generated for the study presented in Chapter 4 enabled me to investigate the dynamics of European PFT diversity over the course of the Holocene. Chapter 5 discusses the increase in PFT diversity, as well as the strengthening of the latitudinal diversity gradient, over the course of the Holocene, in the context of climate dynamics, post-glacial migrational lag, and anthropogenic landscape fragmentation. A journal manuscript for this work is also nearing submission (Collins *et al.* in prep[b]).

1.5
Synthesis of main results

The results presented here suggest that climate and human activity interacted to shape the vegetation of Europe throughout the Holocene.

The Mediterranean region hosted xeric vegetation throughout the Holocene, but this does not preclude the possibility that human activity may have impacted that vegetation. Temperate deciduous vegetation was more widespread at the mid-Holocene than it is in modern times. The fact that arboreal tree taxa overall are less abundant in modern times, with the exception of *Olea*, which shows greater distribution and abundance in modern times than at the mid-Holocene, suggests perhaps a human signature in the form of land clearance and arboriculture of economically valuable trees. Soil erosion following overgrazing and vegetation removal could have changed the land's ability to support less drought-tolerant vegetation, as demonstrated by the BIOME1 modelling study.

In Europe as a whole, climate and migration-rate limitation seem to have been the main forces shaping European vegetation during the first half of the Holocene. However, human activity was probably already a significant driver by 6,000 years ago, likely through land clearance and by intentionally (and unintentionally) aiding the dispersal and establishment of some taxa over others.

1.6
Broader relevance

This research provides insight into both how the European vegetated landscape looked over the Holocene, as well as what forces shaped it to bring it to its modern conditions.

Better understanding of the drivers and processes shaping vegetation can be useful for improving process representation in vegetation models used to anticipate how vegetation might respond to future changes in climate and human land use.

Understanding past patterns in European vegetation could be valuable to the conservation management community, because the decision for how to manage landscapes often requires information on what the "natural" vegetation of the area would be. If human influence has been an important driver of European vegetation patterns since the mid-Holocene, this can have important implications for deciding what "natural" really means, which is relevant for setting conservation priorities. Working at the continental scale is further useful to the conservation community because it provides perspectives at the same scale as continental-scale conservation efforts such as the Natura 2000 network (Osterman 1998).

The results presented here can be used as benchmarking material for evaluating the performance of earth system models, or as input data to better parameterize past land surface conditions. This is important for improving model representation of the role of the land surface in the climate system, which has been identified as a priority for future work in the latest IPCC report (IPCC 2007).

1.7
Outlook and recommendations

The results presented here suggest that it would be worthwhile to further explore the importance of human land use and soil degradation in Holocene vegetation dynamics by incorporating both processes into dynamic vegetation models at the continental spatial and Holocene temporal scales.

In addition, this thesis has not fully explored the potential of pollen-based vegetation reconstructions. The following ongoing projects demonstrate additional applications for pollen database research.

1.7.1
The European Modern Pollen Database, biomization, and climate reconstructions

The relationship between actual vegetation cover and that reconstructed from pollen data depends on a variety of factors, such as depositional environment or pollen productivity and transport. Therefore, comparison of Holocene vegetation reconstructed from pollen data against modern vegetation cover as determined from satellite data or botanical surveys can be problematic. However, such comparisons could be more informative if the modern vegetation cover were also reconstructed from pollen data, as then the pollen data/land cover relationship would be more consistent between the Holocene and modern reconstructions. The same holds true for climate reconstructions based on pollen data.

Though comprehensive in time and space, the European Pollen Database contains only fossil pollen data. To improve the quality of past-present vegetation comparisons and to facilitate the reconstruction of climate anomalies, Dr. Basil Davis initiated a project to assemble a database of Eurasian modern pollen data (surface samples and core-tops), building on the work already done by Doris Barboni (*personal communication*). My role in this effort involved contacting palynologists, soliciting their data, harmonizing the incoming data, designing and managing a database structure with Marco Zanon, and jointly hosting a workshop with Dr. Davis and Mr. Zanon to assemble and construct the database. Figure 1.8 shows the spatial distribution of the data in the database.

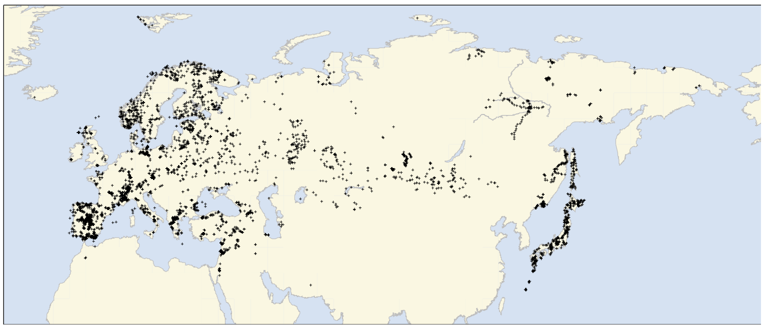


Figure 1.8. Spatial distribution of all data sites incorporated into the European Modern Pollen Database, as well as Asian sites also incorporated during the workshop. Image credit: Achille Mauri. ARVE lab.

Using the same methodology as presented in Chapters 3 and 4 of this thesis, I then biomized the resulting modern pollen dataset (Figure 1.9) and supplied the output to Achille Mauri (along with the fossil biomizations presented in Chapter 4 of this thesis), who has used them to generate the climate reconstructions central to his thesis research with the ARVE lab. The database assembly project highlights the value of standardizing methods in collection, analysis, and representation of pollen data, as differences in pollen taxonomic resolution and methods of determining and reporting pollen abundance and concentration can have significant consequences for the structure and utility of the resulting database.

The modern pollen workshop and resulting database are presented in Davis *et al.* (accepted), and the fossil and modern biomization results have been used for climate reconstructions in Mauri *et al*. (in prep) and Mauri *et al*. (submitted).

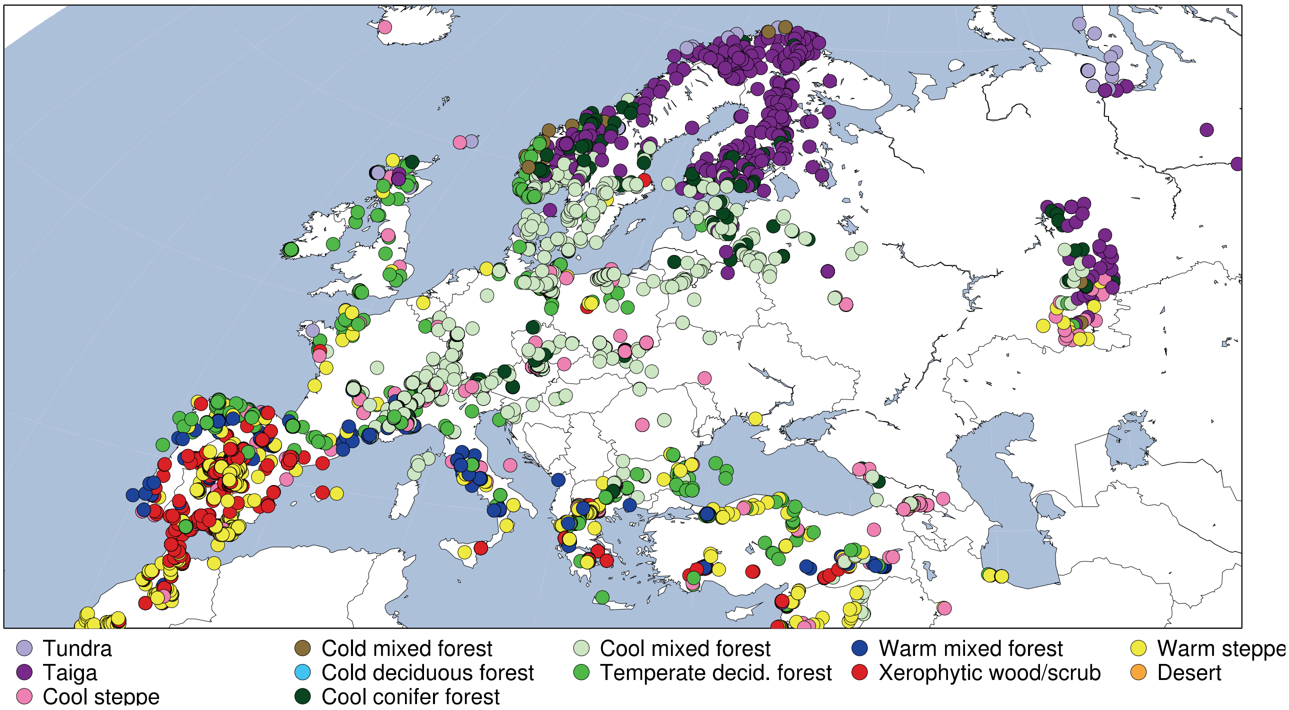


Figure 1.9. Biomization of European Modern Pollen Database, using method of Peyron *et al*. (1998).

1.7.2
Quaternary biogeography of Alpine plants

Between the Last Glacial Maximum (~ 21,000 years ago) and the present, the climate of Europe underwent dramatic changes, transitioning from full-glacial to full-interglacial conditions. As part of a project on the spatial and temporal response of Alpine plants to such dramatic changes, I am working with Dr. Nadir Alvarez, of the Ecology and Evolution department at the University of Lausanne, on reconstructing the late-glacial and Holocene distribution and abundance of nearly 30 Alpine plant taxa. This project is in its beginning stages.

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2 Could anthropogenic soil erosion have influenced Mediterranean vegetation distribution over the Holocene?

Collins, P.M., Kaplan, J.O. & Davis, B.A.S. (2010) *Could anthropogenic soil erosion have influenced Mediterranean vegetation distribution over the Holocene?* IOP Conference Series: Earth and Environmental Science, vol. 9, 8 pgs.

Abstract. The circum-Mediterranean region is characterized by a strongly seasonal climate with rainy winters and intense summertime drought, steep topography, and a multi-millennial history of intensive human land use, all of which make its soils vulnerable to erosion. The historical and stratigraphic record documents severe and long-term soil erosion in several locations in the Mediterranean. A forest-to-scrub transition in Mediterranean vegetation between the mid-Holocene (6,000 yr BP) and the present is evident in the observational palaeorecord. Debate as to the causes of this shift is ongoing. This study seeks to test the sensitivity of large-scale vegetation patterns to changes in soil physical properties such as depth, content of coarse fragments, and organic matter content using the Mediterranean region as a case study. We find that simulated biomes are sensitive to changes in some soil physical properties at some locations, but that threshold values for soil change to affect vegetation are very high. Additional work is required to analyze the role that other soil physical properties, and climate change, played in influencing Holocene land cover change in the Mediterranean, and to improve model representations of relevant processes.

2.1
Introduction

Today, the lands bordering the Mediterranean Sea are largely characterized by coarse-textured shallow soils and sclerophyllous xeric vegetation [1]. Yet pollen records from the mid-Holocene (6,000 yr BP) suggest that several places currently dominated by xerophytic (drought-tolerant evergreen) vegetation once supported extensive deciduous forests [2, 3]. Evidence suggests that the northern limit for xerophytic woodland and scrub in southern Europe was located up to three degrees of latitude farther south as compared to its present position [4]. The debate about the extent [5] and causes [6-8] of this observed northward expansion of xerophytic scrubland vegetation in the Mediterranean region between the middle and late Holocene is ongoing. Long-term changes in regional climate may have been the main driver, as orbitally forced changes in atmospheric circulation resulted in alterations in temperature [9] and precipitation [10] patterns in space and time and affected seasonal moisture regimes. Alternatively, the influence of changing human land use patterns may have played a role, as deforestation, grazing, crop cultivation, and use of fire exerted strong anthropogenic selection pressures on natural vegetation communities [11, 12]. As the combined effects of anthropogenic disturbance and climate change can dramatically alter soil moisture content by promoting soil erosion in uplands and sediment deposition in lowlands (for an overview, see [13]), our work attempts to contribute to this debate by posing the questions, “Do Mediterranean vegetation communities respond to changes in soil physical properties? If yes, how sensitive is the vegetation?”

Moisture availability often limits plant growth in seasonally arid environments such as the

Mediterranean. Here, soils can play a prominent role in determining land cover by acting as moisture reservoirs during periods of drought [14]. Land cover and soil characteristics control the partitioning of precipitation into runoff and infiltration, and soil depth and texture influence the proportion of soil moisture lost to evaporation and drainage versus that retained in the soil matrix. Under identical climatic conditions, differences in soil depth and texture in adjacent patches can cause marked differences in vegetation density [15, 16] and species distribution [17].

Though modern Mediterranean upland soils tend to be coarse, shallow, and poor in organic matter content, evidence suggests that this was not always the case. The Global Assessment of Soil Degradation classifies the soils of much of the circum-Mediterranean region as moderately or severely degraded (approximately 97,000 km^2 in Spain, 70,000 km^2 in Italy, and 40,000 km^2 in Greece [18]), with regions of very severe degradation [18, 19], implying that conditions were once quite different. During the classical periods of Greek and Roman civilization (ca. 2-3 ka BP), currently degraded landscapes such as those near ancient Carthage (Mediterranean north Africa) were once productive enough to feed cities and empires [20].

The combination of steep terrain, strongly seasonal and episodic precipitation, and a multi-millennial history of continuous and often intensive human land use make the Mediterranean region particularly prone to upland erosion and lowland sedimentation. Alluvial stratigraphic records show several distinct events of elevated soil erosion throughout the Mediterranean during the Holocene; they vary in both duration and severity by location and may be correlated with fluctuations in both climate and regional civilizations [21, 22, 23] (for a review, see [13]).

Research programs such as ARCHAEOMEDES [24] and MEDALUS (Mediterranean Desertification and Land Use) [25] had the aim of qualitatively understanding land degradation in the Mediterranean on a regional or site-by-site basis in historical times and the present day, respectively. As yet, however, there has been no attempt to investigate the impact of changing soil depth and texture on vegetation cover across the Mediterranean region in a systematic, quantitative manner. This study does not attempt to explain the changes in Mediterranean land cover over the Holocene observed in the pollen record, nor does it intend to make comparisons between pollen-reconstructed and model-calculated vegetation cover. Rather, it contributes to the ongoing debate about the causes of Mediterranean land cover change over the Holocene by testing the sensitivity of Mediterranean vegetation to changes in soil physical properties using a simple modeling approach.

2.2
Methods

To simplify our analysis and focus on those areas where we might expect changes in soil physical properties to have influenced vegetation cover in the past, we used the paleoecological record to identify a number of sites where vegetation changed from forest to non-forest types from the mid-Holocene to present. At 34 sites from across the Mediterranean region, we used the SoilMod soil physical model and the BIOME1 equilibrium vegetation model [14] to quantify the sensitivity of biome-scale vegetation to changing soil physical properties. The sites where we ran our model are broadly representative of the range of Mediterranean climate and soil characteristics, from mountains to coastlines and from semi-mesic to xeric environments. A detailed description of our methods follows.

2.2.1
Site description

The Mediterranean region lies roughly between 30°N and 40°N latitude and 10°E and 40°W longitude and has been defined as the region in which olive trees can be cultivated, the northern boundary of which is roughly determined by the 5°C January isotherm [26]. It is a tectonically young landscape with several steep mountain ranges. The climate is seasonal, with summers characterized by clear skies and drought due to the falling limb of the Hadley cell and winter weather dominated by the prevailing westerlies that deliver cyclonic precipitation with high spatial and temporal heterogeneity due to the varied topography. Average annual precipitation ranges from approximately 100 to 900 mm (two-thirds of which fall between September and March [1]), and the mean annual temperature is 15 ± 5 ˚C [4].

2.2.2
Data sources and study sites

To identify specific sites that experienced a change in land cover between the mid-Holocene and the present, this study uses a published pollen-based reconstruction of Mediterranean land cover classified into 12 biomes (following [27]) at 122 sites for both the present day and the mid-Holocene [4]. We classified the biome assignment for each site for both time periods as forest or non-forest, according to each biome's annual moisture requirement index α (Priestly-Taylor coefficient, or ratio of actual to potential evapotranspiration, AET/PET) as described in [14] (forest: $1 \geq \alpha \geq 0.65$; non-forest: $0.65 > \alpha \geq 0$). Thirty-four sites shifted from forest to non-forest between 6 ka BP and the present (figure 2.1), 3 sites did the reverse, and 85 sites did not cross the $\alpha = 0.65$ threshold in either direction. For each of the 34 sites that shifted from forest to non-forest, we extracted late 20th century soil data (depth, particle size distribution, organic matter content, percent of coarse fragments) at the 1 km gridcell nearest to each site from the Harmonized World Soil Database (HWSD) [28] and late 20th century mean climatology (temperature and precipitation values as used in [14]) from the WorldClim database [29]. The pollen data are not used again in this study after this site-selection step.

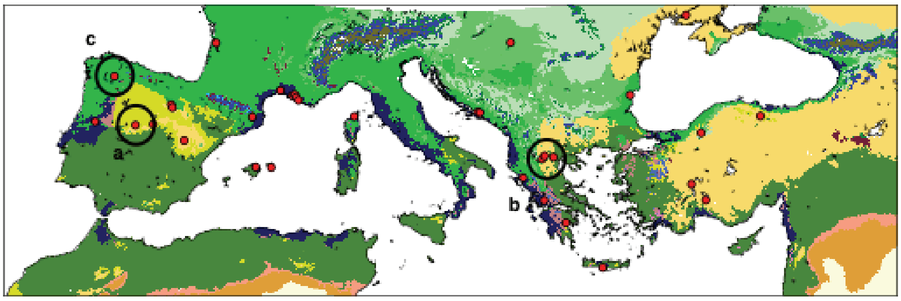

Figure 2.1. Potential natural vegetation of the Mediterranean study area simulated by the BIOME1 model. Each red circle represents a sediment core where pollen data indicate a forest biome at 6 ka BP and a non-forest biome in the present day [2]. Results for circled sites a, b, and c are presented in figures 2.2 and 2.3.

2.2.3
Models and calibration

We employed two models in this study. First, we used a soil physical model (SoilMod) driven by the HWSD parameters listed in section 2.2. This model consists of a series of pedotransfer functions [30-34] and calculates soil bulk density, water holding capacity (defined as the difference between field capacity, or water remaining in the soil under -33 kPa water potential [Ψ], and wilting point, or water remaining in the soil at Ψ -1,500 kPa), and saturated hydraulic conductivity for the region surrounding each of the 34 sites analyzed.

Next, we used a global biogeography model (BIOME1) driven by WorldClim climate data [29] and the output from SoilMod (see above). For each gridcell or data point, BIOME1 uses these data to determine the presence or absence of each of 13 distinct plant functional types (PFTs) based on their physiological requirements, namely minimum and maximum thresholds of temperature and moisture availability [14]. The latter is determined by the moisture availability index α, calculated as the ratio of actual to potential evapotranspiration (AET/PET) [14, 35]. AET is proportional to soil water content in a single-layer "bucket" type soil, which is a function of soil water holding capacity (as calculated by SoilMod) and precipitation (from WorldClim). PET is calculated using the equations in [35] with temperature data from WorldClim and % sunshine data from the CRU CL2.00 climatology [36]. Manipulating the soil physical properties for a given location changes the size of the soil "bucket" and therefore leads to a change in the calculated α value for that location, which in turn may alter the location's suitability for a given PFT. Finally, a unique biome name is assigned to each combination of present and absent PFTs (figure 2.1; PFTs as in [14]).

To calibrate BIOME1, we used it to generate a gridded map of potential natural vegetation represented as biomes (figure 2.1) and then refined our model parameterizations until the map output satisfactorily matched the modern potential vegetation distribution for the Mediterranean [37].

2.2.4
Sensitivity tests

As depth and content of coarse fragments (% v) both influence the total volume of fine soil material that is available to retain water, and soil organic matter content (% w) affects a mineral soil's ability to retain water, these were the three soil physical parameters we chose to manipulate. Changing these three parameters alters the resulting bulk density, water holding capacity, and saturated hydraulic conductivity as calculated by SoilMod, which in turn modifies the α value used by BIOME1 to calculate the biome for each combination of parameters. Assuming that soil degradation would decrease depth and organic matter content and increase the percent of coarse fragments, we explored a wide range of parameter space that could represent both "degraded" and "improved" conditions relative to present-day soil conditions.

First, we varied the simulated depth of all soils from 0.1 m to 2.0 m and calculated soil water holding capacity using SoilMod, keeping all other soil characteristics constant. Then, we held depth constant at HWSD (present-day) values and simultaneously varied simulated soil organic matter from 0% to 20% (w) and content of coarse fragments (lithic material > 2 mm in diameter) from 100% to 0% (v) for all test sites, again using SoilMod. For both sets of experiments, we ran the new calculated soil bulk density, water holding capacity, and conductivity values through BIOME1 and checked the resulting simulated biome to see if a "degradation" or "improvement" in soil physical parameters under constant climatic conditions led to a change in the calculated biome assignment at any of our test sites.

2.3
Results

Of the 34 sites analyzed, the simulated biome was insensitive to any "improvement" in soil physical properties at all but three sites (figures 2.1, 2.2, 2.3). Each of these three sites was sensitive to a decrease in the content of coarse fragments, but only two were sensitive to an increase in depth, and none responded substantially to an increase in soil organic matter (figures 2.2, 2.3). Sensitivity was expressed by a change in the calculated biome for a site, e.g. from drought-tolerant open conifer woodland to drought-sensitive temperate deciduous forest (figures 2.2, 2.3).

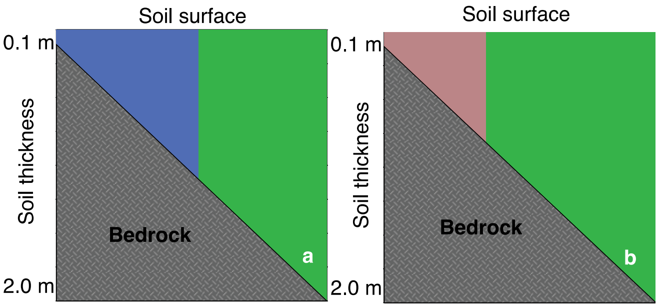

Figure 2.2. Increasing soil depth from 0.1 m to 2.0 m led to a biome shift at two of our 34 test sites. Letters correspond to circled sites in figure 2.1. Colors indicate biome types. Green: temperate deciduous forest; blue: evergreen broadleaf and needleleaf forest; rose: evergreen broadleaf and needleleaf woodland. For biome descriptions, see [14].

For this study, the majority of sites appear insensitive to increases in soil depth and organic matter and decreases in the content of coarse fragments. There are three potential explanations for this outcome: 1.) Changes may have occurred in the relative percentages of PFTs present, or even in levels of net primary productivity, but the resolution of our biome-level analysis was too coarse to pick up these subtleties; 2.) Soil water holding capacity is more sensitive to changes in soil texture (which we have not yet tested) than to soil depth, stoniness, or organic content; 3.) We tested the correct parameters and analyzed the output at the appropriate level of complexity, but in fact Mediterranean vegetation is insensitive to changes in soil physical properties.

The 3 sites that did respond to an "improvement" of soil physical properties were likely already near the threshold between two different biome classes (figure 2.1). However, all 34 sites responded to a "degradation" of soil physical properties; when soils approached a threshold level of 95%-97% (v) coarse fragments, biomes shifted uniformly to desert conditions.

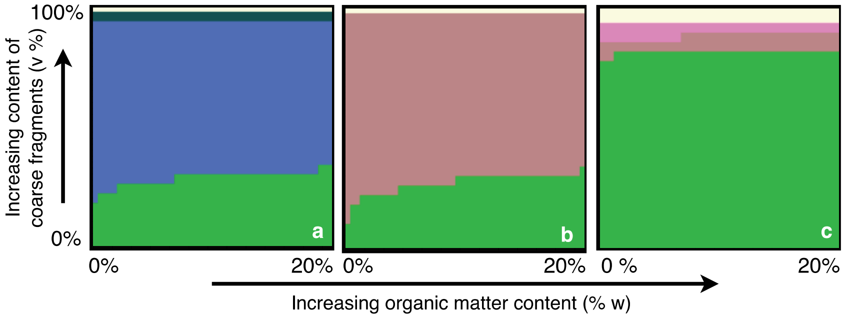

Figure 2.3. Changing soil organic matter content and content of coarse fragments caused a shift in simulated biome at three of our 34 test sites. Letters correspond to circled sites in figure 2.1. Change in color indicates biome shift. Pale Yellow: desert; dark green: temperate conifer forest; pink: open conifer woodland. For other colors, see Figure 2.

Rather than analyzing the entire circum-Mediterranean region in a gridded manner, this study works with 34 individual points distributed across the entire region that are assumed to be representative of the full range of Mediterranean climate and soil characteristics. This was done to simplify our approach; we acknowledge that future work would benefit greatly from analyzing the entire gridded region and intend to do so in the future. The biome scheme used in BIOME1 is not analogous to the biome scheme used with the pollen data, making direct comparisons between biomes from model output and biome assignments from pollen data impossible. This discrepancy will be remedied in future work. For this study, we are more interested in whether or not a shift from one biome type to another occurs in response to changes in soil physical properties; the actual biome assignments are of secondary interest.

2.4
Discussion and Conclusions

Our results suggest that at least under certain circumstances, “improving” soils by increasing soil depth and organic matter content and/or decreasing the content of coarse fragments can lead to the simulation of more moisture-loving biome types (i.e. a shift from evergreen to deciduous vegetation) without requiring a change in climate, and reversing the direction of these changes can lead to the simulation of desert. However, the threshold levels for these changes are quite high and suggest that further study is required to improve our model representations of the processes involved in soil-vegetation-climate interactions.

This study attempts to quantify the sensitivity of vegetation under Mediterranean conditions to soil thickness, stoniness, and organic matter content. Though all 34 sites analyzed demonstrate a clear transition from forest to non-forest biomes between the mid-Holocene and the present in the pollen record, only three respond to changes in modeled soil stoniness and organic matter content (figure 2.3), and just two of these show a change in biome in response to changing soil depth (figure 2.2). These results could suggest that Mediterranean vegetation is relatively insensitive to changes in soil physical properties. However, only a small number of soil parameters were tested for a limited number of locations, and more complex analysis over a wider area may reveal greater sensitivity.

We will follow up on this preliminary work with a more in-depth analysis of the environmental factors relevant at our study sites, and we will extend our analysis to additional sites. We will expand our experimental design to analyze soil texture (relative proportions of sand, silt, and clay), we will use an alternative soils dataset [38, 39] that provides more detailed information on soil depth at the present day, and we will analyze vegetation response at the levels of net primary productivity and plant functional types. We will also incorporate potential soil-climate feedbacks and interactions in future work.

The question of vegetation sensitivity to changes in soil physical characteristics is not merely academic. It may have serious implications for the concepts of sustainable land use and resilience of land to abuse and degradation. How much soil can be lost (or gained) before a region’s natural vegetation community shifts from one stable state to another? Is the process reversible? Do thresholds differ between ecosystems? Though much work has been done on the annual to decadal detrimental effects of soil erosion on agricultural productivity [40-43], little quantitative data is available on how centuries or millennia of human land use alter the land’s capacity to support natural vegetation or human activities. The circum-Mediterranean region is a drought-limited, seasonal environment prone to erosion that has been heavily used by humans for millennia. In many places, Mediterranean soils have experienced dramatic erosion since the mid-Holocene. The debate about what caused the observed shift in vegetation from forest to non-forest between the mid-Holocene and the present in many areas of the Mediterranean is still open. Any attempt to understand the dynamics of vegetation over long timescales should not ignore the potential impact of changes in soil physical properties under human, or even natural, influences.

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3 The mid-Holocene vegetation of the Mediterranean region and southern Europe, and comparison with the present day

Collins, P.M., Davis, B.A.S. & Kaplan, J.O. (2012) The mid-Holocene vegetation of the Mediterranean region and southern Europe, and comparison with the present day. *Journal of Biogeography*, vol. 39, 1848-1861.

Abstract

Aim. To contribute to the intense debate surrounding the relative influence of climate and humans on Mediterranean-region land cover over the past 6,000 years, we assess the Holocene biogeography and vegetation history of southern Europe by means of an extensive pollen record dataset.

Location. The Mediterranean biogeographical zone and neighbouring parts of Iberia, the Alps, and Anatolia, between 30° N, 48° N, 10° W and 45° E.

Methods. We compiled a southern European pollen record dataset using available pollen databases (124 sites) and other sources (74 sites), with improved spatial coverage and dating control compared with earlier studies. We used only those sites that had pollen data for both 0 ka and 6 ka. We reconstructed mid-Holocene and present-day biomes, arboreal pollen percentages, and distribution and relative abundance of 11 key woody taxa, with anomaly maps.

Results. Northern temperate forest biomes extended further south at the mid-Holocene than at present, but not as far as earlier studies suggested. Sclerophyllous vegetation occurred along the Mediterranean coast throughout the region at 6 ka. Arboreal pollen percentages were up to 50% higher than at present. At 6 ka, *Olea*, *Fagus* and *Juniperus* had smaller distributions and/or abundances; *Abies*, *Cedrus* and both deciduous and evergreen *Quercus* had larger distributions and/or abundances; *Phillyrea*, *Pistacia* and *Cistus* showed minimal difference; and *Pinus* showed a cosmopolitan distribution with variable abundance.

Main conclusions. Temporal difference analysis is more meaningful when only sites containing samples for all time slices are analysed. During the mid-Holocene, southern Europe was more heavily forested with temperate vegetation than it is at present, but drought-tolerant xeric vegetation was still widespread along the southern margins of the region. Although human land use may have caused land degradation between the mid-Holocene and the present, the mere presence of xeric vegetation in the Mediterranean region does not require human impact. This challenges the commonly held belief that modern Mediterranean vegetation represents a "degraded" state.

3.1
Introduction

The Mediterranean Basin has been subjected to human-induced deforestation, repeated fires, overgrazing and erosion for nearly the entire Holocene (Van Overloop, 1986). Yet the cumulative impact of anthropogenic activities on Mediterranean vegetation assemblages observed today is still debated (de Beaulieu *et al.*, 2005). Have millennia of cumulative impact generated a 'ruined landscape' (Attenborough, 1987), or has human activity instead stabilized or even diversified Mediterranean ecosystems (Grove & Rackham, 2001; Blondel, 2006)? Improved understanding of past Mediterranean vegetation is essential because it informs our understanding of its current state, its sensitivity to climate and human impact, and the potential responses to future changes in climate and/or land use patterns in this biodiversity hotspot (Médail & Quézel, 1999; Montmollin & Strahm, 2005; Petit *et al.*, 2005; Médail & Diadema, 2009).

In this study we focus on a comparison of vegetation patterns in the Mediterranean between the mid-Holocene (6 ka) and the present day. The mid-Holocene is a recognized benchmark period for palaeoenvironmental research (Huntley & Prentice, 1988; Prentice *et al.*, 1996; Braconnot *et al.*, 2007; Wanner *et al.*, 2008), because by this time the Pleistocene ice sheets had retreated to near present-day conditions, sea level and atmospheric CO_2 concentrations had stabilized at pre-industrial levels (e.g. COHMAP, 1988; Kaplan *et al.*, 2003), and evidence suggests that humans had not yet begun to significantly alter the natural environment at the continental scale, at least in the central and western Mediterranean (Kaplan *et al.*, 2011).

While a great deal of previous research has attempted to characterize changes in Mediterranean vegetation over the Holocene, these efforts generally suffered from a limited number of sites, poor spatial coverage in complex terrain, and/or imprecise and limited dating control (Huntley & Birks, 1983; Gliemeroth, 1997; Jalut *et al.*, 2000; Cordova *et al.*, 2009, Sadori *et al.*, 2011). Previous studies that focused specifically on comparisons between the mid-Holocene and the present day generally used all data available for either time slice, making it impossible to determine whether differences between time slices were due to vegetation change or to the presence/absence of sites in a time slice (Prentice *et al.*, 1996, 2000; Jolly *et al.*, 1998; Gachet *et al.*, 2003; Gritti *et al.*, 2004; Cheddadi & Bar-Hen, 2009).

To overcome the limitations of previous work on Holocene land cover change in the Mediterranean, we have: (1) compiled a new pollen database for the Mediterranean, including several new sites published in the last 5 years, with improved spatial coverage and better documentation of sites, sources, and dating control; (2) applied strict chronological control to the data we used; (3) mapped the potential distributions of arboreal pollen (AP) and plant taxa in space using a novel, three-dimensional interpolation technique; and (4) made direct site-by-site comparisons of changes in vegetation between the present day and the mid-Holocene. Consequently, we are able to describe a picture of Holocene vegetation change across the entire Mediterranean Basin that is more complete and reliable than any previous attempt. We here addressed the following questions.

1. How did Mediterranean vegetation at the mid-Holocene differ from that of the present day?
2. Will our novel treatment of all available data, with more sites and better quality control, challenge the commonly accepted paradigm of a "ruined" Mediterranean?

3.2
Materials and methods

Vegetation cover in palynological studies is typically characterized either by assessing the distribution and/or abundance of one or a few taxa of particular interest, or by grouping taxa into categories and assessing the distribution and/or abundance of the categories. Common examples of categories include arboreal versus non-arboreal, xerophytic versus mesophytic, or evergreen versus deciduous taxa. Another approach groups taxa into climate-specific vegetation assemblages such as 'plant functional types' or 'biomes' (Prentice *et al.*, 1996). In this study, we used 275 pollen records from the Mediterranean and southern Europe to reconstruct and map vegetation characteristics for the mid-Holocene (6 ka) and the present day (0 ka). We present our results for both 0 ka and 0 ka, with calculated anomalies (0 ka minus 6 ka). We analysed vegetation in terms of biomes, arboreal pollen percentages (AP%), and distribution and abundance of eleven characteristic taxa. We used only sites having pollen data for ***both*** time slices

3.2.1
The dataset

We assembled a dataset of pollen samples for southern Europe and northern Africa for the mid-Holocene and the present. This geographical domain encompasses the entire present-day Mediterranean region as defined in Quézel & Médail (2003), plus contiguous areas such as the Alps and parts of Iberia and Anatolia.

Our complete pollen dataset contains 636 records for the geographical domain of interest. To avoid the problem of comparing sites that are not co-located in space, we used only sites having data for both the 6 ka and 0 ka time slices. If a site lacked a core top sample for the present-day time slice, we substituted a surface sample from the same site or from within 1 km when possible. If either present-day or mid-Holocene pollen data for a site were lacking, the site was excluded from our analysis; 395 sites had to be excluded in this way. A further 43 sites were excluded due to insufficient dating control, leaving us with 198 pollen records: 123 sites from the European Pollen Database (Fyfe *et al.*, 2009), one site from the PANGAEA database (http://www.pangaea.de), 11 sites provided to us by the individual authors (Jahns, 1993; Jahns & van den Bogaard, 1998; Drescher-Schneider *et al.*, 2007; Neumann *et al.*, 2007; Wagner *et al.*, 2009), and 63 other sites for which we digitized the pollen diagrams from directly from the publications. For a complete list of sites, with coordinates, data sources, and maps of geographical and topographical distribution, see Appendices in section 3.6.

The pollen data in our dataset were collected from sediment cores from lakes, mires, and estuarine sites. We excluded marine cores from our analysis due to the large and uncertain extent of their source areas. We assimilated all taxon names to conform to standard European Pollen Database (EPD) taxonomy and checked that all taxa were sorted into the appropriate categories used to distinguish arboreal, non-arboreal, and aquatic pollen types from non-pollen types. 'Arboreal' taxa consist of all taxa having woody tissue and belonging to one of the EPD categories of 'trees', 'shrubs', 'dwarf shrubs', or 'lianas'. 'Non-arboreal' taxa consist solely of taxa belonging to the EPD category 'herbs' (http://www.europeanpollendatabase.net). We ignored aquatic and marshland taxa and used only terrestrial taxa for our analyses. Incorporation of both arboreal and non-arboreal pollen into the terrestrial pollen sum is crucial for better understanding the openness and character of vegetation cover.

Samples were selected for the mid-Holocene (6 thousand years ago, ka) and the present (0 ka) using age–depth models based on calibrated radiocarbon dates. Age–depth modelling and interpretation followed that of the original author or the EPD where available; for all others a simple linear interpolation between bracketing dates was used. Radiocarbon dates were calibrated using OXCAL 3.10 with the IntCal04 radiocarbon calibration curve (Ramsey, 2005; Reimer *et al.*, 2004). Where dating problems such as marine and terrestrial hard-water errors or differences between materials occurred, we followed the authors' recommendations or those documented in the EPD. We defined the mid-Holocene as 6000 ± 500 cal. yr BP, as is commonly adopted in palaeoenvironmental analyses, and the present as 0 +60/-500 cal. yr BP, corresponding to AD 1950. For each time slice, we selected the sample closest to the target date.

3.2.2
Biomes

To translate pollen counts into biome assemblages, we followed the biomization methodology described by Peyron *et al.* (1998), as adapted from Prentice *et al.* (1996). This biomization procedure categorizes 39 arboreal pollen taxa and 39 non-arboreal pollen taxa into 22 plant functional types, which are then combined into 12 biomes. Pollen counts for taxa not belonging to a plant functional type were excluded from the analysis. The computer code of the biomization program is available upon request from the corresponding author. For comparison, we also mapped both the modern potential natural vegetation cover (Fig. 3.1) and the BIOME 6000 data (Prentice *et al.*, 2000) (version 4.2, available for download at: http://www.bridge.bris.ac.uk/projects/BIOME_6000) (Fig. 3.2).

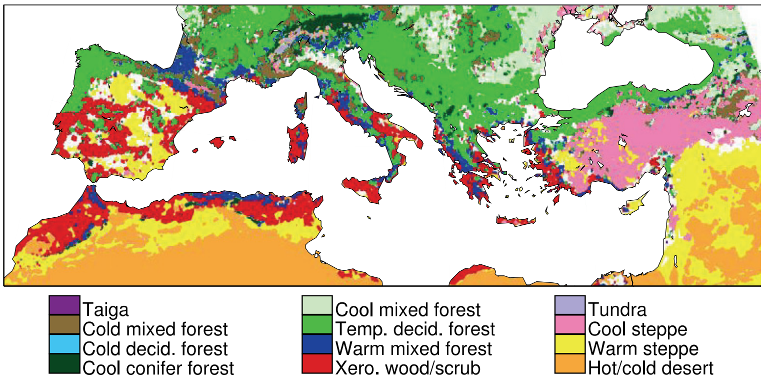

Figure 3.1. Potential natural land cover of present-day southern Europe and the Mediterranean, reclassified into biomes (Prentice *et al.*, 1996; Peyron *et al.*, 1998) from the Olson (1994) remote sensing-based land cover data set following Roberts *et al.* (2004). White areas on land denote no available data. All maps in this paper use a Lambert Azimuthal Equal-Area projection centred on 15 °E, 40 °N.

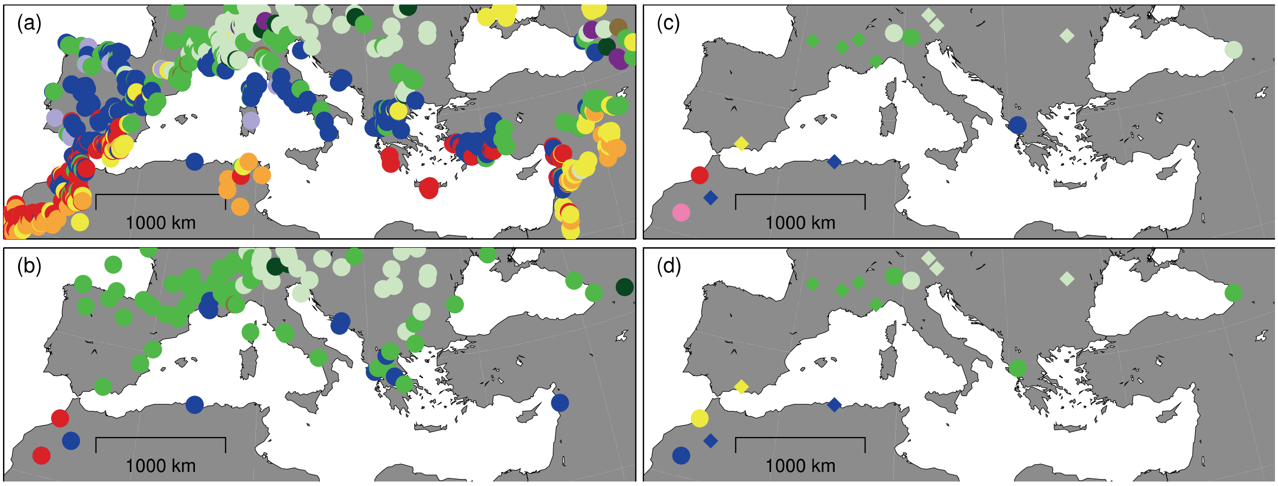

Figure 3.2. Mid-Holocene (6 ka) and present day (0 ka) southern European and Mediterranean biomes reconstructed from pollen data by Prentice *et al.* (2000) in the BIOME 6000 project. Panels (a) and (b) show all 0 ka and 6 ka data (respectively) reported in Prentice *et al.* (2000). Panels (c) and (d) represent the same data as panels (a) and (b) but were filtered to show only sites having calculated biomes for both time slices, consistent with the methodology used in this paper (cf. Fig. 3.3). Not all sites can be shown, due to overprinting of sites in close proximity to one another. Circles indicate sites where biome differs between time slices; diamonds indicate sites where biome is the same at both time slices. Colours as in Fig. 3.1, with the exception of yellow, which here represents 'steppe' undifferentiated between 'warm' and 'cool'.

3.2.3
Arboreal pollen percentages

While biome reconstruction gives a general idea of potential vegetation type, AP% provides quantitative approximations of closed versus open vegetation cover. We investigated the distribution and abundance of forest cover as approximated by AP%, calculated as the percentage of the total terrestrial pollen sum belonging to arboreal pollen taxa. The terrestrial pollen sum is calculated as the sum of pollen counts of all non-aquatic and non-wetland taxa, both arboreal and non-arboreal. The arboreal pollen sum is the sum of the pollen counts belonging to arboreal pollen taxa. AP% offers a continuous, numerical approximation of relative landscape openness, although it does not directly translate to on-the-ground forest cover (Tarasov *et al.*, 2007).

To provide a more spatially coherent visualization of our results, we mapped an interpolated surface between the analysed sites. Interpolations were generated with a 3D thin plate spline (tension $\lambda = 0$), using elevation as the third dimension of the interpolation (Fields Development Team, 2006). To avoid over-interpretation of the interpolated surfaces, we masked the surfaces beyond a radius of 150 km around each pollen site.

3.2.4
Taxon pollen percentages

We assessed the distribution and abundance of 11 of the most important woody taxa in the Mediterranean region (*Fagus*, *Abies*, deciduous and evergreen *Quercus*, *Pinus, Cedrus, Juniperus*, *Olea*, *Pistacia*, *Phillyrea* and *Cistus*) by mapping their pollen percentages. Using a method similar to that of our AP% analyses, we calculated abundance as the percentage of the terrestrial pollen sum represented by each taxon. The distribution and abundance of individual taxa provide continuous, numerical information on the taxa that might be driving the trends observed in our biome and AP% reconstructions.

Our approach differs from that of Huntley & Birks (1983), who calculated their taxon abundances as percentage of arboreal, rather than terrestrial, pollen. We chose our approach because we were interested in actual taxon abundance relative to the entire vegetation assemblage. Our interpolation and plotting methods were identical to those used in our AP% analysis. The minimum presence/absence percentage thresholds were selected on a taxon-by-taxon basis, following Huntley & Birks (1983).

3.3
Results

3.3.1
Biomes

Biome distributions reconstructed for 0 ka (Fig. 3.3a) are broadly consistent with the satellite-derived land cover map (Fig. 3.1), given that the satellite image represents the landscape at a coarser spatial resolution than the pollen reconstruction. The pollen-based biome maps show that temperate deciduous forest (TDF) was more widespread at 6 ka than at 0 ka (Figs 3.3b,c). Of the 197 sites in our dataset, 64 sites were TDF at 6 ka and 33 sites were TDF at 0 ka. In the Mediterranean region at 6 ka, TDF extended further south into Italy and Spain, into areas currently occupied by drought-tolerant biomes such as warm mixed forest, xerophytic wood/scrub, warm steppe, or cool steppe (Fig. 3.3). North of the Mediterranean region, TDF occupied areas that are currently cool mixed forest, cool steppe, or warm steppe. In southern France and in mountainous, northern parts of Spain, Italy, and Greece 26 sites remain TDF at both time slices. Throughout the

Mediterranean region, 49 sites were classed as one of the more drought-tolerant biomes at both time slices. In northern Spain, three sites were classed as drought-tolerant biomes at 6 ka but are TDF at 0 ka. In Turkey, one site (Sögüt Gölü) appears as TDF at 0 ka but not at 6 ka.

Both the present study (Fig. 3.3) and BIOME 6000 (Fig. 3.2) found the boundary between TDF and drought-tolerant vegetation to be located farther south at 6 ka than at 0 ka (Prentice *et al.*, 1996; Jolly *et al.*, 1998). However, BIOME 6000 shows TDF dominating southern Europe and extending to the shores of Mediterranean Sea at 6 ka, while our analysis clearly shows drought-tolerant vegetation occupying many southern European sites at 6 ka.

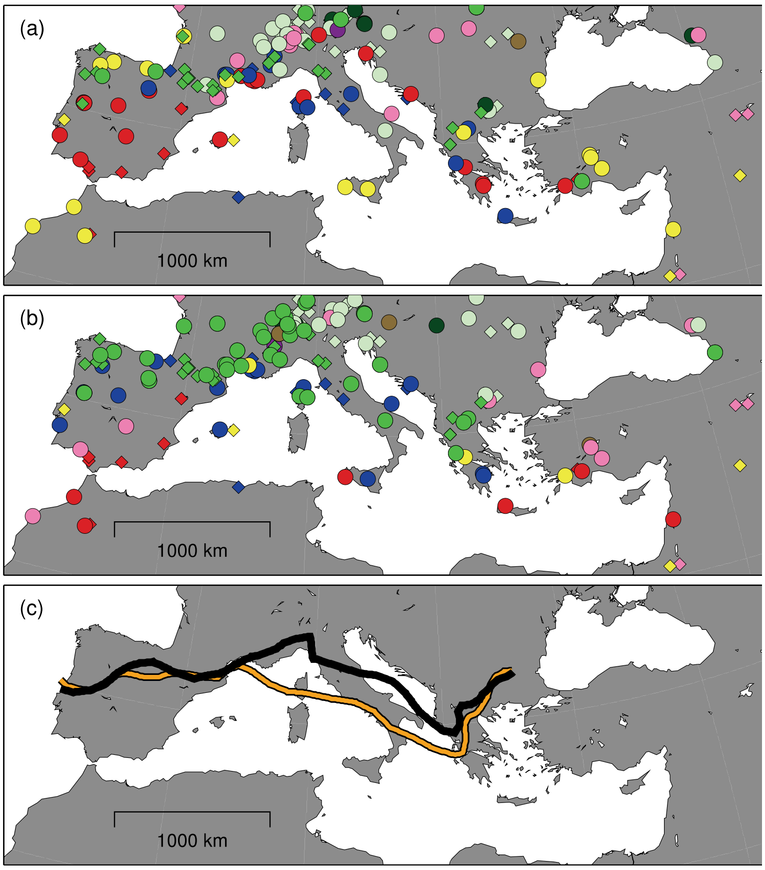

Figure 3.3. Southern European and Mediterranean biomes reconstructed from pollen data for the present day, 0 ka (a), and mid-Holocene, 6 ka (b), following Peyron *et al.* (1998). Circles indicate sites where biome differs between time slices; diamonds indicate sites where biome is the same at both time slices; colours as in Fig. 3.1. For clarity, sites having biome 'temperate deciduous forest' have been plotted on top of all other sites. (c) Southern limit of temperate deciduous forest biome at 0 ka (black) and 6 ka (orange).

3.3.2
Arboreal pollen percentages

The percentage of total terrestrial pollen belonging to arboreal taxa at the mid-Holocene does not suggest a uniform forest cover over the entire Mediterranean region (Fig. 3.4). However, vegetation cover was generally much more closed throughout southern Europe at 6 ka than it is at 0 ka. Northern Africa, along with much of Spain, France, Italy, the Balkan states and areas to the north, had up to 35% greater AP% at 6 ka than at present; in some areas, this difference exceeds 50%. Scattered throughout the Mediterranean are sites showing little change, where AP% differs by less than 15% between the mid-Holocene and the present. Southern Greece, southern Turkey and the Levant show lower AP% at 6 ka compared to 0 ka: up to 15% less AP for Greece and the Levant, and up to 50% less AP in south-western Turkey.

3.3.3
Taxon pollen percentages

The relative abundance of *Fagus* (Fig. 3.5a & Fig. 3.7 in Appendix 3.6.3) within its 6 ka range was greater at 6 ka than at 0 ka. At 6 ka, *Fagus* was limited mostly to southern France, northern Italy, and areas to the north and east of these, whereas at 0 ka it extends further north and east to Bulgaria, Romania, and Greece, and west to northern Spain. Both the distribution and relative abundance of *Abies* (Fig. 3.5a, Fig. 3.7) were greater at 6 ka than at 0 ka. At 6 ka, *Abies* occurred throughout Italy and extended into France, Spain, Germany and the Balkan states. At 0 ka, it is restricted to isolated patches of this range, at much lower relative abundance. Deciduous *Quercus* (Fig. 3.5a, Fig. 3.7) was as widely distributed throughout southern Europe at 6 ka as it is today, but its relative abundance was larger at 6 ka throughout its range. The range of evergreen *Quercus* (Fig. 3.5a, Fig. 3.7) (North Africa, Spain, France, Italy, Greece, Turkey) was the same between the two time slices. Its relative abundance was greater at 6 ka than at 0 ka throughout almost its entire range, with the exception of eastern Greece, central Spain, and the Appenine mountains of Italy, where the reverse was true.

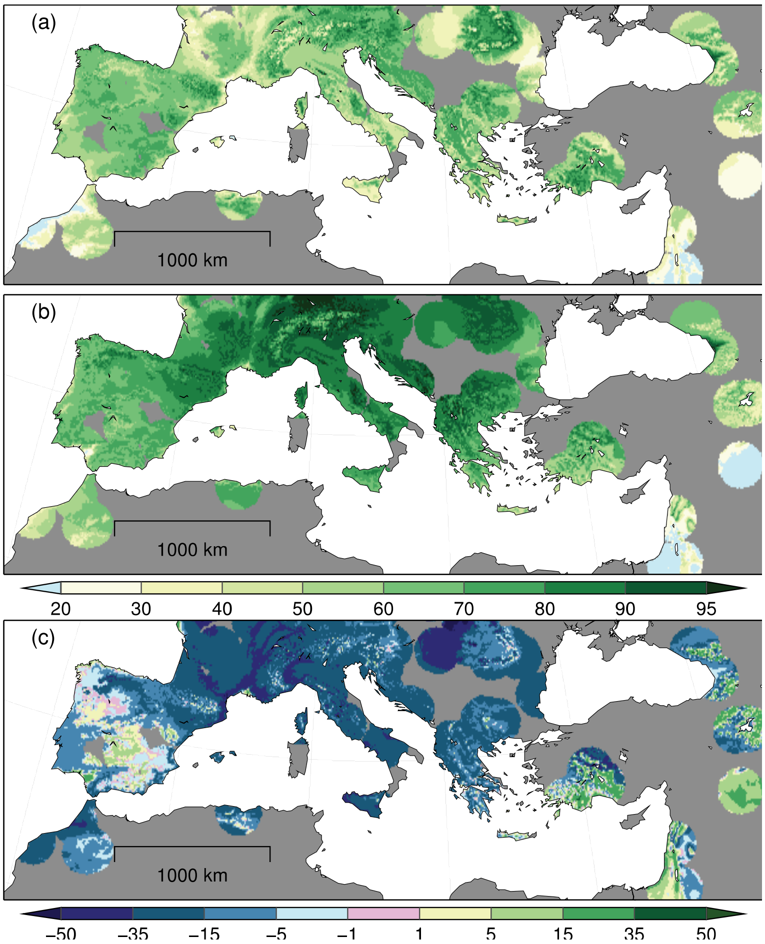

Figure 3.4. Arboreal pollen (all woody vegetation, including trees, shrubs, dwarf shrubs, lianas) calculated as a percentage (AP%) of total terrestrial sum (excluding aquatic and marsh taxa) for 0 ka (a) and 6 ka (b). Colours indicate AP%; darker green: higher AP%, lighter green: lower AP%, blue: AP% < 20%. Sample sites used are same as in Fig. 3.3. Panel (c) shows anomaly between time slices (calculated as 0 ka AP% minus 6 ka AP%). Colours indicate magnitude and direction of anomaly; green: 0 ka AP% > 6 ka AP%, blue: 0 ka AP% < 6 ka AP%, pink: < 2% difference between 0 ka and 6 ka. All surfaces were interpolated using a 3D thin plate spline, third dimension elevation, tension = 0. Grey areas indicate no data (> 150 km from a data point).

High percentages of *Pinus* pollen occurred across the entire study area at both time slices (Fig. 3.5b, Fig. 3.7). Relative abundance was lower at 6 ka than at 0 ka in many areas of southern Europe, especially in the parts of south-western Turkey that also showed lower AP% at 6 ka. Unlike *Abies* or *Pinus*, the evergreen needle-leaved *Cedrus* was not distributed throughout the Mediterranean region at either time slice (Fig. 3.5b, Fig. 3.7). It occurred in north-west Africa, south-eastern Europe, and Turkey, in both time slices. Abundances in Turkey were noticeably higher at 6 ka than at present, while abundances in northern Africa were lower. Abundances were equally low for both time slices in the rest of its range. *Juniperus* (Fig. 3.5b, Fig. 3.7) occurred throughout the Mediterranean region and southern Europe at the mid-Holocene but at lower abundance compared with 0 ka levels in most places. Exceptions include south-western Spain, the margin of the Adriatic Sea, and southern parts of France and Turkey, where abundance was greater at the mid-Holocene.

Olea (Fig. 3.5c, Fig. 3.7) was less widely distributed and had lower relative abundance at 6 ka than at 0 ka. At 6 ka, *Olea* was not present in large areas where it is found today, namely in northern Spain and Italy, large areas of southern France, and the northern Balkan states. At 6 ka, the relative abundance of *Olea* in the southern parts of Spain, Italy and Greece, and in northern Africa, was lower than it is at present. The areas in Spain where the difference in relative abundance of *Olea* was greatest correspond with the areas where AP% was lower at 6 ka than at 0 ka.

Apart from its absence from the Levant, *Pistacia* (Fig. 3.5c, Fig. 3.7) had a similar 6 ka distribution to *Olea*. *Pistacia* was present in northern Africa and southern parts of Spain, France, Greece and Turkey. While 6 ka relative abundance was slightly higher at some sites and slightly lower at others as compared with present, there was generally little difference between distribution and relative abundance at 6 ka and 0 ka. At 6 ka, *Phillyrea* (Fig. 3.5c, Fig. 3.7) occurred mainly in northern Africa and southern Spain, but it was also present at scattered sites in Italy, Greece, and southern France. Relative abundance at 6 ka was slightly greater in northern Africa and slightly smaller in Italy, southern France, and southern Greece. *Cistus* (Fig. 3.5c, Fig. 3.7) occurred mainly in Spain, Crete, and the southern areas of Italy and Greece at 6 ka. It was more abundant in Crete and western Spain at 6 ka than at 0 ka but less abundant in eastern Spain.

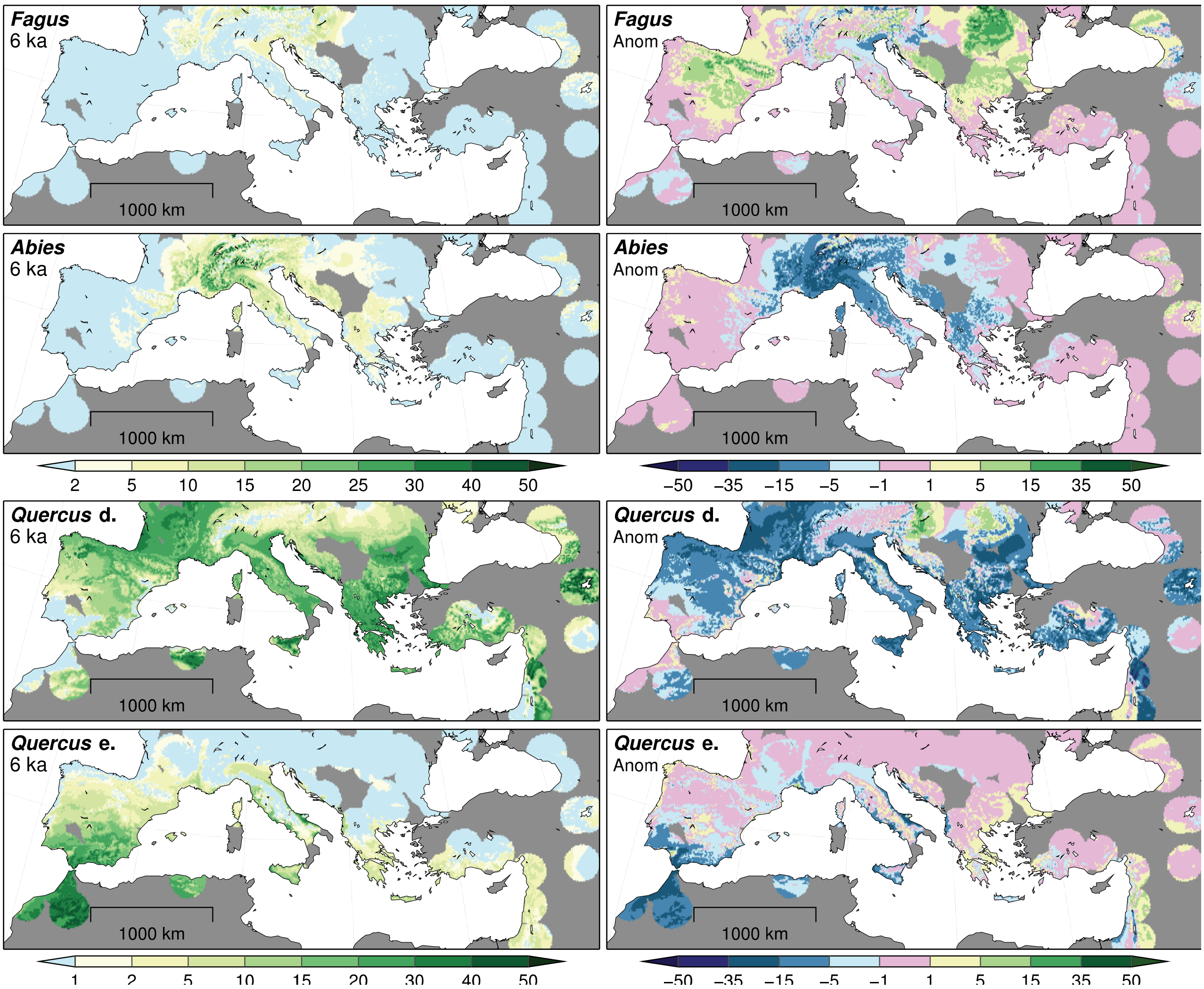

Figure 3.5a. Distribution and abundance of 11 southern European and Mediterranean woody taxa, calculated as a percentage of total terrestrial sum (excluding aquatic and marsh taxa) for the mid-Holocene (6 ka, left column). Colours indicate abundance; darker green: higher % of total terrestrial sum, lighter green: lower % of total terrestrial sum, blue: below presence/absence threshold. Anomaly calculated as 0 ka taxon % minus 6 ka taxon % (Anom, right column). Colours as in Fig. 3.4c. (a) *Fagus, Abies, Quercus* d. (deciduous), *Quercus* e. (evergreen). (b) *Pinus, Cedrus, Juniperus*. (c) *Olea*, *Pistacia*, *Phillyrea*, *Cistus*. Sample sites used are same as in Fig. 3.3. Interpolation as in Fig. 3.4.

3.4
Discussion

3.4.1
Biomes

The biome maps presented in this study are an improvement on those generated from the BIOME 6000 project for several reasons. First, the present study uses a greater number of sites with better spatial coverage in the Mediterranean region. Second, the maps in this study show only sites with pollen data for both 6 ka and 0 ka, allowing for meaningful assessment of real differences between time slices. The large difference in the number of sites shown in the filtered versus unfiltered BIOME 6000 datasets (Fig. 3.2) highlights the novelty of the present study and suggests that caution is required when drawing conclusions about vegetation change from comparison of the BIOME 6000 published 0 ka and 6 ka maps, or indeed from comparison of any time slice maps with temporally inconsistent data locations. Third, BIOME 6000 classified all undifferentiated *Quercus* pollen into the temperate summergreen PFT.

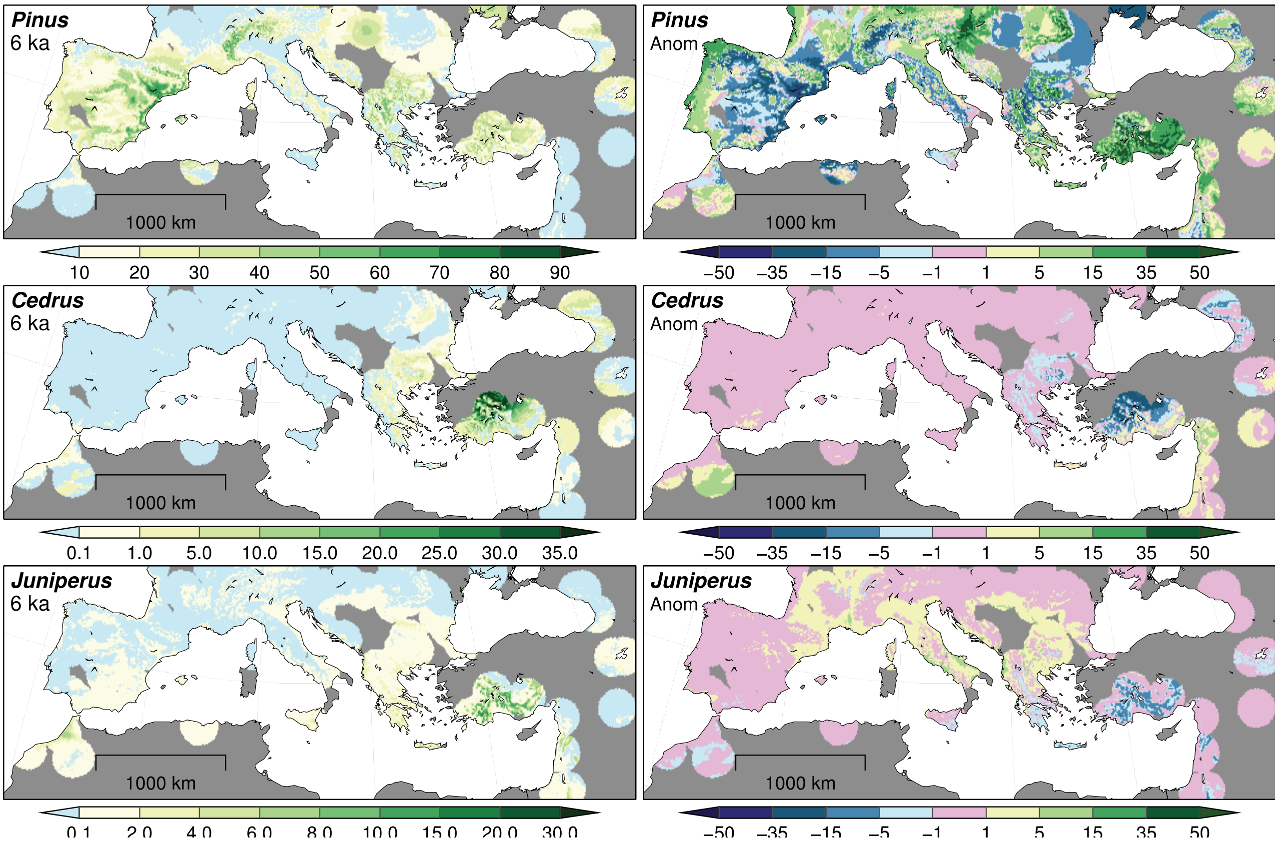

Figure 3.5b.

In contrast, the present study avoids this ambiguity by excluding from the biomization calculations any *Quercus* pollen not clearly identified as predominantly evergreen or summergreen. Finally, we used the biomization scheme of Peyron *et al.* (1998), while BIOME 6000 used the scheme from Prentice *et al.* (1996). The two schemes differ in that the former includes many herbaceous taxa while the latter does not and is therefore biased towards forest biomes. Thus, our results are more consistent with the relative distributions of drought-tolerant versus drought-intolerant biomes found for EPD data at 0 ka and 6 ka by other studies (Guiot *et al.*, 1996; Gachet *et al.*, 2003; Gritti *et al.*, 2004; Roberts *et al.*, 2004). However, the interpolated biome maps of Guiot *et al.* (1996), based on Prentice *et al.,* (1996), reconstructed TDF for mid-Holocene Sicily, where we reconstructed xerophytic biomes. This is probably because our reconstructions contain two recently collected Sicilian pollen records that did not exist when Guiot *et al.* (1996) was published.

As mentioned in the Results, one site in Turkey (Sögüt Gölü) appeared as TDF at 0 ka but not at 6 ka. At this site, high quantities of *Pinus* pollen (60% and 85%, respectively) co-occur with low quantities of pollen from temperate deciduous taxa (7% and 0.6%, respectively) at 0 ka. Due to a limitation of the Peyron *et al.* (1998) biomization scheme, such a scenario can yield a biome such as TDF when in fact the landscape would be better characterized as conifer woodland.

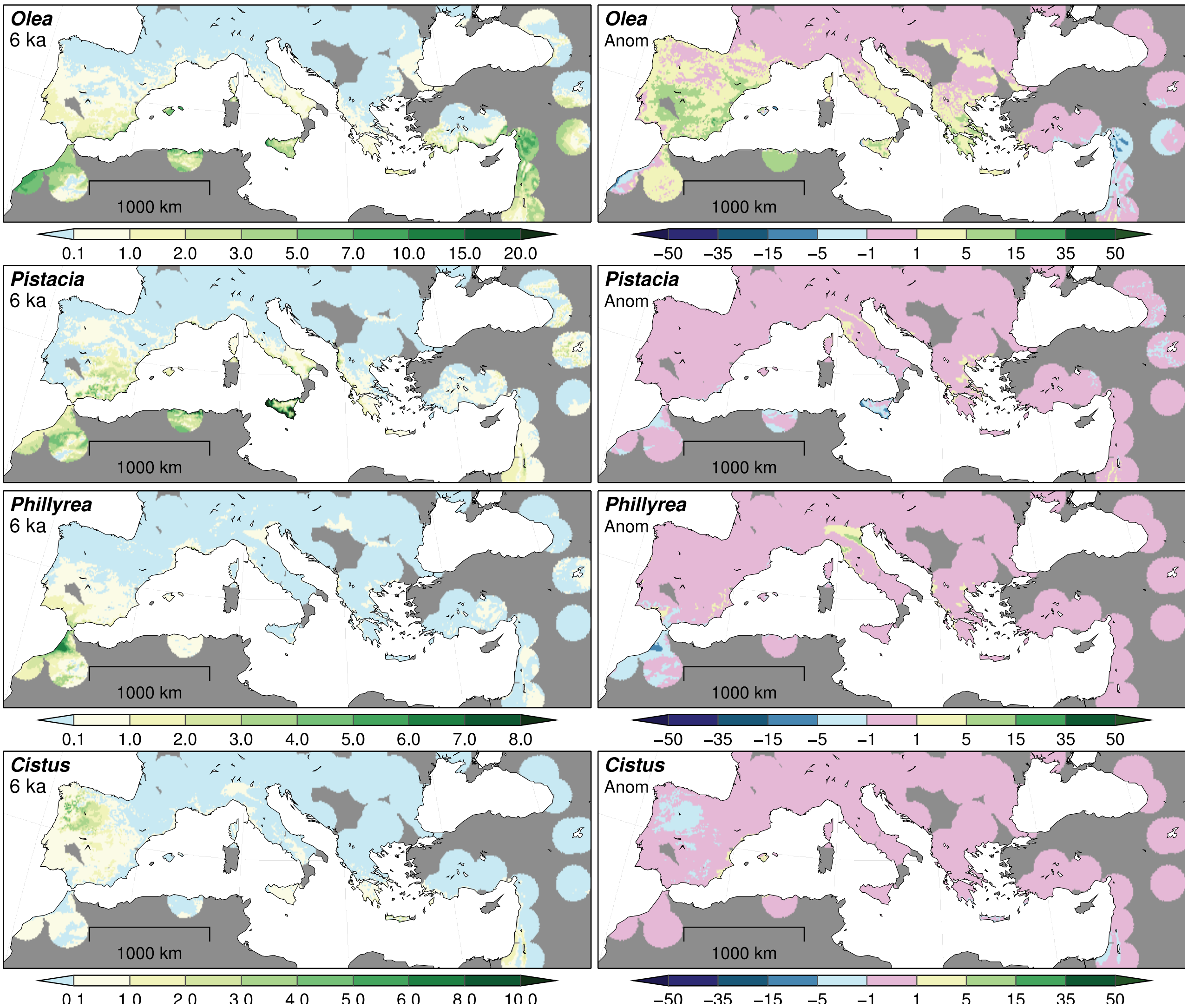

Figure 3.5c.

3.4.2
Arboreal pollen percentages

As mentioned in the Results, some Mediterranean areas show lower AP% at 6 ka compared with 0 ka. These differences are driven by the lower abundance of *Pinus* at 6 ka compared with 0 ka in these regions. However, the majority of the study area showed greater AP% at 6 ka when compared with present, with differences of up to 50% in lowland regions, suggesting that a major driver of differences in biomes between time slices could be deforestation.

The broad patterns of our results match the distribution of forest density observed for Western Europe at 5 ka (1000 years after our time slice) by Cheddadi & Bar-Hen (2009). Interestingly, the model predictions of tree cover simulated by Kleinen *et al*. (2011) for 8000 cal. yr BP (2000 years before our time slice) show almost a complete absence of forest cover in the Mediterranean region, although the authors observe that their model over-predicts forest cover. Model predictions of mid-Holocene (6 ka) vegetation cover carried out by Wohlfahrt *et al.* (2004) also show a predominance of open non-forest vegetation types in the central and northern parts of Spain, Italy and Greece. These discrepancies between model predictions and pollen-based reconstructions illustrate the difficulty of predicting vegetation patterns in the complex and heterogeneous Mediterranean region.

3.4.3
Taxon pollen percentages

3.4.3.1
Fagus and Abies

Our interpolation overestimates the present-day distribution of *Fagus* in Spain relative to our dataset and as reported by Giesecke *et al.* (2007) from the *Atlas Florae Europaeae* (Jalas & Suominen, 1972–99). This overestimation is an artefact of the interpolation methodology. However, our mid-Holocene reconstructed distributions broadly match those reconstructed from pollen data by Magri (2008) for 6000–5000 ^{14}C yr BP, Giesecke *et al.* (2007) for 5000 ^{14}C yr BP, and Pearman *et al.* (2008) for 6000 ^{14}C yr BP.

Giesecke *et al.* (2007) and Pearman *et al.* (2008) also modelled the mid-Holocene distribution of *Fagus*. The model used by Giesecke *et al.* (2007), STASH, used species-specific bioclimatic requirements and climate model output to predict the presence or absence of a given species. Pearman *et al.* (2008) used a model based on a machine learning technique called ‘gradient boosting’, where presence/absence probabilities were calculated based on existing pollen data and climate model output. The STASH model result overestimated the distribution of *Fagus* at the mid-Holocene (Giesecke *et al.*, 2007) relative to the pollen data presented in that paper, while the gradient boosting approach yielded distribution maps matching the pollen data presented by Pearman *et al.* (2008) fairly well. Our mid-Holocene reconstruction corresponds well to the modelled distribution of Pearman *et al.* (2008), while we also find the modelled mid-Holocene distribution observed by Giesecke *et al.* (2007) to be an overestimate.

Our mid-Holocene reconstruction for *Abies* is consistent with the distribution reconstructed by Terhürne-Berson *et al.* (2004) for 6000 ± 500 ^{14}C yr BP. The mid-Holocene distribution observed and modelled by Pearman *et al.* (2008) was restricted compared with our observations, due to a limitation in their methodology that excluded samples from southern Italy and the Balkan states.

3.4.3.2
Quercus

Quercus (Fig. 3.5a, Fig. 3.7 in Appendix 3.6.3) is a very diverse genus with species having a wide range of physiological requirements. Because *Quercus* pollen can be distinguished between evergreen and deciduous types, we were able to analyse these separately, which aids in the interpretation of the drivers of environmental change during the Holocene. Overall, we observed lower pollen abundance in both *Quercus* types at 0 ka compared with 6 ka. The spatial distribution of the negative anomalies (i.e. 0 ka abundance < 6 ka abundance) for both types of *Quercus* pollen closely matches the spatial distribution of the negative anomalies for AP% (Fig. 3.4c), which suggests that the difference in *Quercus* abundance between the two time slices is due to deforestation, rather than replacement by other tree species. We suspect this deforestation to be primarily anthropogenic in origin because we did not observe one type of *Quercus* expanding into the range of the other between the two time slices, as might have been expected had climate change been the primary driver of the negative anomalies.

3.4.3.3
Other conifers

Pinus (Fig. 3.5b, Fig. 3.7) pollen was widespread and abundant at both time slices, reflecting its ability to occupy a wide range of habitats within the Mediterranean region, while also producing a prodigious amount of pollen compared with many other taxa. Substantial reductions in *Pinus* pollen between 6 ka and 0 ka are seen in the Ebro basin and western Alps; both aridity and conversion to cropland were important in the former region (Davis, 1994), while plantation forestry in the latter favoured other tree species, e.g. *Picea abies*. In contrast, increases in *Pinus* pollen are visible in the eastern Mediterranean where forest cover actually expanded in areas of Turkey in the late Holocene either as a result of a more favourable climate or edaphic conditions (Roberts *et al*., 2004). It should be noted, however, that *Pinus* pollen percentages of 25–50% can still occur in the absence of local *Pinus* populations due to long-distance transport (Huntley & Birks, 1983), particularly when local vegetation is sparse or the site sampled was a very large water body.

Cedrus (Fig. 3.5b, Fig. 3.7) pollen is restricted to a relatively small area of the eastern Mediterranean at both time slices. This is probably due to the fact that *Cedrus* is closely associated with moist Mediterranean montane environments, which are found primarily in North Africa and the eastern Mediterranean (Cheddadi *et al.*, 1998). Conversely, the broad distribution of *Juniperus* (Fig. 3.5b, Fig. 3.7) at both time slices occurs because the genus is very diverse, with species ranging in form from trees to dwarf shrubs and in habitat from the Mediterranean to the Arctic (Huntley & Birks, 1983).

3.4.3.4
Other xerophytic sclerophyllous taxa

The xerophytic sclerophyllous taxa *Olea*, *Phillyrea*, *Pistacia* and *Cistus* have similar bioclimatic requirements and are grouped into the same plant functional type in our biome analysis. They are drought-tolerant and cold-intolerant; for example, *Olea* is restricted to climates where mean temperature of the coldest month is no lower than approximately 3°C (Walker, 1960). As their temperature tolerances are similar to the climate of the Mediterranean, the distribution of the xerophytic sclerophyllous taxa, especially *Olea*, have traditionally been used to define the boundaries of the Mediterranean region (e.g. Semple, 1931).

Therefore, it might be expected that distributions and relative abundances for all taxa should be similar for a given time slice. While this is true for 6 ka, at 0 ka *Olea* pollen is found in greater abundance and with a wider distribution compared with *Phillyrea*, *Pistacia* and *Cistus* (Fig. 3.5c, Fig. 3.7), which show little change between the time slices. Because *Olea* cultivars are of commercial/agricultural importance and have been widely planted across the Mediterranean at least since classical times, with particularly large increases in Spain over the past several hundred years, we do not interpret the increase in *Olea* pollen to be necessarily indicative of a change in Mediterranean climate; rather, the differences observed in *Olea* pollen distribution and abundance are more likely to be due to human activity (Davis, 1994).

As noted, *Pistacia*, *Phillyrea* and *Cistus* (Fig. 3.5c, Fig. 3.7) show small changes in pollen abundance and distribution between 0 ka and 6 ka. These taxa produce low to moderate levels of poorly dispersed pollen (Huntley & Birks, 1983; Fernández, 1994) and are not cultivated, with the exception of *Pistacia vera*. The low relative abundances of these taxa may make them appear under-represented in both distribution and abundance relative to more prolific and well-distributed *Olea* pollen from late Holocene monoculture olive groves, and therefore it may be difficult to use *Pistacia*, *Phillyrea* and *Cistus* as indicators of broader environmental change. Nevertheless, we interpret the continuity of the distribution of these taxa as providing further evidence, along with *Quercus*, of the general stability of the distribution of non-cultivated Mediterranean vegetation (if not its abundance) between 6 ka and 0 ka.

3.5
Conclusions

Mediterranean topography, climate and history are complex and heterogeneous, and individual pollen records are influenced by many factors. This makes it difficult to draw accurate conclusions about region-wide trends based on one or a few sites. Here we have presented a series of vegetation reconstructions based on terrestrial (arboreal and non-arboreal) pollen data from 275 sites in southern Europe and the Mediterranean region for the mid-Holocene (6000 ± 500 cal. yr BP) and the present (0 +60/-500 cal. yr BP), with comparisons between the two time periods.

These reconstructions used a greater number of sites, with better spatial coverage and better-documented dating control than has previously been available. This allows us to offer a new and more detailed way of addressing the very old question of how, or whether, the past vegetation of southern Europe (particularly the Mediterranean region) differed from present-day conditions. It should be noted that the differences between our 0 ka and 6 ka vegetation reconstructions say nothing about the trajectory of change between the two time slices, which has been shown at individual sites to have been strongly nonlinear (Finsinger *et al.*, 2010).

Our results show that, contrary to the findings of the BIOME 6000 project (Fig. 3.2), xerophytic vegetation was widespread in southern Europe at the mid-Holocene (Fig. 3.3), even under conditions of what is thought to be low to negligible human impact. Thus, we do not find support for the hypothesis that the mid-Holocene Mediterranean region was dominated by temperate deciduous forests that have since been ‘ruined’ by human activities.

Nevertheless, the northern temperate deciduous biomes did extend somewhat further south into the Mediterranean region during the mid-Holocene than they do at present (Fig. 3.3). Mid-Holocene forest cover was generally denser and more extensive, but some areas of Spain and Turkey had lighter cover at 6 ka compared with the present (Fig. 3.4). *Abies,* deciduous and evergreen *Quercus*, and *Cedrus* were more abundant within their ranges than they are at present. *Fagus*, *Olea* and *Juniperus* had smaller ranges and were less abundant. Distribution and abundance of *Pistacia*, *Phillyrea* and *Cistus* were slightly lower than at present. The cosmopolitan *Pinus* (Fig. 3.5b, Fig. 3.7) showed very fragmented patterns of distribution and abundance due to anthropogenic deforestation in some areas and afforestation from natural post-disturbance colonization as well as human-mediated plantation in others. Overall, our results suggest that the differences in vegetation cover and taxonomic composition observed between 6 ka and 0 ka were probably influenced by both late Holocene climate change and anthropogenic activity, but that they were not as extreme in magnitude as has previously been suggested.

Thus, this study calls into question the general perception, based largely on the results of BIOME 6000 (Fig. 3.3), that southern Europe was covered by substantial areas of temperate deciduous forest at the mid-Holocene. This perception of change is evident in interpretations of palaeoecological data (Prentice *et al.*, 1996; de Beaulieu *et al.*, 2005) and in the choice of boundary conditions for regional climate modelling studies (Reale & Shukla, 2000; Gates & Liess, 2001; Dermody *et al.*, 2011). In contrast, our results reinforce the idea that changes in biomes between the mid-Holocene and the present in many parts of the Mediterranean were more subtle. Our study, with new data and high quality control, makes a strong case against this unrealistic view of a mesic Mediterranean and provides a useful, reliable, and much needed baseline (Masson *et al.*, 1999) for future modelling studies.

Future work to synthesize the palaeoecological record should concentrate on extending the biome, AP%, and taxon reconstructions to provide continuous coverage of the entire Holocene. Only a transient analysis of the palaeoecological record covering a large spatial domain, i.e. a domain relevant for the development of mesoscale climate, will provide us with enough information to draw conclusions on the mechanisms of Holocene land cover change in the Mediterranean. Expansion of modern pollen datasets will facilitate more comprehensive present–past comparisons

(B.A.S. Davis *et al.,* in prep.). A comparative analysis of the performance of various biomization methods should also be carried out to assess the consequences of choosing one scheme over another.

Finally, it would be useful to develop continental-scale relationships between forest cover as observed with satellite imagery and modern AP% derived from surface sample and core top pollen data. This would allow continental-scale reconstructions of palaeovegetation structure and would complement the regional-scale LOVE/REVEALS methodology of the LandClim Project, which requires pollen productivity estimates (Gaillard *et al.*, 2010). Our reconstructions will be available in graphical and data form from the corresponding author in the hope that the results of this study will be useful as visual qualitative benchmarking tools for the earth system modelling community.

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3.6
Appendices

Appendix 3.6.1. Table of sites used in this analysis, with coordinate and reference information.

Table 3.1. Details for all sites used in this analysis, with coordinate and reference information (full reference list in Appendix 3.6.2). D, digitized; R, raw; c, coretop; ss, surface sample.

Long.	Lat.	Elev. (m)	Site name	Type	Reference	6K Top	6K Bottom	0k	Notes:
34.81	30.61	773	Atzmaut	D	Babenko et al., 2007	3780±120	4837±97	c	zoogenic deposit
4.07	43.62	3	Augery	D	Triat-Laval, 1978	5350±150	6450±100	c	
2.80	43.55	1000	Baissescure	D	de Beaulieu, 1978	6000±150	see paper	c	
17.65	43.03	10	Bajovci	D	Brande, 1973	TOP 0	6915±350	c	
4.71	43.69	1	Barbegal II	D	Triat-Laval, 1978	5160±230	6860±340	c	
-4.97	40.67	1180	Baterna	D	Ruiz-Zapata et al., 1996	TOP 0	5830±100	c	
22.69	46.64	1400	Bergerie	D	Bodnariuc et al., 2002	5665±120	6680±80	c	
-0.08	43.03	409	Biscaye	D	Reille & Andrieu, 1995	5950±55	7215±70	c	EPD #765, restricted
26.70	45.55	890	Bisoca	D	Tantau et al., 2009	5120±50	7760±50	c	
15.23	44.18	25	Bokanjacko Blato	D	Gruger, 1996	TOP 0	3755±120	c	
5.38	43.50	0	Borely	D	Triat-Laval, 1978	3775±400	6380±595	c	
-3.92	39.02	600	Castillo de Caltrava	D	García et al., 1986	1730±80	6240±190	c	
4.87	44.09	32	Courthezon	D	Triat-Laval, 1978	4250±250	7350±170	c	
5.07	43.52	0	Etang de Berre III	D	Laval & Médus, 1989	4250±139	5635±165	c	
9.55	42.15	1	Etang del Sale	D	Reille, 1988	5650±190	5920±190	c	
4.93	43.45	0	Fos	D	Triat-Laval, 1978	TOP 0	5600±150	c	
1.44	42.80	1350	Freychinede	D	Jalut et al., 1982	5140±110	6420±130	c	
14.41	45.73	550	Gorenje Jezero	D	Andric & Willis, 2003	2670±40	8710±40	c	
12.66	37.61	6	Gorgo Basso	D	Tinner et al., 2009	4470±80	6440±40	c	
2.22	42.63	2080	Gourg Nègre	D	Reille & Lowe, 1993	4490±210	7050±210	c	
-0.37	42.72	1682	Ibon de Tramacastilla	D	Montserrat-Marti, 1992	4210±40	9900±80	c	
41.80	41.87	2	Ispani 2	D	Klerk et al., 2009	970±200	4065±39	c	
4.97	36.60	1230	La Chataigneraic	D	Salamani, 1991	6340±70	7960±150	c	
-0.47	43.47	40	La Moura	D	Oldfield, 1964; Reille, 1993	5865±170	6295±130	c	

8.95	42.20	1280	Lac de Creno 8	D	Reille et al., 1999	5410±80	6285±150	c	
9.35	45.80	226	Lago Annone	D	Wick & Mohl, 2006	see paper	see paper	c	^{14}C dates in Wick, in prep.
16.13	41.91	10	Lago Battaglia	D	Caroli & Caldara, 2007	2584±25	5590±50	c	
11.54	45.47	23	Lago Fimon	D	Valsecchi et al., 2008	4840±40	5860±35	c	
8.93	46.00	337	Lago Muzzano	D	Gobet et al., 2000	4600±60	5960±60	c	
14.31	37.52	667	Lago Pergusa	D	Sadori & Narcisi, 2001	4400±105	7475±65	c	
10.82	44.18	1307	Lago Pratigano	D	Watson, 1996	5780±40	8715±40	c	
9.27	45.83	374	Lago Segrino	D	Gobet et al., 2000	5730±45	6630±70	c	
-8.77	38.30	3	Lagoa Travessa I	D	Mateus, 1992	4910±50	6560±70	c	EPD #926, restricted
-7.28	42.25	1340	Laguna de las Lamas	D	Maldonado-Ruiz, 1994	5620±100	7770±100	c	
-2.88	41.91	1820	Laguna del Hornillo	D	Gomez-Lobo, 1993	5020±80	6150±90	c	
23.46	42.13	2320	Lake Ostrezko	D	Tonkov & Marinova, 2005	3510±40	4830±40	c	
0.78	42.64	2240	Lake Redon	D	Pla & Catalan, 2005	see paper	see paper	c	
23.32	42.20	2216	Lake Trilistnika	D	Tonkov et al., 2008	4560±45	6835±50	c	
2.44	42.16	440	Las Palanques (Olot)	D	Pérez-Obiol, 1988	2230±95	7340±80	c	
-2.97	42.03	1850	Las Pardillas	D	Sanchez-Goñi & Hannon, 1999	3220±45	6460±45	c	
8.66	42.42	10	Le Fango	D	Reille, 1988	4450±140	5630±190	c	EPD #889, restricted
-0.02	43.05	394	Le Monge	D	Reille & Andrieu, 1995	5810±55	6760±45	c	EPD #838, restricted
5.20	43.40	0	Le Vallet Neuf	D	Triat-Laval, 1978	TOP 0	7340±270	c	
-0.08	43.03	430	Lourdes	D	Reille & Andrieu, 1995	2110±50	6470±45	c	EPD #834, restricted
4.09	43.63	2	Meyranne	D	Triat-Laval, 1978	5010±430	8010±605	c	
15.21	45.50	140	Mlaka	D	Andric & Willis, 2003	3480±40	7350±40	c	
-7.51	43.59	605	Montes del Buyo	D	Van Mourik, 1986	4740±40	7725±50	c	
23.43	41.68	1800	Mozgovitsa	D	Tonkov, 2003	5700±80	8040±100	c	
16.01	46.63	240	Noricka Graba	D	Andric & Willis, 2003	1420±30	10730±40	c	
-3.68	36.95	785	Padul	D	Pons & Reille, 1986	5980±70	6340±70	ss	ss: Davis et al. 2003
3.90	43.57	1	Palavas	D	Planchais, 1987	5440±100	6180±70	ss	ss: Davis et al. 2003
1.97	42.87	880	Pinet 2	D	Reille & Lowe, 1993	5260±140	7170±120	c	
-7.11	42.71	1330	Pozo do Carballal	D	Muñoz-Sobrino et al., 1997	5320±60	10360±210	c	
14.08	45.42	480	Prapoce	D	Andric & Willis, 2003	5250±60	8360±40	c	
-8.08	41.97	900	Riba Lama de Mira	D	Ruiz-Zapata et al., 1996	5845±105	see paper	c	
9.20	42.72	15	Saleccia	D	Reille, 1988	5160±100	5690±100	c	EPD #861, restricted

-5.00	33.05	2080	Sidi Ali	D	Lamb et al., 1999	CAV 3703	CAV 5120	c	
-6.50	34.42	25	Sidi Bou Rhaba	D	Reille, 1979	TOP 0	6520±110	c	
42.08	38.65	1500	Sogutlu	D	Bottema, 1995	2810±60	7135±180	c	
24.12	35.58	0	Tersana	D	Moody et al., 1996	2110±130	5800±100	c	
-5.35	32.90	1626	Tigalmamine	D	Lamb & van der Kaars, 1995	4415±100	6865±140	c	
17.50	43.08	4	Vid I	D	Brande, 1973	1785±200	7145±175	c	
35.49	30.63	360	Wadi Dana	D	Hunt et al., 2007	5700	6400	c	^{14}C dates; ± not in paper
35.67	33.25	940	Birket Ram	R	Neumann et al., 2007	4140+35	5440+35	c	
29.60	37.13	930	Gölhisar Gölü II	R	Eastwood et al., 1999	4900±75	6305±50	c	
10.89	42.99	157	Lago dell'Accesa 1	R	Drescher-Schneider et al., 2007	4130±50	5565±35	ss	
-6.83	37.15	3	Laguna de las Madres II	R	Stevenson & Harrison, 1992	2580±80	3590±90	c	
-6.10	36.85	60	Laguna Tollos	R	Davis, unpublished data	4785±290	10050±50	c	
-9.05	32.75	1	Lagune de Oualidia	R	Ballouche (PhD Thesis)	TOP 0	6420±190	ss	ss: Ballouche (PhD Thesis)
22.73	37.58	0	Lake Lerna	R	Jahns, 1993	5880±435	6875±175	c	
20.77	40.94	693	Lake Ohrid 2	R	Wagner et al., 2009	4490±35	6145±35	c	
20.83	38.87	0	Lake Voulkaria	R	Jahns, 2005 (PANGAEA)	4415±53	6146±66	c	
-0.89	38.50	470	Las Salinas	R	Davis, unpublished data	2830±60	7400±60	c	
17.35	42.78	0	Malo Jezero	R	Jahns & van den Bogaard, 1998	4370±45	5300±50	c	dates from Jahns, 2002
20.48	39.97	1800	Rezina Marsh	R	Willis, 1992	4440±150	6320±130	c	
7.54	46.65	989	Aegelsee	R	EPD #980	4130±80	7540±50	c	
3.12	39.79	0	Albufera d'Alcudia	R	EPD #891	2440±60	6270±70	c	
8.01	46.23	2017	Aletschwald	R	EPD #1056	3800±80	8010±110	c	
8.01	46.23	2017	Aletschwald 2	R	EPD #1058	POL 5000 Cal	POL 6200 Cal	c	
7.59	46.23	2330	Alp Lüsga Belalp 1	R	EPD #1064	1920±90	4240±80	c	
7.58	46.23	2290	Alp Lüsga Belalp 2	R	EPD #1065	6130±110	3240±100	c	
8.52	46.44	1892	Alpi di Robièi 316, Val Bavona	R	EPD #1148	1480±100	4920±90	c	
-1.55	43.25	500	Atxuri	R	EPD #80	1920±80	2710±60	c	
24.38	45.72	400	Avrig	R	EPD #18	5120±50	13880±90	c	
8.01	46.40	2265	Bachalpsee	R	EPD #1061	2955±80	7505±75	c	
23.67	41.75	2240	Besbog 2	R	EPD #113	3730±80/2740±80	8420±160	c	
31.50	37.54	1120	Beysehir Gölü I	R	EPD #114	6090±75	n/a	c	
7.59	46.20	1030	Bitsch-Naters	R	EPD #1068	4170±120	7420±160	c	

7.58	46.21	1970	Bodmen 2, Alp Bel	R	EPD #1070	POL 5000 Cal	POL 6000 Cal	c
7.58	46.21	1970	Bodmen 3, Alp Bel	R	EPD #1071	POL 4000 Cal	POL 5000 Cal	c
7.84	46.26	2061	Boehnigsee Goldmoos	R	EPD #133	4740±100	10430±150	c
41.18	35.23	200	Bouara	R	EPD #136	TOP 0	5730±120	c
11.30	47.06	2285	Buntes Moor	R	EPD #1200	3150±120	3150±120	c
-7.58	40.34	1409	Charco da Candieira	R	EPD #894	5730±100	6185±35	c
12.93	43.03	752	Colfiorito	R	EPD #179	4120±50	8900±70	c
11.00	47.10	1880	Dortmunder Hütte	R	EPD #1179	4170±100	8300±130	c
23.53	42.05	1900	Dry Lake II (Rila Mountain)	R	EPD #635	5680±75	10575±120	c
11.46	46.64	2080	Dura-Moor	R	EPD #1195	2050±70	10020±190	c
8.98	47.78	432	Durchenbergried	R	EPD #1025	5100±55	13075±135	c
13.87	47.17	1700	Dürrenecksee-Moor	R	EPD #208	4840±75	8760±160	c
21.95	40.82	350	Edessa	R	EPD #19	5260±65	6385±55	c
3.00	43.27	6	Etang d'Ouveillan	R	EPD #737	4310±85	8870±190	c
7.48	46.31	1500	Etang d'y Cor, Montana	R	EPD #1169	4436±41	8980±60	c
8.92	47.75	407	Feuenried	R	EPD #1026	5250±30	13220±85	c
11.88	47.35	2115	Franz Senn-Hütte	R	EPD #1198	3000±200	9630±95	c
13.90	47.12	1680	Fuchsschwanzmoos	R	EPD #242	1555±60	9520±105	c
13.27	47.78	663	Fuschlsee	R	EPD #1259	4381±42	5430±70	c
9.23	47.10	1320	Gamperfin	R	EPD #1089	4570±100	9800±125	c
12.14	47.24	1590	Gerlos	R	EPD #1213	2240±110	12290±110	c
12.36	47.47	820	Giering	R	EPD #1189	5085±465	13130±190	c
8.06	46.12	1635	Gondo Alpjen	R	EPD #1092	3740±120	4670±130	c
7.50	46.12	1710	Grächen See	R	EPD #1095	5010±80	7520±90	c
7.50	46.12	1710	Grächen See 51	R	EPD #1094	4490±100	4950±100	c
13.90	47.17	1750	Grosses Überling Schattseitmoor	R	EPD #669	3565±75	12900±300	c
11.45	47.03	2190	Grünau Moor	R	EPD #1199	POL 5732 Cal	7350±130	c
5.28	45.79	410	Hières sur Amby 86	R	EPD #59	5800±130	10110±240	c
8.01	46.15	2017	Hopschensee	R	EPD #1122	5040±150	12580±200	c
4.13	39.88	40	Hort Timoner	R	EPD #284	POL 4954	POL 8000	c
30.88	38.28	920	Hoyran Gölü	R	EPD #949	TOP 0	2470±50	c
10.12	46.39	1805	Il Fuorn	R	EPD #1106	9635±95	4100±100	c

30.80	38.43	1000	Karamik Batakligi	R	EPD #319	TOP 0	6520±70	c	
21.58	40.62	560	Khimaditis Ib	R	EPD #329	3995±60	7110±70	c	
28.64	36.88	20	Köycegiz Gölü	R	EPD #343	465±30	3070±55	c	
24.33	41.98	1300	Kupena 1	R	EPD #352	TOP 0	9000±40	c	
7.09	46.18	2135	Lac Superieur de Fully	R	EPD #1284	4600±55	5320±40	c	
7.76	45.68	820	Lac de Villa	R	EPD #930	1635±60	12720±130	c	
6.87	45.69	2276	Lac du Verney-Dessus	R	EPD #1250	4295±35	12810±70	c	
6.34	44.42	1308	Lac Saint Léger	R	EPD #594	TOP 0	8400±220	c	
7.13	44.23	2240	Laghi dell'Orgials	R	EPD #1041	4670±35	20930±130	c	
-6.15	43.05	1570	Lago de Ajo	R	EPD #33	4113	6963	c	Corr. from 6800±90, 9650±120
12.33	42.12	204	Lago di Martignano	R	EPD #434	3060±220	8180-7260	c	see paper for 6K bottom date
15.60	40.94	1326	Lago Grande di Monticchio 82	R	EPD #453	POL 4921	POL 8105	c	
10.21	44.30	1187	Lago Padule	R	EPD #504	5620±55	7940±50	c	
-7.64	40.36	1650	Lagoa Comprida 2	R	EPD #820	4340±90	8385±50	c	
-6.77	42.22	1608	Laguna de la Roya	R	EPD #366	5230±50	10290±60	c	
-0.17	41.23	150	Laguna Salada Chiprana	R	EPD #919	3410±150	5725±60	c	
2.01	42.55	2000	Lake Racou	R	EPD #1038	5060±45	7360±70	c	
43.00	38.50	1645	Lake Van	R	EPD #677	POL 4450	POL 7350	c	
27.83	43.20	0	Lake Varna (Arsenala)	R	EPD #76	5390±65	7495±95	c	
7.00	47.02	432	Le Loclat	R	EPD #1216	5130±70	8095±80	c	
-1.01	45.40	2	Le Marais de la Perge	R	EPD #609	TOP 0	6700±70	c	
-1.12	45.38	2	Le Marais de la Perge (South)	R	EPD #610	4400±60	6053±172	c	
40.69	43.73	2428	Luganskoe	R	EPD #404	3489±153	4200±80	c	
23.03	41.70	1720	Maleshevska Mtns Peat Bog	R	EPD #427	3205±185	6055±420	c	
11.46	46.67	2050	Malschötscher Hotter	R	EPD #1196	5050±75	8670±130	c	
10.98	47.29	800	Mieminger See	R	EPD #1180	1190±80	4430±90	c	
7.50	46.17	1520	Mittlere Hellelen	R	EPD #1102	4050±50	8470±60	c	
25.92	46.08	1050	Mohos 1	R	EPD #35	5070±220	9750±200	c	
25.92	46.08	1050	Mohos 2	R	EPD #36	4550±100	8740±160	c	
1.65	45.85	720	Moulin de Prugnolas	R	EPD #531	4510±140	5000±130	c	
8.83	47.62	434	Nussbaumer Seen 1	R	EPD #1030	POL 6100 Cal	POL 7000 Cal	c	
8.83	47.62	434	Nussbaumer Seen 4	R	EPD #1031	5230±60	13100±90	c	

8.83	47.62	434	Nussbaumer Seen 8	R	EPD #1032	POL 5300 Cal	POL 6200 Cal	c	
8.15	46.33	2315	Oberaar	R	EPD #1138	4880±80	5100±130	c	
6.18	44.52	975	Pelléautier	R	EPD #513	660±210	4640±190	c	
-1.89	47.02	2	Pierre Folle	R	EPD #963	2520±100	5530±180	c	
6.59	44.96	1850	Plaine Alpe	R	EPD #738	8870±190	4240±50	c	
-8.81	38.07	2	Poço de Barbaroxa de Cima	R	EPD #902	5430±100	6910±60	c	restricted; p.f.a: Queiroz
6.17	46.57	1040	Praz Rodet	R	EPD #1149	5210±60	9780±60	c	
6.59	44.92	1800	Pré Rond	R	EPD #739	3695±50	7660±65	c	
23.54	47.82	730	Preluca Tiganului	R	EPD #1257	4990±40	5760±35	c	
-3.43	43.15	920	Puerto de Los Tornos	R	EPD #660	4620±70	7830±90	c	
41.17	43.67	2726	Quartzevoe	R	EPD #537	5780±120	4370±175	c	
11.49	46.64	1780	Rinderplatz	R	EPD #1194	1495±150	11790±170	c	
11.03	46.84	2260	Rotmoos Obergurgl	R	EPD #1202	4680±100	5170±100	c	
7.84	46.79	1190	Rotmoos-Eriz	R	EPD #1153	POL 5000 Cal	POL 6000 Cal	c	
8.33	47.08	419	Rotsee 170	R	EPD #1145	INT 5732	INT 6295	c	
8.33	47.08	419	Rotsee 240	R	EPD #553	3900±90	7140±100	c	
8.33	47.08	419	Rotsee 250	R	EPD #554	4820±60	10740±130	c	
7.98	46.68	1935	Sägistalsee	R	EPD #1155	4265±75	8005±90	c	
5.63	45.43	650	Saint Sixte	R	EPD #592	4570±230	5600±150	c	
-2.72	43.05	625	Saldropo	R	EPD #572	3590±90	5630±70	c	
-6.73	42.10	1050	Sanabria Marsh	R	EPD #44	TOP 0	8200±90	c	
11.43	46.67	2033	Schwarzsee	R	EPD #1197	1550±75	9370±150	c	
7.28	46.67	1046	Schwarzsee FR	R	EPD #1159	POL 5900 Cal	POL 6000 Cal	c	
12.30	47.65	664	Schwemm A3	R	EPD #741	3790±100	9360±140	c	
12.30	47.65	664	Schwemm B1	R	EPD #742	3740±100	4380±100	c	
12.30	47.65	664	Schwemm B5	R	EPD #743	5240±90	10370±80	c	
12.30	47.65	664	Schwemm D3	R	EPD #978	4650±100	10780±230	c	
11.19	47.32	1200	Seefelder See	R	EPD #1184	POL 5732 Cal	POL 8841 Cal	c	
29.90	37.00	1400	Sögüt Gölü	R	EPD #611	2885±35	9180±95	c	
11.68	46.76	870	Sommersüss	R	EPD #1193	3585±60	12700±200	c	
8.20	47.80	1000	Steerenmoos	R	EPD #1028	5198±59	7593±62	c	
23.54	47.81	790	Steregoiu	R	EPD #1258	3680±70	6425±75	c	

7.40	46.73	1520	Süfternen-Grönegg	R	EPD #1165		POL 2000 Cal	POL 4000 Cal	c
6.86	45.70	2415	Torveraz	R	EPD #1253		5060±40	9090±50	c
7.81	45.82	2320	Tourbière de Champlong	R	EPD #905		TOP 0	9030±95	c
2.79	43.58	970	Tourbière de Gatimort	R	EPD #1266		1470±30	5700±40	c
2.97	43.57	1040	Tourbière de la Lande	R	EPD #1267		2405±45	4160±40	c
7.65	45.86	2304	Tourbière de Santa Anna	R	EPD #982		2900±75	9170±215	c
3.60	44.45	1370	Tourbière du Peschio	R	EPD #1273		3030±50	4405±50	c
13.07	47.93	500	Trumer Moos	R	EPD #663		10740±130	2730±80	c
7.73	46.82	980	Wachseldorn Untermoos	R	EPD #1176		5096±45	12915±130	c
7.40	46.43	1885	Wallbach, Lenk	R	EPD #1170		4380±120	11100±50	c
13.10	47.98	505	Wasenmoos beim Zellhof	R	EPD #713		POL 2730	8590±130	c
11.50	47.02	1875	Waxeckalm	R	EPD #1178		3450±90	3600±210	c
11.03	46.86	2150	Zirbenwaldmoor	R	EPD #715		2120±80	8600±150	c
19.99	46.36	92	Zsombo Swamp	R	EPD #717		537±64	9029±98	c

Definitions: "EPD #" = entity # in European Pollen Database; "zoogenic" = created by animals (e.g. dung, bones);
"^{14}C date" = uncalibrated radiocarbon date; "TOP" = "coretop"; "CAV" = average of radiocarbon dates;
"TOP" = top of core; "POL" = date derived from stratigraphic correlation against another pollen core;
"restricted" = permission required to use data; "p.f.a.:" = permission from author

Appendix 3.6.2. List of complete references cited in Appendix 3.6.1.

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Appendix 3.6.3. Maps of topography and site distribution (Fig. 3.6), and 0 ka vegetation cover reconstructed from pollen data (Fig. 3.7).

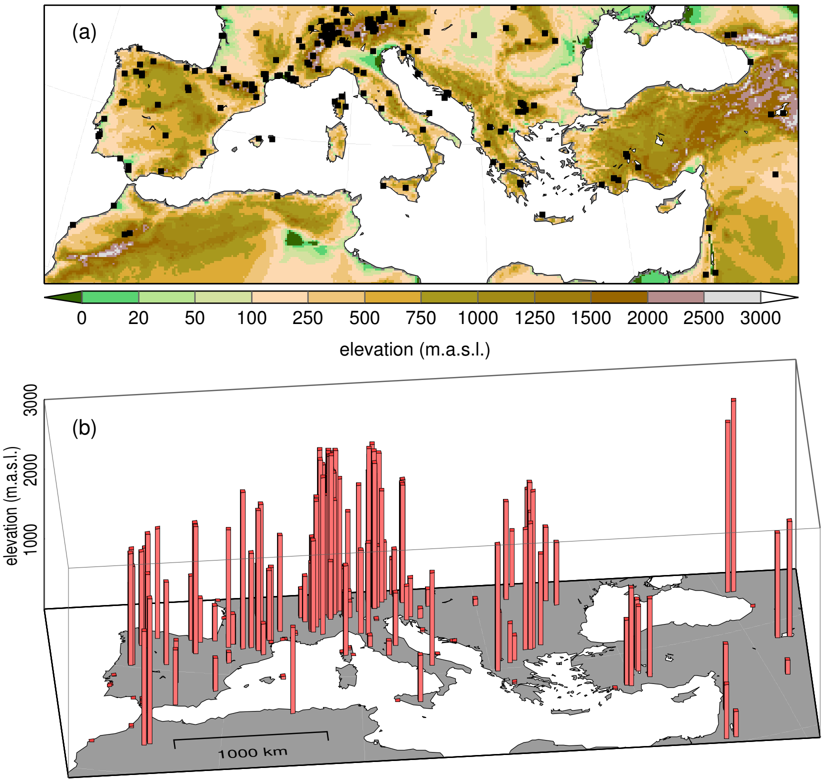

Figure 3.6. Present-day topography of southern Europe with black squares showing sites of pollen records analysed in this paper (a), and red columns showing elevational distribution of sites (b). All maps in this paper use a Lambert Azimuthal Equal-Area projection centred on 15 °E, 40 °N.

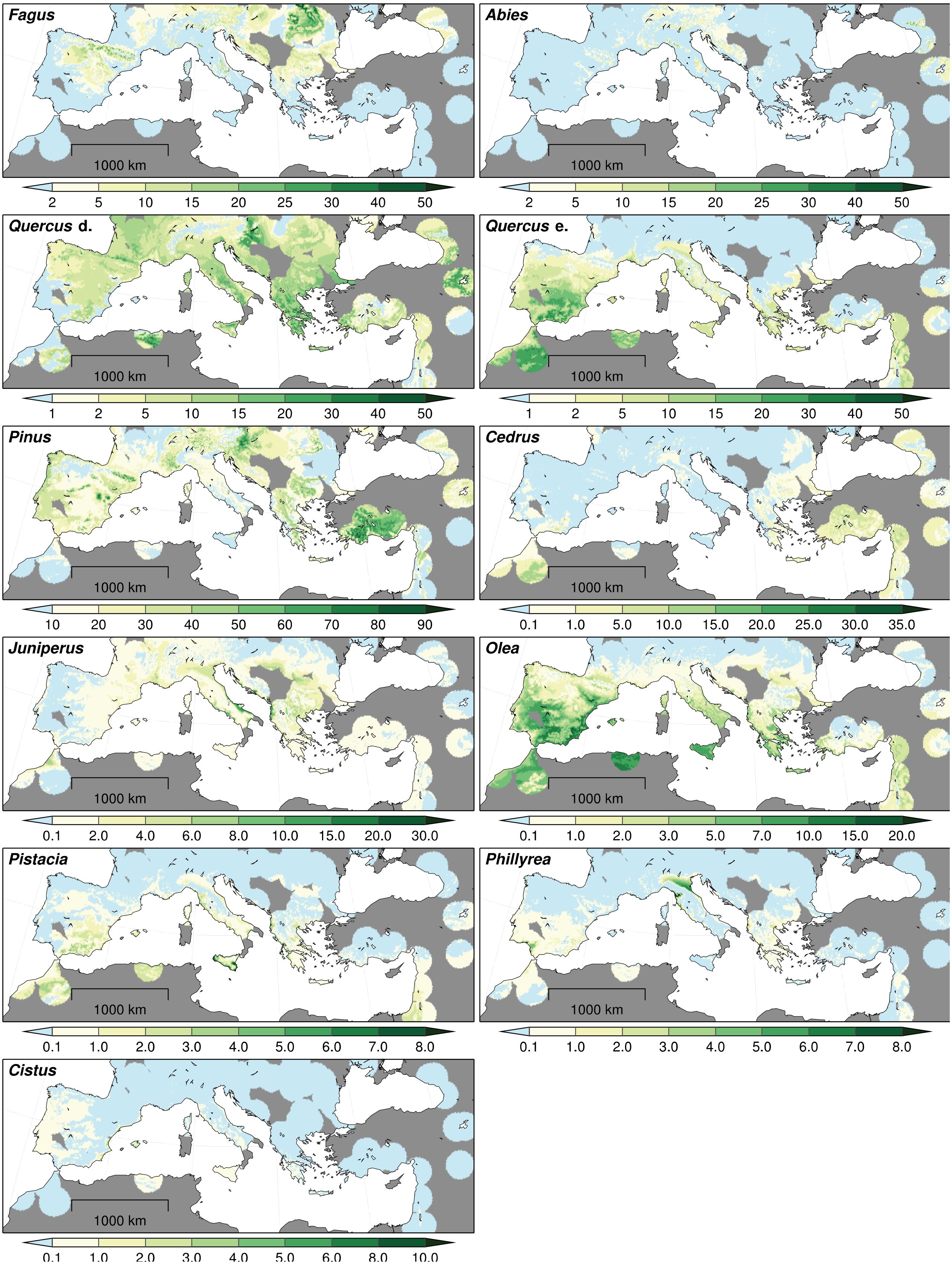

Figure 3.7. Distribution and abundance of individual taxa, calculated as percentage of total terrestrial sum (excluding aquatic and marsh taxa) for 0 ka. Points represent pollen data from individual sites. For *Quercus*, 'd' denotes 'deciduous' and 'e' denotes 'evergreen'. Interpolation as in Figs. 3.4-3.5.

4 The age and post-glacial development of the modern European vegetation: A plant functional approach based on pollen data

Collins, P.M., Davis, B.A.S. & Kaplan, J.O. The post-glacial development of the modern European vegetation: A plant functional approach based on pollen data. Manuscript in preparation for submission to *Global Ecology and Biogeography*.

Abstract. Using pollen data, we quantitatively assess the age of the modern vegetated landscape of Europe and reconstruct Holocene dynamics in biomes and landscape openness. We find that much of the European landscape is 6,000 years old or younger, though much of lowland Europe dates to 2,000 cal yr BP, while some areas have remained unchanged throughout the Holocene. While the plant functional type (PFT) assemblage became continuously more similar to present, biome assemblages changed in different ways in northern vs. southern Europe and stayed relatively constant in central Europe. Landscape openness as approximated by arboreal PFT % increased until the mid-Holocene and then returned to early-Holocene conditions by modern times. The continued dominance of forest biomes through the Holocene suggesting climate favourable to forest cover, in conjunction with the increase in landscape openness between the mid-Holocene and the present, suggests that human activity has significantly shaped European vegetation dynamics since the mid-Holocene. Thus, human activity may have to be included in future conceptions of "natural" European vegetation dynamics.

4.1
Introduction

Human activity has been an integral part of European landscape processes for millennia (Ellenberg 1988; Thirgood 1981; Behre 1988). Thus, the question "what is natural?", often asked in the contexts of vegetation biogeography and conservation science, becomes problematic (Carrión & Fernandez, 2009; Carrión 2010; Farris et al. 2010; Loidi et al. 2010). Are human-influenced landscapes "natural?". Or can landscapes only be "natural" when completely free from human disturbance? Does "completely free from human disturbance" only mean "free from agriculture and pasturing"? Or does it also mean "free from hunter-gatherers setting fires and decimating megafaunal populations"? If the latter, then the European landscape has not been "natural" since behaviorally modern humans arrived 40,000 years ago (cite), at which point the full-glacial climate was radically different from today's mild interglacial (Holocene) conditions. If human activity and climate together have shaped the Holocene vegetation of Europe (e.g. Ruddiman 2003; Bradshaw 2004; deBeaulieu et al. 2005), then the question "what is natural?" appears to lose meaning.

Nevertheless, the size of the human population of Europe, and the magnitude of the human impact on the landscape, have increased exponentially between the beginning of the Holocene and modern times (defined as 1750 AD to the present day) so it is safe to assume that the landscape of the early Holocene experienced much less human impact than did the landscape of the recent Holocene. Rather than asking the question "what is natural?", then, perhaps it is more meaningful to ask "how old is the modern European landscape?". This paper addresses the following questions:

How far back in time must one look for the landscape to appear quantitatively different from modern conditions? When and where did changes occur? Has the trajectory of change been continuous or sporadic? How much change has occurred over time? Is it possible to distinguish between anthropogenic and climatic drivers of vegetation change at continental spatial and millennial temporal scales?

Our study should be of interest to the conservation community, as it contributes to the knowledge of the age and stability (or dynamism) of the protected and non-protected landscapes of Europe (e.g. Froyd and Willis 2008). In the modern era of accelerating anthropogenic landscape- and climate change, knowing how the vegetated landscape of Europe has responded to climate dynamics and human impact in the past is crucial to understanding both how the modern landscape developed and how it might change in the future (Willis and Birks 2006; Hannah et al. 2002, 2007). In addition, the quantitative, data-based, spatially- and temporally-explicit and continuous reconstructions of the vegetation of the whole of Europe for the entire Holocene presented here have never before been attempted, and it is hoped that they will prove of use as benchmarking material for the earth system modeling community. Finally, this study is innovative because it blurs the lines between modern ecology and quaternary science, and between small-scale vegetation ecology and continental-scale biogeography; both of these syntheses have been identified as research priorities for the future development of ecology as a discipline (Beck, et al. 2012; Rull 2012).

The current study contributes to the already vast body of literature on the Holocene vegetation history of the northern hemisphere. Such work includes interpolated maps of broad-scale European vegetation characteristics reconstructed from pollen data, e.g. forest cover (Cheddadi and Bar-Hen 2009) or biomes (Huntley 1990, Guiot et al. 1996), for some or all of the Holocene. Other studies map pollen-based European vegetation reconstructions on a point basis, e.g. biomes (Guiot et al. 1996, Prentice et al. 1996, Prentice et al. 2000, Gachet et al. 2003, Collins et al. 2012), more generalized vegetation assemblages (Huntley 1990b), or plant traits (Gritti et al. 2004) for some or all of the Holocene. Still others focus on mapping individual plant taxa across Europe throughout the Holocene (e.g. Huntley and Birks 1983, Giesecke et al. 2007, Pearman et al. 2008). Pollen-based Holocene vegetation reconstructions at the regional scale abound (e.g. Odgaard and Rasmussen 2000, Andric and Willis 2003, Jalut et al. 2009, Collins et al. 2012), and those at the site scale are too numerous to discuss here.

Alternatives to pollen-based vegetation mapping include modeling European biome distributions for the mid-Holocene (Gallimore et al. 2005) or the pre-industrial present (Prentice et al. 2011), comparing pollen-reconstructed to modeled vegetation (Prentice et al. 1998, Brewer et al. 2009), or assessing the synchronicity of change between Europe and North America (Gajewski et al. 2006). Beyond Europe, a comprehensive assessment of the Holocene vegetation history of eastern North America has been performed based on pollen data, including interpolated maps of taxa, taxon groups, biomes, analyses of difference from present, climate reconstructions, and comparison to vegetation reconstructions based on climate model output (Overpeck et al. 1992, Overpeck et al. 1992, Williams et al. 1998, Williams et al. 2001, Williams et al. 2004).

Though much work has clearly been done on the vegetation history of Europe, the type of thorough assessment that has been performed for North America is lacking. Most of the European studies cited above either synthesize data across Europe for only one or a few time slices, or across the Holocene for a limited spatial range, or they focus on one or a few taxa, or their results are more qualitative than quantitative. Except for the work of Huntley and Birks (1983) and Huntley (1990b), we are unaware of any attempt to map and quantify vegetation dynamics across the whole of Europe for the entirety of the Holocene. And since those two studies were published, great advances have been made in data availability and quality, spatial coverage, dating control, analytical techniques, and computing power. Here, we take advantage of these advances to quantitatively assess the age of the modern vegetated landscape of Europe, to measure change across time using the Squared Chord Distance (SCD) metric (Overpeck et al. 1985), and to map the relative openness of the landscape, as well as the distribution and abundance of biomes, at 500-year intervals throughout the Holocene (11.5 ka to modern times).

We perform large-scale synthesis and statistical analysis of palaeoecological (fossil pollen) data, using the most comprehensive dataset of pollen data currently available, including more sites with better chronological control, and excluding any pre-calculated percentage data (for which it is often impossible to determine how the original sums were calculated). Fossil pollen entrained in freshwater sediments offers the best and most consistent tool available to examine the vegetation of the Holocene and compare it to modern conditions (e.g. Prentice and Webb 1998); by comparison, satellites offer only decades of data and the written record provides at best a few millennia of (often subjective and difficult to interpret) information on vegetation cover (e.g. Thirgood 1981). In addition, several decades of fieldwork in Europe have yielded vast amounts of pollen data, much of which (though by no means all) is publically available for use in studies such as this, in repositories such as the European Pollen Database (EPD; Fyfe et al. 2009), PANGAEA, ALPADABA, NEOTOMA, etc. Though it is important to be aware that the relationship between pollen data and actual vegetation cover can vary and is influenced by differences in pollen productivity and transport (Sugita 1994, Gaillard et al. 2012), fossil pollen analysis remains the most readily available and widely accepted source of information on past vegetation.

There are, however, some disadvantages associated with working directly with raw pollen data. For example, fossil taxonomic resolution and representation vary by conditions, preservation, sample, site, and analyst; there is no standard approach or methodology. When synthesizing pollen data, some researchers deal with this ambiguity by focusing on one or a few clearly defined or easily identifiable taxa, but this has the negative side effect of making most of the counted pollen data (any grains not belonging to the chosen taxa) unusable. The alternative we adopt here, grouping pollen taxa into plant functional types (PFTs), allows us to draw a clearer picture of the vegetated landscape by incorporating a greater number of taxa into our analysis and by blending many taxa from disparate regions; we can thus more inclusively assess changes in the landscape without being bound to certain taxa or being sensitive to pollen taxonomic diversity concerns. In effect, the PFT approach filters noise at the taxon level in favour of signal at landscape level. Definitions of PFTs vary widely (Smith et al. 1997); we use those of Peyron et al. (1998), which are derived from Prentice et al. 1996, because they are useful for the large spatial and temporal scales we work with, and they allow our work to translate to other disciplines such as earth system modelling.

Once the raw pollen data are transformed into PFT assemblages, we mathematically interpolate these to a four-dimensional (space and time) grid with ecologically meaningful scaling factors. This effectively extends the scope of the study area between the sites where the pollen data were collected, in a manner that takes advantage of continuous climate fields and accounts for elevation. Interpolation in time allows each data point to remain where it is in time, relative to the centre of the time slice; this creates a clearer picture of each time slice without the centuries of blurring that are problematic in the time slice batch approach. Thus, four-dimensional interpolation makes it possible to cover the entire continent in a way that can then be quantitatively summarized with area average calculations.

Working on the continental spatial and Holocene temporal scale allows us to reconstruct a history of the entire continent, based on data, with quantitative assessments of change, at the scales on which earth system and climate modelling research are done. SCD is a metric of difference with which we can quantitatively compare landscapes based on how similar or different their plant functional landscapes are (Overpeck et al. 1985; Huntley 1990a). The biomisation methodology (Prentice et al. 1996, Peyron et al. 1998) was designed to reconstruct vegetation in equilibrium with climate and is relatively unbiased by human activity. Landscape openness, by contrast, is largely driven by human activity in areas where the climate is appropriate for forest. Thus, though it is difficult to disentangle the interactions between humans and climate in shaping the vegetated landscape of Europe, assessing changes in biome distribution alongside changes in landscape openness might offer some insight into the timing and importance of human influence on the Holocene vegetated landscape of Europe.

4.2
Methods

4.2.1
Study area and data

The study area covers Europe and Asia Minor and is limited to land falling consistently within 150 km of a data site at every time slice between 6 ka and the modern day. Modern coastlines and ice extent are used throughout. The data come primarily from the EPD, with additional data as described in Collins et al. 2012. Only sites with reliable, calibrated radiocarbon chronologies (Davis et al. 2003) have been used, and all taxonomy has been checked and standardized. There are 1558 sites containing 83018 samples, spanning 11,500 years, and containing 4189 taxa. We performed our analyses for both the entire study area and on the northern (> 55 degrees north latitude), middle (45 – 55 degrees north latitude), and southern (< 45 degrees north latitude) zones separately.

4.2.2
Plant functional types

Multiple algorithms exist for converting pollen taxonomic data into Plant Functional Types, or PFTs (e.g. Prentice et al. 1996, Peyron et al. 1998, Tarasov et al. 1998, Williams et al. 1998). All follow the general procedure of 1) grouping pollen taxa into PFTs based on certain vegetation criteria (e.g. Smith et al. 1997) and 2) calculating the PFT scores as some kind of scaled or non-scaled sum of the raw pollen counts. We chose the method of Peyron et al. (1998), as it is optimized for Europe and makes two key improvements over that of its European predecessor (Prentice et al. 1996).

First, the method of Peyron et al. (1998) is more sensitive to detecting changes in vegetation composition at the PFT level, as it uses more pollen taxa (77, ranging in taxonomic resolution from species to family) and PFTs (22; 14 arboreal and 8 shrub/herbaceous) relative to the method of Prentice et al. (1996) (41 pollen taxa, 17 PFTs). Second, Peyron et al. (1998) permit each pollen taxon to belong to only one PFT (up to 17 taxa per PFT), creating new PFTs to handle ambiguous pollen taxa; in contrast, Prentice et al. (1996) allow some taxa to belong to multiple PFTs, rendering their method less sensitive to detecting vegetation change.

The algorithm operates as follows: For each pollen sample, the abundance of each pollen taxon relative to the total amount of terrestrial pollen present is calculated. These relative abundances are filtered to remove any values lower than 0.5%, square-rooted to amplify the importance of the rare relative to the common taxa, and then summed into scores, using the taxon combinations relevant to each PFT. At the end of the process, every pollen sample has a score for each of the 22 PFTs.

4.2.3
Interpolation

Next, we divided the pollen samples by date into twenty-three 500-year-long Holocene time slices, for comparison against the modern time slice, which encompassed all samples more recent than 1700 AD (0.25 ka). Within each of the 23 Holocene time slices, we interpolated the calculated scores for each of the 22 PFTs onto 1° grids using a 4-D (latitude, longitude, elevation, time) thin plate spline (R 2008). Interpolating in time as well as space gives greater weight to data points closer to the target date and less weight to those at the edges of the time slice, minimizing temporal blurring (Davis et al. 2003). However, as the modern time slice was shorter, we chose to interpolate instead using a 3-D thin plate spline. For all time slices, latitude and longitude were scaled to have equal weight, and we used the scaling ratio between latitude and altitude recommended by Ozenda (1989).

To correct for interpolative bleed and ground-truth the efficacy of the interpolation method, modern spatial distributions of PFTs were checked for plausibility against the distributions of representative taxa in the Atlas Flora Europaea (Jalas & Suominen 1972) and minimum presence/absence thresholds were applied accordingly.

4.2.4
Analyses

We used the interpolated, gridded PFT scores described above to perform three different types of analyses of Holocene European vegetation age and change. All analyses were performed for the entirety of the study area, as well as for the north, middle, and southern zones separately, and all calculations were done individually for each pixel of the grid.

4.2.4.1
Squared chord distance

To determine the age of the modern vegetation and to assess change during the Holocene, we compared the PFT assemblage of each time slice to that of modern conditions using the Squared Chord Distance (SCD) dissimilarity coefficient. This was done using the following formula:

$$d_{ij}= \Sigma_k(p_{ik}{}^{1/2} - p_{jk}{}^{1/2})^2$$

where d_{ij} = the SCD between a pixel in a given time slice *i* and the same pixel at the modern day *j*, and p_{ik} = the proportion ($0.0 \leq p_{i(j)k} \leq 1.0$) of PFT *k* in that pixel for time slice *i* (*j*) (Overpeck et al. 1985).

The calculated SCD can theoretically range from 0 to 2, where 0 indicates a perfect match and 2 indicates maximum possible difference; observed values usually range between 0 and 1 (Overpeck et al. 1991; Huntley 1990a). Though dissimilarity is a continuous concept, a threshold value distinguishing analogous from non-analogous pixel pairs can be empirically derived from the data. We identified a threshold of 0.2 by comparing the SCD scores of pixel pairs having the same biome (c.f. subsection B below) against those of pixel pairs having different biomes (Fig. 4.1). Sixty-seven percent of pixel pairs with SCD < 0.2 (> 0.2) had the same (different) biome while 33% had different (same) biomes. Thus, crossing this threshold is functionally equivalent to passing from one biome to another (e.g. Williams et al. 2001) 67% of the time, or with a probability of roughly one standard deviation.

Though our SCD threshold is determined using changes in biome, the threshold is more informative than simply observing when biomes change across time. Much PFT change can occur within the parameter space of a single biome before causing that biome to change, while a small amount of PFT change at the edge of a biome's parameter space can be sufficient to elicit a biome change; in either case, the change (or lack thereof) in biome would not accurately represent vegetation dynamism at the PFT level.

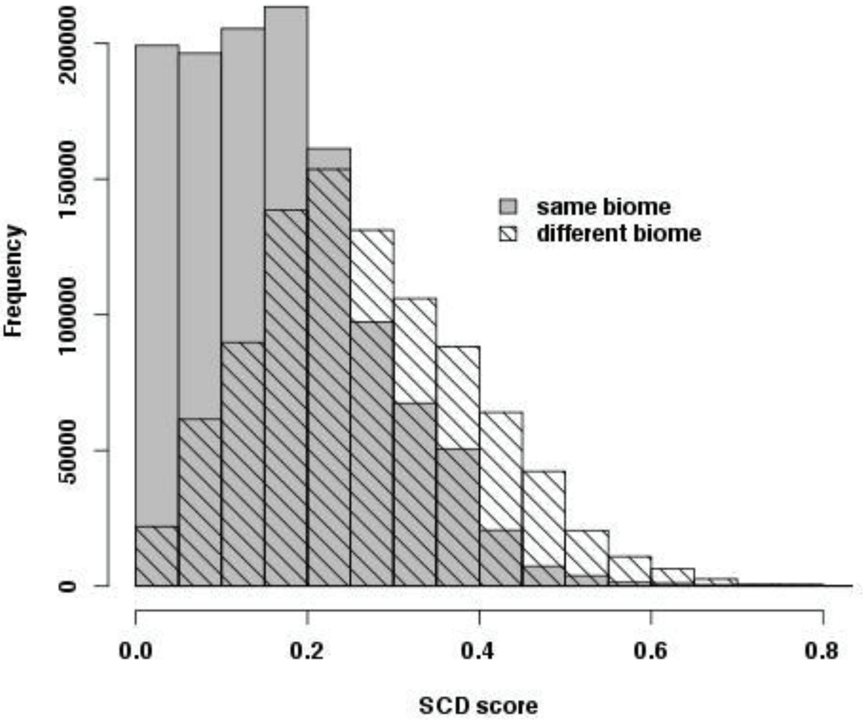

Figure 4.1. Frequency distribution of Squared Chord Distance (SCD) scores used to derive difference threshold of 0.2 (Figs. 4.2, 4.3, 4.4). SCD scores of all pixel pairs having same vegetation type (biome) are compared to all pixel pairs having different vegetation type. Probability of two pixels having an SCD score greater (less) than 0.2 and having different (same) biomes =~ 1 σ (~67%). (Frequency = number of pixel pairs compared).

There is no single established threshold value; Overpeck et al. (1985) and Huntley (1990a) derive SCD analogue thresholds of 0.15 and 0.3 for modern pollen taxa for their pollen datasets from North America and Europe, respectively. Our approach differs from these studies in two ways. First, their calculations were done using point site data, while ours were performed for each pixel of our interpolated surfaces. Second, they performed their calculations using a smaller selection of pollen taxa (~30 woody/10 herbaceous families/genera in Overpeck et al. 1985; ~ 38 woody/6 herbaceous families/genera/species in Huntley 1990a), while we instead transformed a larger selection of pollen taxa (~39 woody/39 herbaceous families/genera/species) into 22 PFTs. Given these methodological differences, it is encouraging to see that our threshold value of 0.2 is nevertheless roughly in agreement with these authors' findings.

4.2.4.2
Biomes

To map vegetation units at each time slice, we converted pollen PFT scores into biomes using the method of Peyron et al. (1998). This was done by assigning each of 12 pollen biomes a score, calculated as the sum of the scores of the PFTs comprising that biome (where each biome is defined as a certain unique combination of PFTs). The biome with the highest score "wins", or is called the "dominant" biome for a given PFT score assemblage. When two biomes had the same score, the biome ranking higher in the dominance hierarchy (c.f. Table 4 in Peyron et al. 1998; Prentice et al. 1996) was chosen as "winner".

4.2.4.3
APFT%

To estimate relative landscape openness at each time slice, we computed the prevalence of arboreal vegetation on the pollen-reconstructed landscape. This was done by dividing the sum of the 14 arboreal PFT scores into the sum of all 22 PFT scores (c.f. Table 2 in Peyron et al. 1998) The result was then multiplied by 100 and is expressed hereinafter as the APFT%, or the percentage contribution of arboreal PFTs to the total PFT sum. A higher APFT% corresponds to a relatively more closed landscape, e.g. a higher percentage of arboreal/woody over herbaceous vegetation. APFT% in this study has not been evaluated against actual land cover data (as required by the REVEALS method; e.g. Gaillard et al. 2010); therefore, we stress that APFT% is a *relative* rather than absolute metric of landscape openness.

4.3
RESULTS

4.3.1
SCD temporal dynamics

The European vegetated landscape begins the Holocene substantially different from modern conditions and converges towards them at a fairly steady rate throughout the study period (i.e. SCD scores start out high and decrease to zero). The northern, middle, and southern zones behave fairly similarly to one another, but subtle differences occur. Variations in the convergence rate at the European and zonal scales suggest dividing the Holocene into five phases (Fig. 4.2).

Starting from the past and working towards the present, the five phases can be characterized as follows: 5) diversity of rates/directions in the trends; 4) generally consistent, and relatively rapid, decrease in SCD scores; 3) reversal (i.e. increase) in SCD scores, followed by period of plateau or gradual decrease; 2) slightly higher rate of decrease; 1) rapid decrease to modern conditions (i.e. SCD score = 0). While the southern zone does experience a plateau/slow rate of decrease during the third phase, this is not preceded by the reversal that the northern and middle zones experienced. Also, the northern zone appears to maintain a steady rate of decrease during the second and first phases, rather than accelerating during the first phase as the middle and southern zones do.

4.3.2
Age of the modern landscape

The age of the modern vegetated landscape of Europe, as determined by the first date in the past at which the 0.2 SCD threshold is crossed, varies strongly by location. On average, the modern European vegetated landscape came into being in phase 2, around 4 ka; this is the date at which the area-weighted average curve for the whole of Europe crosses the SCD analogue threshold of 0.2 (Fig. 4.2). When the northern, middle, and southern zones are analysed separately, different dates emerge. The vegetation of the southern zone is on average older; its area-weighted average curve first crosses the SCD threshold between 5.5 and 6 ka (phase 3) and then oscillates around the threshold until it definitively drops

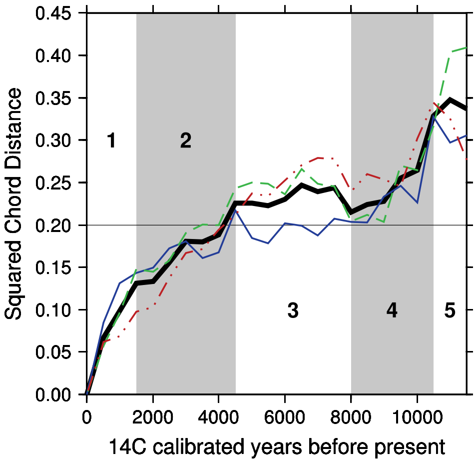

Figure 4.2. Area-weighted average difference (SCD) between the vegetation (PFT assemblage) for Europe at 500-year intervals throughout the Holocene, relative to modern times (black curve). Red, green, and blue curves show the results of the same analysis done respectively for the north, middle, and southern zones (Fig. 4.3). The horizontal line at 0.2 indicates the difference threshold (Fig. 4.1).

below 0.2 between 4 and 4.5 ka (phase 2). The vegetation of the middle zone is on average younger, crossing the SCD threshold between 3.5 and 3 ka (phase 2). The vegetation of the northern zone matches the continental average, crossing the SCD threshold at 4 ka (phase 2).

The geographic distribution of "older" versus "younger" areas is highly variable (Figs. 4.3, 4.4). Parts of south-western Spain, the Alps, Greece, eastern Europe, and northern Fennoscandia already had vegetation similar to modern conditions in the early Holocene, while the vegetation cover of much of central/western Europe dates to 2,000 years ago or less. The majority of the European vegetated landscape appears to be 6,000 years old or younger. By 1 ka, nearly all of Europe had crossed the SCD threshold, meaning the modern European vegetated landscape is at least 1,000 years old, in terms of PFT distribution and abundance.

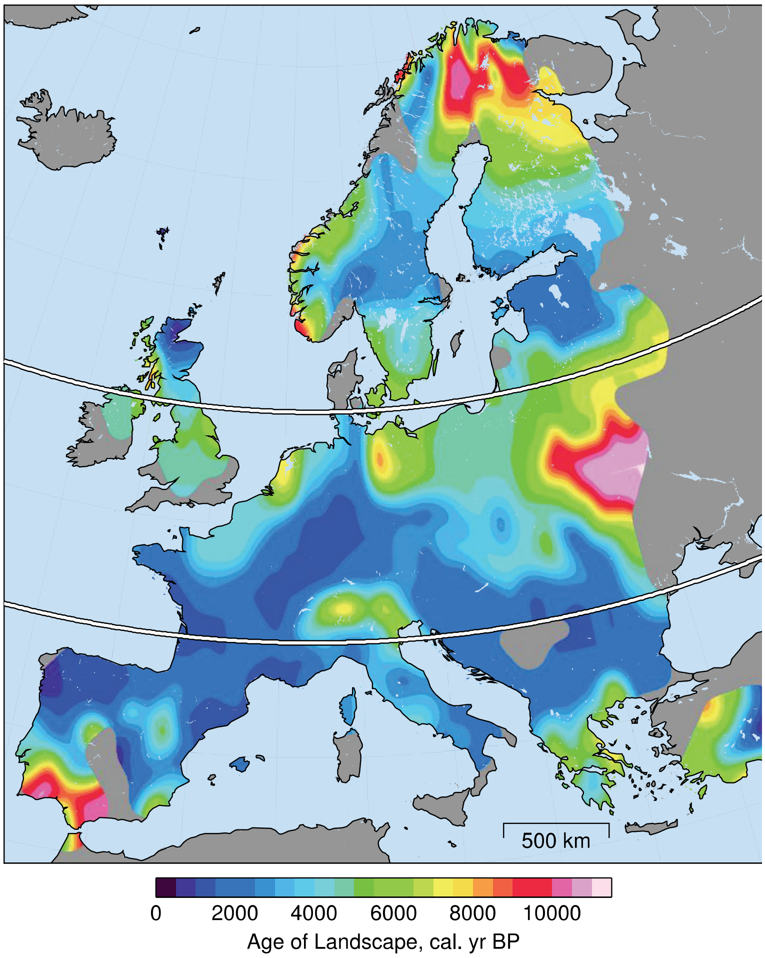

Figure 4.3. Approximate age of the European vegetated landscape. "Age" calculated as date at which SCD relative to modern times (1750 AD to present) first exceeds difference threshold of 0.2 (Fig. 4.1). SCD calculations based on interpolated plant functional type (PFT) assemblages, derived from fossil pollen data. Land area in grey falls outside 150 km radius of a sample site. White latitude parallels mark division between northern, middle, and southern zones as described in the text. All maps in this paper use a Lambert azimuthal equal-area projection centered on 7° E, 52° N with the same scale.

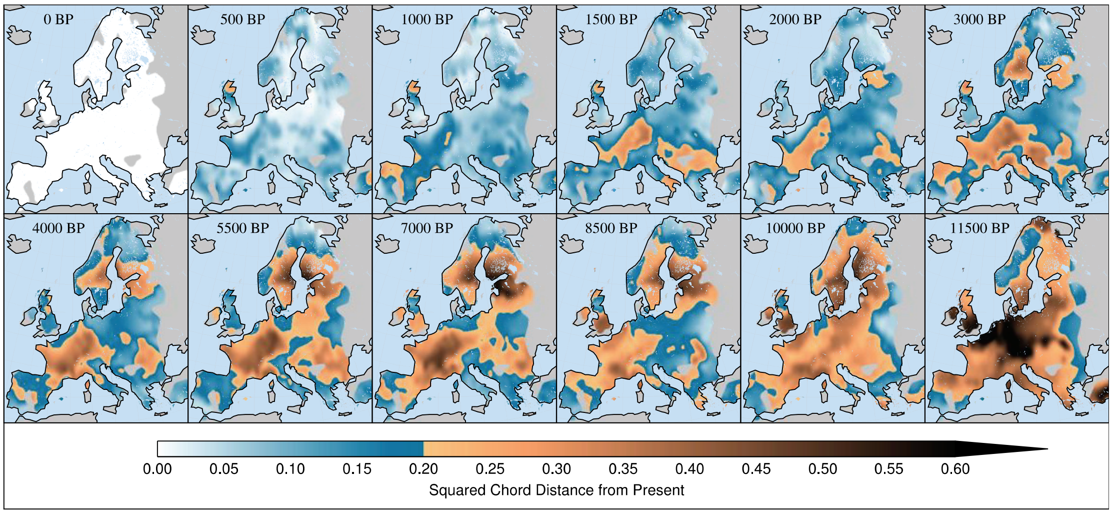

Figure 4.4. Difference (SCD score) between modern and Holocene PFT assemblages. Larger score = greater difference. Threshold dividing "same as modern" from "different from modern" vegetation = 0.2 (Fig. 4.1). Calculations based on 4-D interpolated PFT scores, derived from fossil pollen data.

4.3.3
Biomes and APFT%

The SCD analyses presented thus far allow an estimation of the age of the modern European vegetation and an overview of its Holocene temporal and spatial dynamics, in terms of the difference between the modern vegetated landscape and the landscape of the Holocene past. However, the SCD difference metric says nothing about the ecological nature of the changes. Here, we go beyond the question of "how much change?" to explore the types of vegetation change occurring between the beginning of the Holocene and modern times. Conversion of pollen PFT scores into pollen biomes gives an overview of ecological vegetation units formed primarily in response to climatic conditions, and comparing the ratio of arboreal to non-arboreal pollen PFTs allows an approximation of relative landscape openness, which, for the latter half of the Holocene at least, can be seen as a rough proxy for human impact on the landscape.

4.3.3.1
Biomes

At the European scale, non-forest biomes decrease in relative abundance during the early Holocene (phases 5 and 4) and different cold forest biomes alternate in dominance throughout the Holocene. Relative abundance of *temperate deciduous forest* increases during phase 5 to become the dominant biome by phase 4, which it remains throughout the Holocene (Fig. 4.5a).

The northern and southern zones (Figs. 4.5b, 4.5d) drive the European-scale biome dynamics of the cold forest and non-forest biomes, respectively, while the middle zone (Fig. 4.5c) drives the dominance of the *temperate deciduous forest* biome. In both the northern and southern zones, *temperate deciduous forest* abundance peaks in phase 3, then declines in phases 2 and 1.

In the northern zone, *taiga* is relatively more abundant at the early and late Holocene, *cold mixed forest* is abundant only in the early Holocene, *cool mixed forest* is abundant only in the late Holocene, and *tundra* is present during phase 5 but disappears in phase 4.

In the middle zone, the *temperate deciduous* and *cool mixed forests* dominate in roughly consistent proportions throughout the Holocene, after the *cold mixed forest* and *taiga* disappear in phases 5 to 4 (Fig. 4.5c).

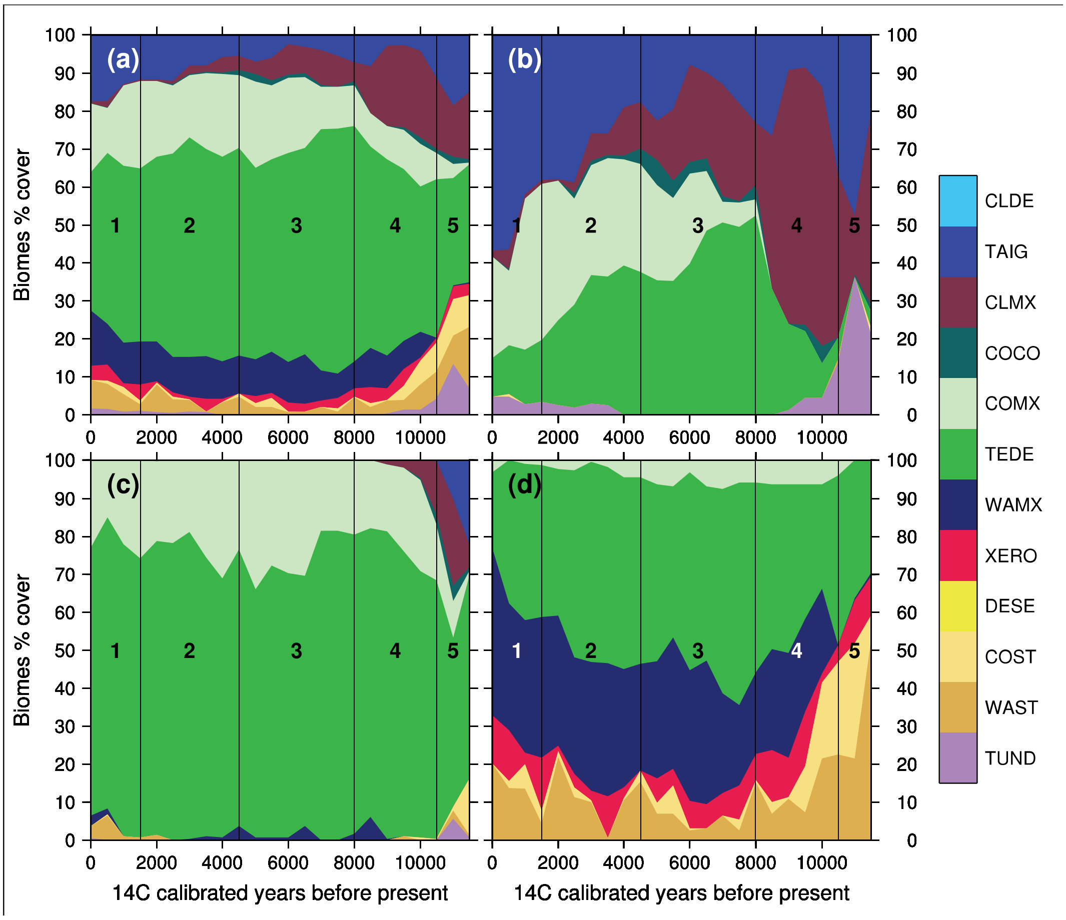

Figure 4.5. Area-weighted average percent cover of biomes at 500-year intervals throughout the Holocene for all of Europe (a), and for the northern (b), middle (c), and southern (d) zones (Fig. 4.2). Biomes as in Peyron et al. 1998 (CLDE = Cold deciduous forest, TAIG = Taiga, CLMX = Cold mixed forest, COCO = Cool conifer forest, TEDE = Temperate deciduous forest, COMX = Cool mixed forest, WAMX = Warm mixed forest, XERO = Xerophytic woods/scrub, DESE = Desert, COST = Cool steppe, WAST = Warm steppe, TUND = Tundra).

In the southern zone, the non-forest *steppe* biomes decrease in relative abundance during phases 5 and 4, reach a low stand in phase 3, then rise again a bit in phases 2 and 1. The *xerophytic* non-forest biome maintains a relatively constant abundance throughout the Holocene. *Warm mixed forest* first appears in phase 4, increases in abundance during phase 3 as the *temperate deciduous forest* declines in abundance, and maintains a constant level of abundance during phases 2 and 1.

Spatially, these trends manifest as a large northward advance and then southward retreat of *temperate deciduous forest* relative to the other cold forest biomes in northern Europe, general spatial stability of forest biome distribution in the middle of Europe, and a subtle advance and retreat of the southern limit of *temperate deciduous forest* relative to the non-forest biomes in southern Europe (Fig. 4.6).

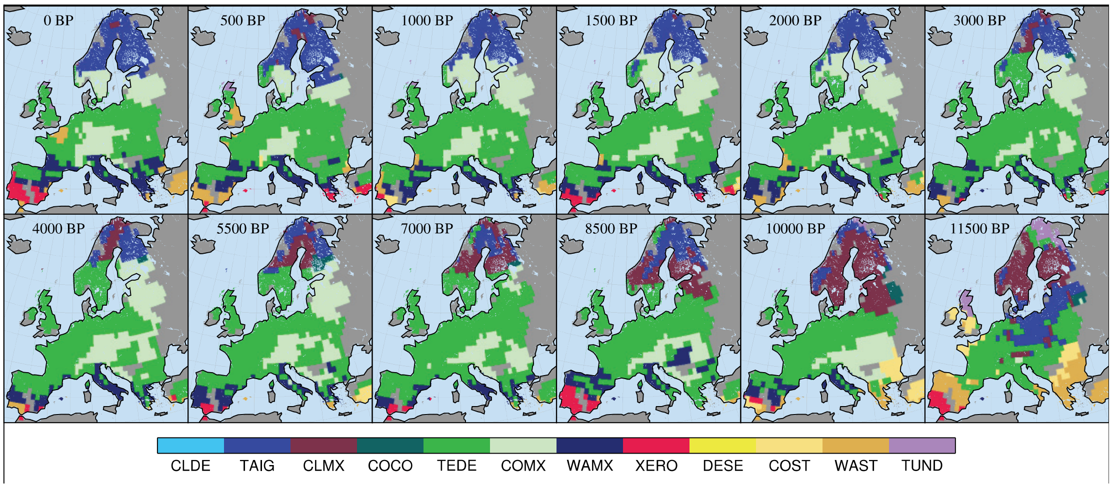

Figure 4.6. Distribution of biomes throughout the Holocene. Calculations based on 4-D interpolated PFT scores, derived from fossil pollen data, following the methodology of Peyron et al. 1998.

4.3.3.2
APFT%

European APFT% increased from less than 60% to 80% between phases 5 and 3, plateaued in phase 3, dropped gradually to 70% in phase 2, then dropped steeply back to 60% in phase 1 (Fig. 4.7). The APFT% of the northern and middle zones follow this same general pattern, with slight differences in timing and magnitude, while the APFT% of the southern zone rises steadily between phases 5 and 3 and then drops steadily between phases 3 and 1.

Throughout the Holocene, APFT% is consistently lowest in the southern zone. The APFT% of the northern zone exceeds that of the middle zone throughout the Holocene, except in phases 5 and 4.

The spatial distribution of low-APFT% areas is similar, though not identical, at the beginning of the Holocene and modern times. In both time periods, western and south-eastern Europe experience the lowest APFT%s, while APFT%s remain higher in northern Europe. However, the low-APFT% areas extend farther north-east into the European Plain at modern times than they did at the beginning of the Holocene (Fig. 4.8).

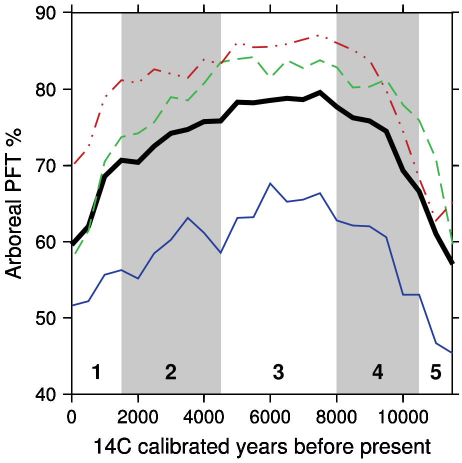

Figure 4.7. Area-weighted average percent of sum of all PFT scores belonging to arboreal PFTs for Europe at 500-year intervals throughout the Holocene (black curve). Red, green, and blue curves show the results of the same calculations done respectively for the north, middle, and southern zones (Fig. 4.2).

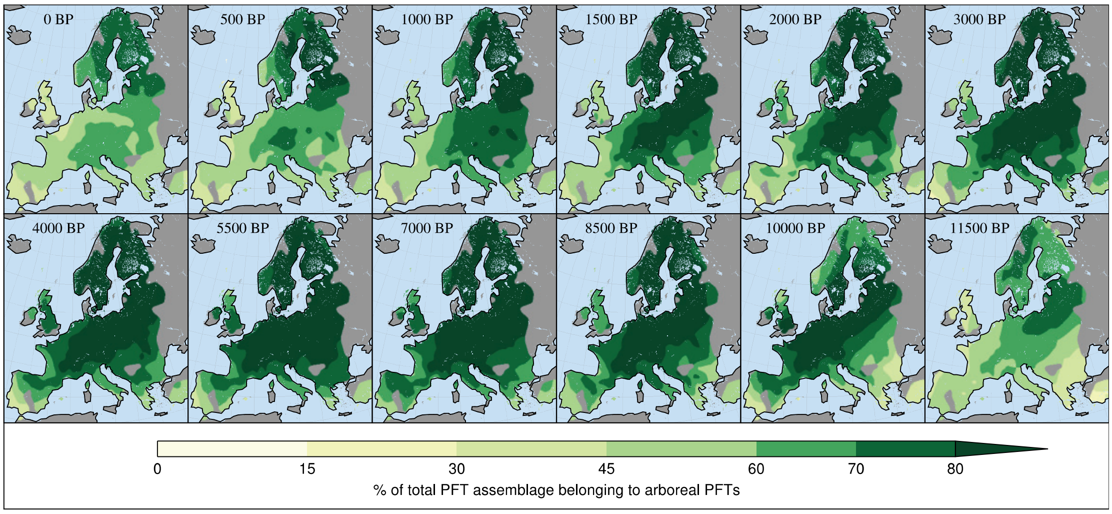

Figure 4.8. Estimated forest cover throughout the Holocene, calculated as percent of sum of all PFT scores belonging to arboreal PFTs. Calculations based on 4-D interpolated PFT scores, derived from fossil pollen data.

4.4
Discussion

4.4.1
SCD temporal dynamics

Though magnitude and timing differ slightly between the continental and the zonal area-weighted averages (Fig. 4.2), the general story appears to be the same for all analyses of Holocene European vegetation dynamics. Between 11.5 and 10 ka, each zone adjusted in its own way to deglaciation. Between 10 and roughly 8 ka, the SCD scores trend downward for all zones, in the direction of modern conditions, likely as the climate settled into the warm Holocene interglacial. But then, at roughly 8 ka, something happened to disrupt this downward trend in SCD scores for all three zones, causing the trend to either plateau (in the case of the southern zone) or reverse and then plateau (in the case of the middle and northern zones) until approximately 4 ka, when the decreasing trend towards modern conditions resumed. Given the timing and relative synchronicity of the disturbance at ~8 ka, we think it not unreasonable to attribute the reversal and subsequent plateau to the final disappearance of the North American ice sheet, which led to a dramatic reorganization of atmospheric circulation. This suggests that, even in the absence of significant human activity (we can assume human populations and levels of land use were small at 8 ka relative to the later Holocene), the European vegetated landscape might have already been fairly similar to pre-industrial modern conditions in the early to mid-Holocene if the North American ice sheet had remained in place.

However, it did disappear, and the next question to address is what might have caused the inflection point at ~4 ka, ending the plateau period (8 to 4 ka) and sending the SCD score trends back in the direction of modern conditions? Again, the synchronicity of the response for all three zones suggests that some climatic event may have played an important role. Though the phases that emerge from our analysis roughly correspond with the Blytt-Sernander Holocene Atlantic/Boreal climate, by 4 ka Neolithic and/or Bronze Age civilizations had established themselves throughout Europe in ever-increasing populations (Harding 2000), so it is possible that human activity could have contributed significantly, either directly through vegetation clearance, or indirectly through the impacts of vegetation clearance on climate (e.g. Reale and Shukla 2001). In any case, the final rapid drop in SCD scores between 1.5 ka and modern times is likely due to human activity, given that human populations (and associated land use) exploded rapidly over this period (Kaplan *et al.* 2009; Kaplan *et al.* 2011).

As Gaillard et al. (2010) point out, changes in the pollen record often underestimate changes in the actual vegetation cover, and so it is possible that the magnitude of the dynamics observed here might be an underestimate of the actual magnitude of vegetation changes over the Holocene.

4.4.2
Age of the modern landscape

On average, the modern European landscape came into being around ~4 ka, with slight differences in timing when the northern, middle, and southern zones are analysed separately. This timing corresponds well with the conclusions drawn by various authors for diverse regions across Europe, who suggest that human activity (land clearing for agriculture, metallurgy, etc) by Neolithic or Bronze Age civilizations created the “cultural landscapes” that were still widespread throughout Europe before the Industrial Revolution (e.g. Odgaard and Rasmussen 2000; Andric and Willis 2003; Bradshaw 2004). For southern/Mediterranean Europe, however, this timing also matches well with an aridification around 5.5 ka observed by Jalut et al. (2009), who suggest that the modern vegetation of that region was established by this climatic process. Grove and Rackham (2003) also argue that the vegetation of southern/Mediterranean Europe was established early due to climatic causes and that human influence played a secondary role. The modeling simulations performed by Reale and Shukla (2001) suggest that anthropogenic removal of vegetation in the southern/Mediterranean part of Europe during the Roman Classical Period (~2 ka) could have had a significant impact on the hydrological cycle (and thus climate) of the region, though Dermody *et al.* (2011) find the opposite. De Beaulieu et al. (2005) conclude that the debate is still open on the relative agency of humans and climate in the development of the vegetation of Mediterranean Europe.

In any case, the spatial distribution of landscape age is far from homogeneous (Fig. 4.M). Indeed, some of the youngest as well as oldest landscapes can be found in the southern, middle, and northern zones of this analysis. There do not appear to be clear trends according to climatic gradients or history of spread of human civilization. As both the calculation of SCD scores from PFT assemblages, and the calculation of PFT scores from pollen assemblages, are non-linear processes, it is not possible to deconstruct the causation underlying the patterns of landscape age in space from the SCD analysis. However, given the location of the three areas (northern Scandinavia, southwestern Spain, and the Bialowieza Forest of Poland and Belarus), one could speculate that the combined impact of human activity and changing climate would have been small in these places. The extreme northern latitudes of northern Scandinavia preclude almost any significant human modification of the vegetated landscape (other than perhaps reindeer herding) and ensure that climate would remain cold throughout the Holocene. The stability of vegetation in south-western Spain suggests that the region remained warm and dry throughout the Holocene, in agreement with the findings of Jalut *et al.* (2009). And the Bialowieza Forest is listed as one of the last remaining stands of old growth forest in Europe; due to its swampy terrain it was never attractive for forest clearance.

It is important to note that landscape “age” merely refers to the most recent date at which the SCD score relative to modern times is greater than the SCD analog threshold of 0.2. As the range of SCD scores in time is a continuum, so usage of a threshold is somewhat arbitrary. This threshold was statistically derived from the distribution of the calculated SCD values for each pixel pair having the same biome compared to the calculated SCD values for each pixel pair having different biomes (Fig. 4.1), with a success rate (true positive vs. true negative, e.g. Gavin et al. 2003) of one standard deviation (or ~66%). This means that, ~33% of the time, a pixel pair having different biomes could have an SCD score greater than 0.2, or a pixel pair having the same biomes could have an SCD score less than 0.2, yielding either a false positive or false negative, respectively. Furthermore, much vegetation change can occur within a pixel without the biome changing (Williams *et al.* 2004; Huntley 1990b), so comparing SCD scores to the case of matching or non-matching biomes may not be the ideal solution. Despite these drawbacks, statistical derivation and usage of a threshold in difference analysis is a common and accepted practice in vegetation reconstructions (Overpeck 1985, Huntley 1990a; Williams et al. 2001; Odgaard and Rasmussen 2000); indeed, we are aware of no better approach.

4.4.3
Biomes and APFT%

4.4.3.1
Biomes

Between 11.5 and 10 ka, both Europe as a whole, and the northern, middle, and southern zones individually, exhibit significant dynamism in terms of changing biomes, as the continent made the transition from glacial to Holocene climatic conditions (Figs. 4.5, 4.6). However, the biome distributions established by 10 ka remained stable right through to the modern day, for the continent as a whole (Fig. 4.5a, 6) and for the middle zone (Fig. 4.5c, 6). As biomes are intended to represent potential natural vegetation in equilibrium with climate conditions, this suggests that Holocene climatic influence on vegetation remained more or less constant between 10 ka and modern times, at least for the middle zone. This is puzzling, considering the early Holocene dynamics of the middle zone SCD curve in Fig 3. However, due to the way biome scores are calculated, it is possible to have a large change in PFT scores that does not incite a biome change, and conversely, a small change in PFT scores can be sufficient to incite a biome change.

Thus, we agree with Williams *et al.* (2004) and Huntley (1990b) that a lack of changing biomes does not necessarily mean stable vegetation. Nevertheless, lack of significant changes in distribution and abundance of biomes in the middle zone does suggest stability of Holocene climate for that zone for most of the Holocene, in agreement with the findings of Davis et al. (2003). Indeed, Huntley (1990) also concluded that the biomes of north-western Europe (within our middle zone) reached modern distribution around 8 ka, but the internal floristic composition of those biomes continued to change throughout the Holocene. Such internal changes, invisible on the biome level, could be driving the SCD dynamics we see in the green curve of Fig. 4.2.

The story is different for the northern and southern zones (Fig. 4.5b and 5d, respectively), which both show important changes in relative abundance of biomes throughout the Holocene and drive the biome dynamics of the European continent as a whole.

In the north, these changes consist of a reorganization of forest types, with *cold mixed forest* dominating early in the Holocene, *temperate deciduous forest* dominating in the middle Holocene, and *cool mixed forest* and *taiga* replacing them both in the late Holocene (Fig. 4.5b, 6). Such dynamics may have been driven by changes in the Latitudinal Insolation and Temperature Gradients, as described by Davis et al. (2003). The timing of the northwestward migration of Norway spruce (*Picea abies)* from the Urals region into Fennoscandia as documented by Giesecke and Bennett (2004) and Seppä et al. (2009) also matches the timing of the rise in dominance of *taiga* and *cool mixed forest*, both of which contain the PFT to which this taxon belongs, at the expense of the *cold mixed* and *temperate deciduous forests*, neither of which contain this taxon.

In the south, these changes consist of an expansion of *temperate deciduous forest* in the middle Holocene (Fig. 4.5d, 6), then its replacement by *warm mixed forest*, *xerophytic wood/scrub*, and *warm* and *cool steppe* in the late Holocene, in agreement with the findings of Collins et al. (2012). It is difficult to say whether these dynamics were more driven by human activity (see subheading “Age of the modern landscape” above, this section) or more by the mid-to-late

Holocene aridification trend observed by Magny et al. (2002). Mostly likely, both processes interacted.

It is noteworthy that the xerophytic wood/scrub and steppe biomes maintained fairly consistent abundance throughout the Holocene as well. This contradicts the conventional wisdom that the presence of xeric vegetation in the Mediterranean is solely a consequence of anthropogenic landscape degradation and is in agreement with the findings of Collins *et al*. (2012). In addition, the mid-Holocene expansion of *temperate deciduous forest* into the northern and southern zones, followed by its late-Holocene retreat back to the middle zone, is in line with climatic reconstructions showing a mid-Holocene climate "optimum" in the north (Davis *et al*. 2003) and relatively more humid conditions in the south (Magny *et al*. 2002).

4.4.3.2
APFT%

While biomes are designed to reconstruct potential natural vegetation and thus to filter out human activity, reconstructing APFT% has no such bias. In fact, since the main activity of humans on the landscape is to preferentially clear forests in favour of non-forest vegetation, assessing APFT% can be considered as a proxy for assessing overall human impact on the landscape.

On average, the development of European APFT% occurred in four phases (Fig. 4.7): an increase in percentage cover from 11.5 to 8 ka, a relatively stable period between 8 and 5 ka, a gradual decrease from 5 to 1.5 ka, and then an abrupt drop between 1.5 ka and the modern day. When the north, middle, and southern zones are analysed separately, the responses differ in magnitude but not in timing. Considering that different climatic processes occurred during the Holocene in the north (changes in insolation), middle (stability), and south (changes in hydrological regime) (Davis et al. 2003; Magny et al. 2002), it is notable that the dynamics of APFT% are synchronized between all three zones.

While APFT% drops off first gradually, then steeply, between 5 ka and the modern day for the north, middle, and southern zones, forest biomes remain the dominant potential natural vegetation throughout this period (Figs. 4.5, 4.6), except for the southern zone, when an increase in scrub and steppe biomes is observed from 6 ka. Since the land remained suitable for forest biomes but the APFT% declined anyway, this suggests that the decline in APFT% between 5 ka and modern times may have been significantly influenced by human activity (land clearance associated with agricultural and/or metalworking civilizations), at least in the northern and middle zones. It is difficult to speculate on the relative agency of climate versus human activity in the decrease in APFT% in the southern zone accompanied by the increase in non-forest biome cover (see Collins et al. 2012 for further discussion of this problem). However, Bradshaw (2004) reviews what is known of European deforestation history and concludes that anthropogenic deforestation has been a dominant disturbance factor in Europe from 5 ka, when Neolithic cultures established themselves. As human civilization established itself much earlier in southern Europe than in the central and northern zones, it seems reasonable that the APFT% curve there begins to drop already at 6 ka.

Though APFT% is similarly low at the beginning of the Holocene and modern times (Fig. 4.7), SCD scores at the beginning of the Holocene differ significantly from modern times (Fig. 4.2), and so does biome cover (Figs. 4.5, 4.6). Thus, the open landscapes of the early Holocene must have been very different in PFT composition from the open landscapes of modern times. The inflection point in the SCD trends (Fig. 4.2) around 8 ka, possibly associated with the final disappearance of the North American ice sheet, may be related to the inflection point at 8 ka in the APFT% curves (Fig. 4.7), when the trend of increasing APFT% plateaus. This might suggesting that a change in PFT assemblages, possibly associated with the climatic event, might have been associated with the levelling off of the APFT% curves. The second inflection point in the SCD curves (Fig. 4.2, at ~4.5 ka, when the plateau period ends and the SCD scores begin to decrease again), also appears to correspond to the point in the APFT% curves where the plateau period ends and the gradual decline begins. Though no known climatic event is thought to have occurred at this point in time, it does roughly correspond with the establishment of agricultural and/or metalworking civilizations in central and northern Europe (they were already established much earlier in southern Europe), suggesting that perhaps anthropogenic land clearance might have been a primary forcing here. In any case, it seems reasonably clear that the final abrupt drop in APFT% between 1.5 ka and modern times, which matches the final abrupt drop in SCD scores for the same time period, was most likely a response to accelerating human land use in that period.

Interestingly, we do not see the increase in APFT% between 9 and 5 ka observed by Cheddadi and Bar-Hen (2009); in our study, APFT% is similarly high at both time periods. However, their forest cover reconstructions were based on the ratio of arboreal to non-arboreal taxa (rather than PFTs, as we have done here), their input dataset is different from ours, and their interpolation methods are unclear. We are aware of no other studies offering quantitative interpolated reconstructions of Holocene European forest cover based on pollen data. However, much work has been done on the topic of the “natural” state (more open or more closed) of the European forest cover (Vera 2000, Svenning 2002, Bradshaw et al. 2003, Bradshaw 2004, Mitchell 2005, Birks 2005). Overall, the conclusion of that debate seems to be that the “natural” state of the European forests would be more closed cover. The results of our analysis appear to support that conclusion, with forest cover percentage increasing from the end of the last glaciation and stabilizing at fairly high levels until around 5 ka, when the decline sets in.

4.5
Conclusions

In this study, we have used plant functional types reconstructed from pollen data to map and analyse the post-glacial development of the modern (1750 AD to present) European vegetation in terms of squared-chord distance from modern conditions, in terms of biomes, and in terms of landscape openness (APFT%). We have shown that the vegetated landscape of Europe was already similar to modern conditions approximately 4-5,000 years ago, around the same time that Neolithic and Bronze Age civilizations established themselves and began clearing the land (slightly earlier in southern Europe). Though correlation is not causation, this timing, combined with the subsequent clear deforestation trend lasting until modern times, suggests that human land use may have been the dominant factor (eclipsing climate and migration) driving changes in European vegetation cover already at the mid-Holocene.

Vegetation dynamics during the first half of the Holocene, by contrast, appear to have been driven more by climate and post-glacial migration, as evidenced by the rapid post-glacial increase in forest cover between 11.5 and 8 ka, and by the abrupt reversal in SCD scores at 8 ka, possibly corresponding with the final disappearance of the North American ice sheet and the associated reorganization of atmospheric circulation.

These conclusions are not completely new; rather, they reinforce the vast body of earlier literature concluding that anthropogenic cultural landscapes similar to those of modern times were already established throughout Europe by Neolithic times (e.g. Bradshaw 2004; Odgaard and Rasmussen 2000). However, the quantitative reconstructions we offer, in the form of maps and time series, have never before been produced for Europe using such a complete dataset or objective methodologies.

Huntley (1990b) points out that the utility of seeking evidence of human activity on such large spatial, temporal, and taxonomic scales is questionable. However, we would argue that, though definitive conclusions cannot be drawn, it is possible to inquire into the intertwining roles of human activity, climate change, and post-glacial migrational lag in shaping the vegetated landscape of Europe by looking at the same dataset in multiple ways, as we have done.

Finally, we note that the concept of landscape "age" is relative and must be interpreted with caution. Nevertheless, for those interested in understanding the history of European vegetation dynamics, maps such as Figs. 4.3 and 4.4 offer a valuable starting point. In particular, Fig. 4.3 could be useful for projects such as the Natura 2000 network, for example in helping to identify the oldest vegetation units of Europe that might be of particularly high conservation value.

This study contributes to the understanding of European vegetation history from the palaeoecological, macroecological, and biogeographical perspectives by presenting a palaeoecological narrative that is quantitatively explicit in space, time, and vegetation type and that allows speculation on the relative agency of these three forcings. The results of this work may interest the earth system modelling community, as it offers potential benchmarking materials at appropriate spatial, temporal, and taxonomic scales for comparison to model output. Mapping the age of the modern landscape should be of interest to the conservation community, as it can help to target conservation efforts to the "oldest" landscapes that might be of higher conservation priority. Finally, studies such as this can contribute to the debate on "what is natural?", and understanding the past development of the European landscape is crucial to understanding both its modern state and its possible future evolution under changing climate and land use patterns.

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5 Rising plant functional diversity in post-glacial Europe: Climate, migration, human impact, and the latitudinal diversity gradient

Collins, P.M., Davis, B.A.S., Mauri, A. & Kaplan, J.O. Increasing plant functional diversity in post-glacial Europe: Climate, migration, human impact, and the latitudinal diversity gradient. Manuscript in preparation for submission to *Ecology Letters*.

Abstract. Understanding how current patterns in biodiversity emerged from historical dynamics is important to anticipating possible future changes; the past is the key to the future. The availability of pollen data covering much of Europe throughout the Holocene makes it possible to study these historical dynamics. Here, we use pollen data to reconstruct European plant functional type (PFT) diversity throughout the Holocene and find that diversity has consistently increased since the Holocene began. Further, it has exhibited a latitudinal gradient whose strength has also increased over the Holocene. We find weak positive correlations between diversity and Holocene trends in temperature and precipitation, suggesting that post-glacial migrational lag due to dispersal limitations did play a significant role in changing Holocene vegetation dynamics and establishing present patterns of diversity. Human impact also seems to have influenced diversity for the last three millennia. These findings imply that future diversity protection policies will have to account for human impact and migrational lag in addition to climate change.

5.1
Introduction

Understanding patterns of biodiversity is a central theoretical concern in macroecology and biogeography. Given the clear positive relationships between biodiversity, ecosystem functioning and services, and human well-being (Balvanera *et al*. 2006; Erskine, *et al*. 2006; Benayas *et al*. 2009; Carpenter *et al*. 2009; Duffy 2009), understanding the forces shaping the diversity of life on Earth also has practical relevance. Floristic diversity in particular influences ecosystem functioning (Grime 1998) and productivity (Erskine *et al*. 2006), as plants are the terrestrial biosphere's primary producers. Functional diversity has been identified as potentially more relevant to ecosystem functioning than simple species richness alone (Hooper *et al*. 2002; Naeem & Wright 2003), and plant functional type (PFT) diversity is becoming recognized as central to ecosystem functioning (Smith *et al*. 1997; Díaz & Cabido 2001).

Human activity has already had significant impact on every facet of the Earth's ecosystems (Vitousek *et al.* 1997). The effects of future human impact and climate change on biodiversity are uncertain and likely will vary by region, but overall changes in distribution and abundance of a wide variety of organisms, including further extinctions, are possible (Huntley *et al.* 1995; Theurillat & Guisan 2001; Bakkenes *et al.* 2002; Thuiller *et al.* 2005; Araújo & Rahbek 2006; Willis & Bhagwat 2009). In the face of rapid and accelerating environmental change, it is essential to improve our understanding of the present patterns of PFT diversity, in order to better anticipate possible future behavior and to adopt appropriate conservation measures (Hannah *et al*. 2002; Hannah *et al*. 2007).

The most universal spatial pattern in biodiversity is the Latitudinal Diversity Gradient (LDG). It occurs throughout the world, on land and in sea, in all kingdoms of life (Hillebrand 2004). Many studies have attempted to understand why biodiversity should be greater at lower than at higher latitudes (Currie 1991; McGlone 1996; Gaston 2000; Koleff & Gaston 2001; Willig *et al.* 2003; Currie *et al.* 2004; Pimm & Brown 2004). Potential causes include energy/moisture availability, land area (for terrestrial diversity), glacial/interglacial cycles and migration rates, and topographic heterogeneity.

In North America, tree species richness was found to be primarily correlated with available energy and moisture, secondarily correlated with topography and distance from sea, and not connected to seasonal climatic variability and glacial history (Currie & Paquin 1987). Adams and Woodward (1989) support this conclusion, but add that glacial extinction does in fact limit floristic diversity in North America and Europe relative to eastern Asia. Kreft and Jetz (2007) use a geostatistical approach to conclude that energy/moisture dynamics primarily determine global patterns of floristic diversity, with other factors (such as topograhic heterogeneity) playing a synergistic role.

In Europe, the debate on the causes of modern patterns in floristic diversity focuses on whether vegetation distribution/migration is in equilibrium with, or lagging, post-glacial climate change. Huntley & Birks (1983) and Huntley and Webb (1989) observed that individual tree taxa migrated independently across Europe throughout the Holocene (the period between the end of the last glaciation, 11,500 years ago, and modern times), continuously changing the species composition of the forests of Europe, and Huntley (1990) concludes that changes in Holocene climate paced this migration. Svenning and Skov (2007), in contrast, found that modern European tree diversity patterns are not in equilibrium with climate and are instead a function of post-glacial migrational lag. Giesecke *et al.* (2012), however, do not find evidence for Holocene changes in vegetation composition at their study sites in Sweden, and they conclude that vegetation changes occurring at their study sites in Germany are attributable to the onset of human agricultural disturbance at 6,000 cal yr BP rather than changing climate or migrational lag.

Thus, species distribution and abundance have changed in Europe throughout the Holocene to create the diversity patterns of the present day, but it is still not clear to what extent variations in Holocene climate, post-glacial dispersal limitation, and human disturbance are responsible for creating these patterns. Species diversity is not the same as PFT diversity, and pollen-based vegetation reconstructions do not yield the same results as do vegetation surveys (Gaillard *et al.* 2010). However, it has been established that pollen data can be used to satisfactorily reconstruct continental- and millennial-scale patterns in terrestrial vegetation (Prentice *et al.* 1996). Indeed, it is the only type of palaeoecological data that can do so over large spatial and temporal scales with sufficient data density and availability (Fyfe *et al.* 2009).

In this study, we use pollen data to quantitatively reconstruct the PFT diversity of Europe for the entire Holocene. By examining PFT diversity, rather than pollen diversity, we overcome the problem of pollen data being highly variable in taxonomic resolution while accessing the question of diversity from the perspective most relevant to ecosystem functioning. For this analysis, PFTs can be thought of as a sort of meta-taxonomic classification. In asking the following questions, we seek to better understand the emergence of modern-day spatial patterns in European vegetation diversity:

- Has European PFT diversity changed over time? If so, how?
- Have rates of change been consistent or variable in space and/or time?
- Has the LDG been constant or variable?
- How, if at all, do Holocene dynamics in PFT diversity compare to Holocene climate dynamics?

5.2
Methods

The study area, source data, PFT calculations, and interpolation methodology have already been described in detail in Collins *et al.* (in prep). In summary, well-dated, quality-controlled pollen data were used to reconstruct the relative abundances (scores) of 22 PFTs from sites across Europe for the entire Holocene, following the methodology of Peyron *et al.* (1998). These site-based PFT scores were then interpolated in time and space to a 1-degree grid at 500-year intervals (time slices) between 11.5 ka and modern times (defined as 200 cal yr BP to present); it is on these gridded surfaces that all subsequent calculations were performed.

First, we summed the number of PFTs present in each gridcell for each time slice. Then, we calculated the area-weighted average number of PFTs for the entirety of Europe, and for the north (> 55 deg N), middle (45 – 55 deg N), and southern (< 45 deg N) zones separately. We derived gridded mean annual temperature and precipitation anomalies from modern times using the interpolated PFT surfaces in conjunction with other paleoclimate proxies, as described in Davis *et al.* 2003 and Mauri *et al.* (in prep).

Latitudinal gradients in PFT diversity, temperature, and precipitation for each time slice were approximated by subtracting the area-averaged value for the southern zone from that of the northern zone. To facilitate comparison, all time series and gradients are presented in terms of anomaly from present values.

We performed correlation analyses using both linear (Pearson's) and rank-abundance (Spearman's, Kendall's) techniques, to capture any potential linear or non-linear relationships in the data.

5.3
Results

5.3.1
Trends in PFT diversity and the LDG

Overall, European PFT diversity increased steadily throughout the Holocene, with a noticeable acceleration between 3 ka and modern times (Figs. 5.1, 5.2). When analyzed by zone, the northern zone shows a steady rate of increase from around 8,000 ka onwards to the present day, with the late-Holocene acceleration absent. In the middle zone, a short period of increase from 11.5 to 9 ka is followed by a plateau in PFT diversity unti around 3 ka, at which point the late-Holocene acceleration becomes clearly evident. In the southern zone, PFT diversity increases steadily throughout the Holocene, with the late-Holocene acceleration also clearly evident.

The latitudinal diversity gradient, calculated as the difference between the area-averaged PFT diversity of the northern and southern zones, has been clearly evident in European PFT diversity throughout the Holocene; however, it was slightly weaker in the early Holocene and has grown stronger towards modern times (Figs. 5.1, 5.2).

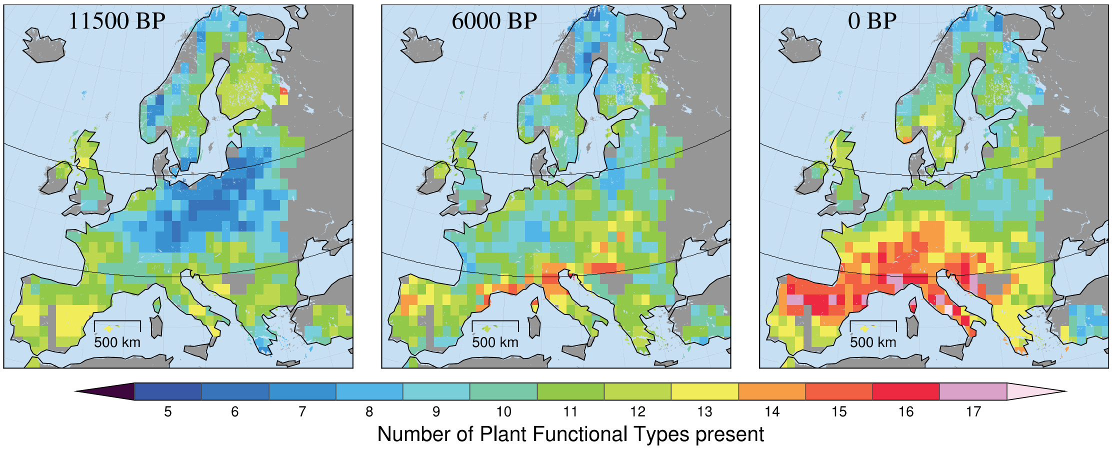

Figure 5.1. Plant functional type (PFT) diversity, in terms of number of PFTs present, at the early (11,500 cal yr BP) and middle (6,000 cal yr BP) Holocene, and modern times (200 cal yr BP to present), interpolated using 4D thin-plate spline onto 1-degree grid from pollen palaeodata. Total number of PFTs in this analysis = 22. Latitude lines delimit northern (> 55 deg N), middle (< 55, > 45 deg N), and southern (<45 deg N) zones used throughout this analysis.

5.3.2
Trends in climate dynamics and gradients

5.3.2.1
Temperature

Overall, annual average temperature was lower than present throughout the Holocene (Fig. 5.2). This general observation, however, does not hold true for the individual zonal analyses. The northern zone experienced lower-than-present temperatures before around 8.5 ka and higher-than-present temperatures for the rest of the Holocene until modern times. The middle zone experienced lower-than-present temperatures before around 8.5 ka and similar-to-present temperatures for the rest of the Holocene. The southern zone experienced lower-than-present temperatures throughout the Holocene, gradually increasing towards modern conditions.

The latitudinal temperature gradient shows a very clear trend of continually increasing strength from 11.5 to around 6.5 ka, after which it decreases to present conditions (Fig. 5.2). The gradient is consistently stronger (meaning relatively cooler at higher latitudes and relatively warmer at lower latitudes) than modern conditions from 10 ka until modern times.

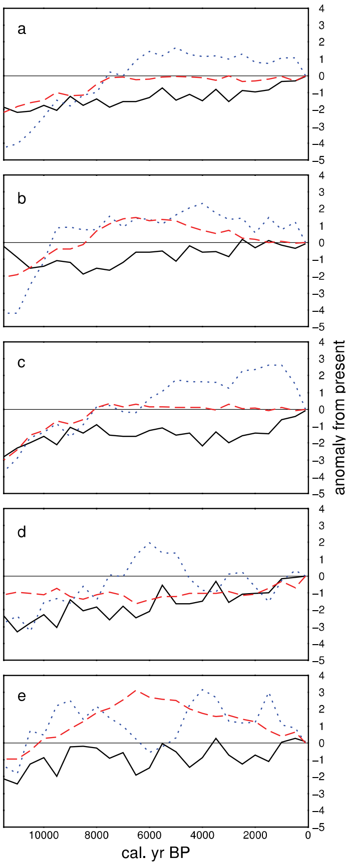

Figure 5.2. Trends in mean annual temperature (deg. C, red dashed curve), mean annual precipitation (mm/day, blue dotted curve), and PFT diversity (mean number of PFTs detected, black solid curve), calculated as area-weighted average anomalies from present values, for all of Europe (a), and for the northern (b), middle (c), and southern (d) zones separately (c.f. Fig. 5.1). Panel (e) shows latitudinal "gradients" (northern minus southern curves) in temperature, precipitation, and PFT diversity in terms of anomaly from present.

5.3.2.2
Precipitation

Overall, annual average precipitation was less than present until around 7.5 ka and then was greater than present for the rest of the Holocene (Fig. 5.2). This general observation also holds true for the northern and middle zones (though the time of crossing the threshold between “less-than-” and “greater-than-present” was earlier for both), but it is not true for the southern zone, which only experienced greater-than-present precipitation between around 7 and 5 ka.

The latitudinal precipitation gradient is highly variable in time, with high uncertainty in the reconstruction, but it appears that for most of the Holocene this gradient was stronger (meaning relatively wetter at higher latitudes and relatively drier at lower latitudes) than it is today, with the notable exception of the mid-Holocene (around 6 ka), when the gradient appeared to be similar to modern conditions, and the very early Holocene (before 10.5 ka), when the gradient was weaker than it is today (Fig. 5.2).

5.4
Discussion

5.4.1
PFT diversity and climate dynamics

The average PFT diversity of Europe increased throughout the Holocene (Figs. 5.1, 5.2). Between 11.5 and 3 ka, the strongest rate of increase occurred in the southern zone, while the middle zone experienced an initial increase followed by a plateau, and the northern zone experienced first a decrease and then an increase in PFT diversity. Between 3 ka and present, the rate of PFT diversity increase accelerated in the southern and middle zones but not in the northern zone. The latitudinal gradient in PFT diversity increased slightly between the beginning of the Holocene and the modern day. The temporal trends observed for changes in annual average temperature anomalies and the latitudinal temperature gradient agree with the seasonal findings of Davis and Brewer (2009), which they explain by invoking changes in the latitudinal insolation gradient.

What role, if any, might changes in Holocene climate have played in these PFT diversity dynamics? Correlation is not causation, but the energy/moisture hypothesis for diversity suggests that patterns/trends in temperature and moisture might be linked with patterns/trends in diversity. Thus, one might expect increases (decreases) in PFT diversity to co-occur with increases (decreases) in temperature and moisture availability.

	Pearson		**Spearman**		**Kendall**	
	t.	p.	t.	p.	t.	p.
a.	*0.61*	*0.62*	*0.52*	*0.60*	*0.38*	*0.41*
b.	*0.05*	*0.12*	*0.04*	*0.17*	*0.00*	*0.13*
c.	*0.57*	*0.46*	*0.23*	*0.40*	*0.15*	*0.27*
d.	*0.46*	*0.36*	*0.25*	*0.30*	*0.18*	*0.21*
e.	*0.21*	*0.35*	*0.09*	*0.19*	*0.04*	*0.14*

Table 5.1. Correlation analysis between PFT diversity and temperature (t.) or precipitation (p.) for each of the panels of Fig. 5.2. Both linear (Pearson) and rank-abundance (Spearman and Kendall) methods were used, to detect any possible linear or non-linear relationships in the data.

However, the correlations between PFT diversity and the reconstructed climate anomalies in temperature and precipitation are only weakly positive when the north, middle, and southern zones are considered individually, and only moderately positive for the continental average. The positive correlation between the PFT LDG and the latitudinal gradients in precipitation and temperature is especially weak (Table 1).

Thus, Holocene climate dynamics alone may not be enough to explain Holocene temporal dynamics in PFT diversity and the LDG, which contradicts Huntley (1990a) and is in line with Kraft and Jetz

(2007) who concluded that climate alone could not completely explain modern-day spatial patterns in biodiversity. This may be because, despite the observed climate variations, Europe nevertheless remained warm and wet enough throughout the Holocene to accommodate a variety of PFTs, so that dispersal-limited migration rates and location of refugia, rather than climate dynamics, drove Holocene PFT diversity dynamics throughout the Holocene. This is consistent with the findings of Svenning and Skov (2007) and inconsistent with the findings of Giesecke *et al*. (2012). However, this does not necessarily imply a simple Mediterranean-to-north migration; vegetation likely recolonized Europe from multiple refugia throughout the continent. Svenning *et al*. (2008) find that boreal tree species likely occurred in refugia north of the Alps even at the Last Glacial Maximum (LGM), and Kullman (2008) concludes that certain boreal tree taxa survived the last glacial period in cryptic refugia even in northern Scandinavia. Nevertheless, we find highest PFT diversity has always been in southern Europe and that the general tendency has been for increasing PFT diversity to creep northwards over the Holocene, which supports previous conclusions (Bennett *et al.* 1991; Hewitt 1999; Médail & Diadema 2009) that most of Europe's PFT diversity took primary refuge in southern Europe.

The acceleration of the rate of increase in PFT diversity in the southern and middle zones during the last three millennia, despite opposing trends in temperature and precipitation, begs explanation, as a few thousand years is much too short for evolution to alter dispersal rates. Human activity, however, is very effective at rapidly dispersing and establishing functionally diverse agricultural, silvicultural, ornamental, and weedy plants far beyond their historical ranges, as well as at increasing landscape (and, therefore, PFT) heterogeneity through forest fragmentation. As human impact on European landscapes has only been intensifying for the last 5-6 millennia (Olofsson & Hickler 2008; Kaplan *et al.* 2009; Kaplan *et al.* 2011), we suggest that the observed acceleration in the rate of increase of European PFT diversity between 3 ka and present is attributable to human activity, which contradicts Huntley's (1990a) conclusion that human influence on European vegetation is invisible at the continental scale. The lack of acceleration in the northern zone could be due to the fact that anthropogenic land cover change there was never as significant as in the middle and southern zones (Olofsson & Hickler 2008; Kaplan *et al*. 2009; Kaplan *et al.* 2011). We note that human-induced extinctions of the last few centuries due to industrialized landscape homogenization and total habitat destruction would not show up in this analysis, both because of the longer time scales of the time slices, and because the PFT-level analysis would not detect species-level extinctions unless the extinction removed all representatives of a PFT in a gridcell.

5.4.2
Trends in the LDG, and links to climate dynamics

As the Latidutinal Diversity Gradient is one of the most universal patterns in macroecology (Hillebrand 2004), it is not surprising that it should be observable in the PFT diversity of Europe throughout the Holocene. However, it is interesting that the strength of the gradient should increase with time. Multiple factors controlling the strength of the gradient have been proposed: land area, topography, energy/moisture gradients, distance from a continental margin (c.f. Introduction). In this study, all of those factors are held constant over time, except for the energy (as assessed by temperature) and moisture (as assessed by precipitation) gradients, which we observed to be only weakly positively correlated with the PFT diversity gradient in time (Table 1).

An increase in the strength of the PFT diversity gradient with time implies that PFT diversity is increasing faster in the southern than in the northern zone. This could simply be because the starting stock of available PFTs at the beginning of the Holocene was larger in the southern zone than in the northern zone, or it could be because the southern zone has greater topographic heterogeneity than the northern zone, or it could be that human activity has had more significant impact through dispersal and disturbance-induced landscape fragmentation/heterogeneity over longer timescales in the southern zone than it has in the northern zone. These results disagree with those of Slivertown (1985), who found a similar strengthening of the European LDG in woody plants over the Holocene, but concludes it to be driven by climate rather than post-glacial migrational lag or human activity. These results further disagree with those of Haskell (2001), who concluded that the European LDG at the plant family level remained constant throughout the Holocene.

5.5
Conclusions

In this time of changing climate and ever-intensifying human land use, improving our understanding of the patterns and drivers of modern day biodiversity will be important to adapting conservation measures to future environmental conditions. Land use and climate change are already potentially committing many taxa to extinction (Thomas *et al.* 2004), and though future changes are highly uncertain (Sommer *et al.* 2010), it is possible that protected areas may no longer be located appropriately for the flora they are intended to protect (Hannah *et al.* 2002; Hannah *et al.* 2007).

The study of past vegetation dynamics offers unique insight into present patterns and possible future behavior in response to environmental change (Willis & Birks 2006; Rull 2012). Here, we have used pollen data to reconstruct latitudinal and temporal trends in the PFT diversity of the European vegetated landscape throughout the Holocene. We find that European PFT diversity increased throughout the Holocene, and that rates of increase differed between the southern, middle, and northern zones of Europe, leading to a strengthening of the LDG. We also observe an acceleration in the rate of increase in PFT diversity in the middle and southern zones during the most recent three millennia, which we attribute to human impact, in contradiction to Huntley's (1990a) assertion that human impact is not visible in Holocene vegetation history at the European continental scale.

The fact that temporal and spatial trends in PFT diversity are only weakly correlated with Holocene climate dynamics suggests that European vegetation (in terms of PFTs) is not in equilibrium with climate; this agrees with the findings of Svenning & Skov (2004) and Araújo & Pearson (2005). Also in agreement with Svenning & Skov (2007), we conclude that post-glacial migrational lag and human impact, rather than Holocene climate dynamics, shaped Holocene and modern European PFT diversity

The observed strengthening in the European PFT LDG over the Holocene contradicts the findings of Haskell (2001) that the gradient was constant throughout the Holocene. While our findings regarding trends in changes in the European PFT LDG are similar to those of Silvertown (1985), our results do not support that author's conclusions that climate causes the changes.

Much research effort has focused on where Europe's interglacial vegetation found refuge during glacial periods, as well as how quickly they could have spread out from these refugia during warm inter-glacial periods. It is generally accepted that most European vegetation found refuge in the south (Bennett *et al.* 1991; Hewitt 1999; Médail & Diadema 2009), but evidence also exists for northern refugia for various taxa (Kullman 2008; Svenning *et al.* 2008). While not precluding the significance of northern refugia, this study reinforces the importance of southern refugia by showing that southern European PFT diversity has been high relative to that of middle and northern Europe throughout the Holocene.

The fact that European PFT diversity is not in equilibrium with climate, but rather shows evidence of migrational lag throughout the Holocene influenced by human impact in recent millennia, has implications for conservation. In particular, it suggests that anticipating future patterns of diversity will be much more complex than modeling future climates, successional phases, and biogeochemical cycling as was done by Hickler *et al.* (2012); it will require incorporating the effects of dispersal lag and human activity as well, which may be difficult to incorporate into modelling efforts.

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**My professional goal is to use
my passion for nature conservation,
my diverse international experience,
my strong environmental science background, and
my excellent communication and interpersonal skills
to work for the protection of the Earth's
flora, fauna, and wild places.**

Education

2008 – present **Ph.D, environmental science**, École Polytechnique Fédérale Lausanne (EPFL), Switzerland.
Topic: *Vegetation change, climate, and human impact in Europe since the last glaciation*.
Graduation date: *26 March 2013*.

2003 – 2007 **Bachelor of Arts, *cum laude***, Dartmouth College (Ivy League university), USA.
Senior honors thesis: *Ecotoxicity and microbial biogeochemistry in Antarctic soils*.[1]
Double major: *Ecology, Environment*. Study abroad programs: *Africa, Mesoamerica*.

1999 – 2003 **First in class, GPA 4.0/4.0**, Amphitheater High School, Tucson, Arizona, USA.
Independent research project: *Water resources management in a desert city*.

Professional Experience

2008 – present **Doctoral research assistant,** *École Polytechnique Fédérale Lausanne, Switzerland*.

- Designed and executed studies resulting in 4 peer-reviewed publications (2 in prep[2,3], 2 published[4,5]) on changes in European vegetation, soil, climate, and human land use since the last glaciation (10,000 years ago). Work required data mining and analysis, writing and trouble-shooting computer code in multiple programming languages, and making maps.
- Co-organized 1-week workshop of 20 participants to study modern European vegetation patterns. Managed team of 10 people to assemble database from over 60 data contributors. Workshop resulted in 1 peer-reviewed publication[6] and a publicly-available database representing nearly 5000 localities.
- Organized weekly lab research seminars and 3 networking events for EPFL graduate students.
- Designed and delivered 3 earth science workshops for elementary school students. Participated in 5 conferences and 1 summer school, presenting research results and organizing group projects. Taught 3 years of undergraduate lab in GIS & Remote Sensing.
- Prepared and presented invited talks at World Meteorological Organization, UN, Geneva; Civil and Environmental Engineering Department, EPFL; Departments of Biology and Geosciences, University of Lausanne.

2012 **Invited speaker, assistant program coordinator**, *Planet Under Pressure conf., London*.

- Spoke as 1 of 6 panelists in main conference session on solutions-oriented sustainability policy to audience of over 3,000 people.
- Spoke as 1 of 5 panelists in breakout session on value of communication and networking in earth system science to audience of 30 people.
- Directed committee to draft young scientist conference declaration aimed at 2012 UN Conference on Sustainable Development. Planned and organized meetings, established protocols, created and managed blog to collaboratively draft group statement with team of 30 people. Delivered statement onstage to over 3,000 conference delegates.
- Organized and presided over young scientist networking event attended by 70 delegates.

- Wrote contribution to conference blog; created and moderated young scientist web forum; invited columnist for scientific journalism publication.[7]

2007 – 2008 **Park ranger**, *Sequoia National Park, California, USA.*
Designed and delivered educational talks and guided nature tours on forest and cave ecology to approx. 20,000 visitors (including elementary school groups) over 9 months. Assisted park scientists in bear tracking, cave surveys, invasive species management, fire risk evaluation, air quality assessment, and snowpack monitoring.

2007, summer **Mountain hut guardian**, *Moosilauke Ravine Lodge, New Hampshire, USA.*
Provided hospitality to guests and maintained facilities. Designed and delivered educational talks on topics in local ecology and geology to approx. 800 visitors over 5 months.

2007, winter **Student researcher**, *Dartmouth foreign studies in Costa Rica and Little Cayman Island.*
Designed and executed 8 collaborative and 1 independent field study on topics in terrestrial and marine ecology with a team of 15 colleagues in 6 distinct ecosystems over 3 months. Analyzed data, wrote peer-reviewed reports, assisted in editing the resulting 254-page summary publication[8]. Served as team's Spanish-English translator.

2005 – 2006 **Research intern**, *U.S. Army Corps of Engineers, New Hampshire, USA.*
Collected soil samples on military installations, performed chemical laboratory analyses of explosives and heavy metals contamination, analyzed data, presented results relevant to groundwater quality through 2 written reports and 1 poster session.

2005, winter **Student researcher***, Dartmouth foreign studies in South Africa, Namibia, Swaziland*.
Surveyed topics in land use, water resources management, wildlife conservation, ecotourism, sustainable development, and social justice through field excursions over 3 months. Collaboratively managed a team of 20 colleagues in writing a 192-page summary report on issues in southern African food security[9].

Computer Skills

PostgreSQL, Fortran90, R, GMT, netCDF, CDO, AWK, GRASS GIS, Unix/Bash, Windows/Mac

Languages

English (native language), French (fluent), Spanish (limited working proficiency), German & Italian (beginner)

Activities

I love ***learning*** new skills and ***perfecting*** old ones, and I highly value ***fitness*** and ***exploring*** the outdoors. By practicing a variety of mountain, water, and ***endurance*** sports, I am always ***testing my limits***. During the week I run or swim, and on weekends I ski-tour, climb, hike, or cycle. I have raced in several running, cycling, and triathlon ***competitions***. I also enjoy ***team sports*** like soccer, volleyball, and badminton, and my ***creative side*** comes out through reading, photography, piano, dance, and cooking.

Publications

[1]Collins. (2007). ***Fluoride in Victoria Land, Antarctica, and its impact on soil biota***. Dartmouth College thesis, 52 pgs.

[2]Collins, Davis, Mauri, Kaplan. (in prep.) Increasing plant functional diversity in post-glacial Europe: Climate, migration, human impact, and the latitudinal diversity gradient. *Ecol. Lett.*

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[4]Collins, Davis, Kaplan. (2012) The mid-Holocene vegetation of the Mediterranean region and southern Europe, and comparison with the present day. *J. Biogeogr*., vol. 39, 1848-1861.

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[7]Collins. (2012). Feeling good about being green. *Research Europe*, vol. 344, 8.

[8]Peart, Barrow, Fownes, et al., eds. (2007) *Dartmouth Studies in Tropical Ecology*. Contributing author, Dartmouth Ecology Foreign Studies Program, 254 pgs.

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