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3 **Pan-Mediterranean Holocene vegetation**

4 **and land-cover dynamics from synthesised pollen data**

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## 26 **ABSTRACT**

27

### 28 **Aim**

29 The Mediterranean is characterised by diverse and spatially-heterogeneous mosaic  
30 landscapes. Within this study a cluster analysis-based method is developed for the  
31 classification of Mediterranean vegetation types based on modern and fossil pollen datasets.  
32 The application of this approach to multiple pollen records spanning the Mediterranean  
33 region has allowed temporal variations in vegetation dynamics to be explored throughout the  
34 Holocene. We ask how far back stable baseline vegetation communities can be identified in  
35 the pollen record, and whether those types considered to be characteristic of the  
36 Mediterranean landscapes have been present in the past as well as at the present.

### 37 **Location**

38 The research location includes the land areas surrounding the Mediterranean Sea. The pollen  
39 sites are principally located in mainland Spain, southern France, Greece and Turkey, Italy,  
40 North Africa, the Levant, and some Mediterranean islands.

### 41 **Methods**

42 5641 samples from 158 fossil pollen records (cores) and 1799 modern pollen surface samples  
43 were harmonised taxonomically and pollen count data summed into 200-year time windows  
44 on a common timescale from 11,000 BP to the present-day. Cluster analysis and community  
45 classification was used to identify major vegetation types along with other approaches to  
46 explore patterns in ecological datasets, such as Simpson's diversity index and non-metric  
47 multidimensional scaling.

### 48 **Results**

49 The pollen datasets were classified into eleven closed forest/woodland and five open or  
50 scrubland vegetation types. Closed vegetation clusters declined from the mid-Holocene with

51 a marked increase in open or human-modified vegetation types since 3500 BP and with an  
52 increasing rate of vegetation change and habitat diversity through time.

53 **Main conclusions**

54 The Mediterranean has been a dynamic landscape throughout the Holocene with frequent  
55 changes in land cover identified in the pollen datasets. The pollen-inferred clusters reveal a  
56 wider range of Mediterranean vegetation types than identified in previous studies; for  
57 example, including both beech and alder woods. Evergreen Oleaceae-dominated shrubland is  
58 much better represented in modern than in fossil samples while mesic forest was abundant in  
59 the past but is uncommon today.

60

61 **Keywords:** Disturbance; Holocene; Human impacts; Land-cover; Landscape structure;  
62 Mediterranean; Pollen; Vegetation

63

64

## 65 INTRODUCTION

66

67 Pollen analysis offers a valuable tool for exploring long-term changes in vegetation and land  
68 cover (Jackson & Blois 2014; Edwards et al., 2017). Numerous studies have mapped and  
69 classified European vegetation using fossil pollen for discrete time intervals through the  
70 Holocene in relation to climate and major environmental gradients (e.g. Huntley, 1990;  
71 Prentice et al., 1996; Peyron et al., 1998). This has led to the description of plant functional  
72 types, the identification of ‘biomes’ and their spatial and temporal distribution (e.g. Marinova  
73 et al., 2017), climate reconstruction based on pollen and vegetation modelling (e.g. Guiot &  
74 Kaniewski, 2015) and geographical mapping of individual taxa (Brewer et al., 2017).  
75 Understanding patterns of vegetation dynamics and biogeographic change allows improved  
76 knowledge of the habitats within ecoregions and their responses to disturbance and  
77 environmental change, which can provide frameworks for biodiversity conservation policies  
78 and ecological modelling (Blasi et al., 2014). Previous studies have often focused on  
79 continental scales. For example the ‘BIOME 6000’ mapping project (Prentice et al., 1996;  
80 Prentice & Webb, 1998) provided a pollen-based landscape reconstruction for Europe for two  
81 time periods (6000 and 0 BP) based on modern and fossil data, notably for climate-biosphere  
82 modelling. However, continental-scale descriptions of vegetation types can be less  
83 informative about ecologically diverse sub-regions, such as the Mediterranean. There is  
84 potential for more detailed classification and reconstruction of Mediterranean ecoregions (e.g.  
85 Collins et al., 2012), which can allow exploration of how vegetation types developed in  
86 relation to human land modification.

87

88 The present vegetation of the Mediterranean region is the product of a distinctive climate and  
89 natural environment transformed by human activities over many millennia (Jalut et al., 2009).

90 Improved understanding of the unique vegetation assemblages that characterise the  
91 Mediterranean landscape and how these have changed over millennia has potential value in  
92 identifying vegetation types at risk from future land use change. Much of the modern  
93 Mediterranean vegetation has been altered by deforestation, over-grazing, erosion and  
94 burning (Vogiatzakis et al., 2006). In recent decades these factors have led to a shift from  
95 highly heterogeneous landscapes maintained by multiple different land uses, to more  
96 homogeneous landscapes, for example, following land abandonment on some European  
97 shores of the Mediterranean (Pausas, 1999). Wildfires are also an important feature of  
98 Mediterranean ecosystems and their associated disturbance regimes (Rundel et al., 1998).  
99 Animal grazing has been a constant disturbance factor throughout the Holocene, and has been  
100 important in maintaining open and mosaic landscapes (Blondel, 2006). Plant distribution is  
101 also restricted by environmental factors such as species' climatic tolerances and interspecific  
102 interactions (e.g. García-Valdés et al., 2015). Climate is an important driver of vegetation  
103 turnover through previous interglacial periods (e.g. Langgut et al., 2011) and some studies  
104 employ pollen analysis as a tool to reconstruct past climate (e.g. Mauri et al., 2015). Since the  
105 mid-Holocene, the increasing impact of human land use has been demonstrated in numerous  
106 studies (e.g. Colombaroli & Tinner, 2013). Consequently, disentangling the impacts of  
107 climate and human land use on vegetation shifts can be complex, notably for recent  
108 millennia.

109

110 The aims of this study are to: 1) develop a data-led method for the classification of vegetation  
111 types based on modern and fossil pollen datasets across the Mediterranean region; 2) identify  
112 temporal and spatial variations in the abundance of different vegetation types and explore  
113 whether stable baseline vegetation communities can be identified in the pollen record; and 3)  
114 compare these results with previous studies that have classified and mapped vegetation from

115 pollen data and modern vegetation associations. These aims will be achieved via use of  
116 cluster analysis to derive a numerical classification of vegetation types from pollen taxa  
117 associations. This approach has the potential to be applied to multiple sequences covering  
118 broad geographic regions and is flexible enough to accommodate additional datasets in the  
119 future. Databases of modern pollen samples (Davis et al., 2013) and fossil pollen (e.g. Fyfe et  
120 al., 2009) have been used for this macro-ecological study.

121

## 122 **METHODS**

123

### 124 **Modern and fossil pollen datasets**

125

126 Pollen count data have been obtained from the European Modern Pollen Database (Davis et  
127 al., 2013) and the European Pollen Database for fossil records (version: May 2016) (Leydet,  
128 2007-2017). The analyses are based on 1799 modern surface samples and 158 fossil pollen  
129 records (cores) from 143 sites (Supplementary Information 1). Only pollen sequences with  
130 reliable chronologies (sensu Giesecke et al. 2013) were used. These provide more  
131 independent age control for the mapping of vegetation change than has been possible in  
132 previous studies. The pollen count data from each site have been summed into 200-year time  
133 windows from 11000 BP to present. These allow vegetation changes of sub-millennial  
134 duration to be identified, avoid ‘smoothing’ that might result from using longer time windows  
135 (Fyfe et al., 2015) and enable direct temporal comparison among sites. The modern (i.e.  
136 surface) pollen and most recent (200 BP - present) fossil samples are separated in the  
137 analyses. The majority of the modern pollen samples derive from moss polsters or soils and  
138 there is no duplication of core top samples between the modern and fossil datasets. This has  
139 resulted in 3852 fossil samples distributed across 55 time windows, and a total of 5641

140 modern/fossil pollen samples. Pollen sites located in areas with characteristic Mediterranean  
141 climate and vegetation have been selected for analysis (Fig. 1), as defined using the  
142 vegetation zones illustrated by Izdebski et al. (2015) and Ozenda & Borela (2000). Pollen  
143 sites from the Rhone Valley in southern France were also included in the initial cluster  
144 analysis to identify land-cover types at higher elevation, but these sites were subsequently  
145 removed for analysis of patterns in the Mediterranean, leading to 105 fossil records and 1610  
146 modern samples.

147

148 The taxonomy of the modern and fossil datasets has been harmonised and simplified using  
149 the EPD nomenclature (Leydet, 2007-2017). Different levels of taxonomic resolution were  
150 chosen for specific purposes. For example, key indicator species; i.e. taxa that are associated  
151 with certain land use types, such as arable weeds, were grouped at the species level (e.g.  
152 ribwort plantain (*Plantago lanceolata*)), whereas other taxa were combined at a higher  
153 taxonomic level, such as all evergreen oak species and varieties (e.g. *Quercus ilex* and  
154 *Quercus suber*). There are challenges for pollen analysts in subdividing the *Quercus* group  
155 based on the morphology of the pollen grains. For example, *Quercus cerris/suber* types,  
156 which represent both evergreen and deciduous types, are often combined by analysts due to  
157 difficulties in distinguishing them using a light microscope. Certain assumptions are required  
158 when utilising large databases that have been compiled from the work of numerous different  
159 analysts, for example, '*Quercus* undifferentiated' could represent evergreen or deciduous  
160 *Quercus* when not identified to species level. Within the dataset presented here, deciduous  
161 *Quercus* appears in 150 sequences and evergreen *Quercus* has been identified in 125  
162 sequences, therefore in the majority of cases analysts have separated different oak types.  
163 Only taxa with >1% occurrence that occur in >50 samples were included, resulting in 260  
164 pollen taxa. The geographical coverage of this dataset is good for most of the European



165 Mediterranean but poorer for the African side. This needs to be taken into account when  
166 interpreting results, as all phytogeographical conditions may not be represented. The terms  
167 ‘vegetation clusters’ and ‘vegetation/pollen assemblages’ are used interchangeably and  
168 ‘cluster group’ is used to describe the resulting collection of pollen samples that fall into a  
169 particular ‘cluster’ number.

170

## 171 **Data analysis**

172

173 Ward’s hierarchical agglomerative clustering method (Ward, 1963; Murtagh & Legendre,  
174 2014) has been applied to the amalgamated modern and fossil pollen dataset using the ‘Rioja’  
175 R package (Juggins, 2015). This unsupervised data-driven approach was used to assign pollen  
176 samples to cluster groups based on the similarity of their taxa assemblages without excluding  
177 any land pollen taxa from the dataset (other than those <1% with fewer than 50 occurrences).  
178 Whilst many approaches exist for classification of multivariate data, these generally produce  
179 similar results in pollen datasets (Felde et al., 2014; Felde et al., 2016). Cluster analysis  
180 allows hierarchical aggregation at different classification levels (García-Madrid et al., 2014).  
181 Detailed comparison of the pollen samples and assemblages at different clustering levels has  
182 allowed exploration of the cluster groups that separate at a lower clustering level (e.g. six  
183 clusters) and are represented by more distinct vegetation groups (Table 1). Unsupervised  
184 cluster analysis assigns pollen samples into a predetermined number of groups. The ratio of  
185 change between cluster groups through time, which may represent a measure of community  
186 turnover, was calculated by identifying the number of pollen samples that switch to a new  
187 cluster or remain within the same cluster between successive time windows and transforming  
188 these values into a ratio of change to non-change.

189

190 After assigning pollen samples to clusters statistically, a phytosociological classification  
191 approach was used to identify the frequent and abundant taxa within each group based on the  
192 number of occurrences of the taxon, the average percentage, median and interquartile range  
193 (IQR). The resulting community tables were used to facilitate the selection of interpretive  
194 name descriptors for each cluster based on the most frequent/abundant taxa along with  
195 comparisons with other classification systems (Küchler & Zonneveld, 1998; Bossard et al.,  
196 2000; Allen, 2009). The pollen cluster groups have also been compared against land cover  
197 and land use types defined by the Corine (COoRdination of INformation on the Environment)  
198 remotely-sensed land cover maps (European Environment Agency (EEA), 2016) and the  
199 results of previous studies (Huntley, 1990; Prentice et al., 1996; Guliot et al., 1996; Peyron et  
200 al., 1998). An individual taxon's frequency is determined by calculating its number of  
201 occurrences divided by the number of samples in the cluster and assigning one of five  
202 frequency classes based on cut-off values between each group, which follows the method  
203 used by Perez et al. (2015). If a taxon appears in 81-100% of all samples in the cluster group  
204 it is assigned the highest frequency class. The relative proportions of samples in each cluster  
205 group have been calculated for each fossil pollen 200-year time window and the modern  
206 pollen surface samples.

207

208 Non-metric multidimensional scaling (nMDS) was applied to the data using the R 'vegan'  
209 package (Oksanen et al., 2016) as a complementary method to summarise major variation in  
210 the dataset. Kernel density plots of nMDS scores have been produced to show the overlap or  
211 distinctiveness of cluster groups in ordination space with contours to highlight greater density  
212 of samples. Simpson's diversity index has been calculated for each pollen sample using raw  
213 pollen percentage data. This diversity index was selected as it takes both species richness and  
214 evenness into account (Simpson, 1949) and is frequently used to explore diversity change in

215 pollen datasets (e.g. Morris et al., 2014). Although species diversity indices provide only  
216 limited information about community ecology and species abundance (Chiarucci et al., 2011)  
217 this index provides a complementary method and has allowed diversity change in the pollen  
218 datasets to be explored independently of the cluster analysis approach. The differential pollen  
219 productivity of different plant types is not accounted for in the methods presented here;  
220 therefore, some high pollen producers, such as *Pinus*, may be over-represented in some  
221 clusters. Lower pollen producers are recognised within the method, as they may appear  
222 consistently represented in certain clusters as frequent taxa in spite of their lower abundance  
223 values.

224

## 225 **RESULTS**

226

### 227 **Defining pollen cluster groups**

228

229 After analysing the community classification of various groups of sites at different  
230 hierarchical levels (Table 1) within the dendrogram, 16 clusters have been chosen as a  
231 suitable number to reflect the range of land cover types represented in the pollen dataset  
232 (Table 2). These are based on a hierarchical classification that aggregates the 16 clusters into  
233 eight major groups. Preston et al. (2013) suggested that decisions about the number of  
234 clusters should be “based on the purpose of the study because there is no single ‘correct’  
235 classification”. Choosing 16 clusters allows us to address the aims of this study and identify  
236 changes in key vegetation assemblages through time. Some of the open land cover clusters  
237 are composed of complex mixtures of relatively low abundance, but frequently occurring  
238 taxa, whereas forest (closed vegetation) clusters are usually distinguished by one or two  
239 dominant arboreal taxa (Fig. 2). The open vegetation clusters include both ‘anthromes’

240 (anthropogenic biomes; Ellis, 2015), such as grassland, with indicators of arable and  
241 disturbed land, and naturally occurring open land cover types, such as steppe. Some clusters  
242 were composed entirely of either fossil or modern samples, i.e. indicating the possible  
243 existence of non-analogue vegetation assemblages. Clusters are presented according to their  
244 corresponding ‘super group’, i.e. a broader group that they are statistically assigned to at a  
245 lower clustering level (Table 1). Many of the pollen records do not cover the entire Holocene;  
246 therefore some periods of time are represented by fewer sites than others. The number of sites  
247 does not drop below 30 for any time interval, which is a suitable number for calculating  
248 averages. However, site numbers do drop below 30 when split by elevation group, and  
249 interpretations need to be made with caution when site numbers are very low for a particular  
250 time window.

251

252 Some cluster groups comprise pollen samples that are similar to one another while other  
253 cluster groups are more diverse when mapped by nMDS scores (Fig. 3). For example, all of  
254 the open vegetation clusters occupy a larger area in nMDS space while the forested clusters  
255 occupy smaller areas on the plots. The nMDS stress value was 0.224, which indicates that the  
256 analysis cannot adequately collapse the variability within the 260 taxa across the samples into  
257 two dimensions. This explains the overlap of clusters within the nMDS ordination space and  
258 highlights the value of the cluster analysis approach in providing a more detailed and useful  
259 way to identify major vegetation types.

260

## 261 **Defining Mediterranean vegetation types**

262

263 *Open vegetation assemblages*

264 The pollen taxa assemblages derived for clusters 1.1 (sclerophyllous parkland), 1.2  
265 (evergreen oak shrubland: Oleaceae), 1.3 (sclerophyllous steppe/parkland) and 1.4  
266 (parkland/grassland) are typical of open landscapes, which are often recognised as being  
267 human modified (Table 1; see Fyfe et al., 2018). Cluster 1.1 is a very mixed group with  
268 median values below 8% for all frequently-occurring taxa, while cluster 1.2 has high values  
269 for Oleaceae, which includes both cultivated olive groves and wild trees. The most frequent  
270 and abundant taxon in cluster 1.3 is goosefoot family (Chenopodiaceae), a typical steppe-land  
271 type, but this cluster also includes frequent occurrence and relatively high abundance of pine  
272 (Pinaceae), grass (Poaceae) and mugwort/wormwood (*Artemisia*). Cluster 1.4  
273 (parkland/grassland) is a very large group that includes 583 pollen samples. The cluster  
274 includes high values for grass, with frequent occurrence of pine, deciduous/evergreen oak  
275 (*Quercus*), arable and grassland indicators. Many of these taxa have broad IQR values  
276 indicating a mixed and varied group. Within cluster 2.0 (evergreen shrubland/woodland:  
277 *Quercus*), certain taxa have higher IQR than others, for example, evergreen oak has a fairly  
278 narrow IQR, while grass in contrast has a large IQR, indicating that evergreen oak is the  
279 distinctive taxon for this cluster.

280

281 The removal of aquatic pollen taxa and spores (such as *Myriophyllum*, *Menyanthes*,  
282 *Sphagnum*, *Potamogeton*) from the dataset means that identifying wetlands is restricted.  
283 However, sedges (Cyperaceae) include both aquatic and dryland plants, so this taxon has  
284 been included in the dataset. Cluster 3.0 (pasture/wetland) is distinguished by high values of  
285 sedge and also includes frequent occurrence of pine and grass. It is common at sites above  
286 500 masl, where it appears to represent pastureland, as well as some lowland sites where it is  
287 more likely to be indicative of wetlands.

288

289 *Pine forests/woodlands*

290 Clusters 4.0 (pine forest), 5.1 (pine woods), 5.2 (pine steppe) and 7.0 (fir forest) are  
291 dominated by pine (Table 1), which produces high amounts of pollen that can travel great  
292 distances (Broström et al., 2008) and can be over-represented in pollen records. There are  
293 many Mediterranean pine species with contrasting ecologies, ranging from *Pinus sylvestris*,  
294 which is typical of cooler montane environments, to *Pinus halepensis* that grows in coastal  
295 regions. These different species of pine may not always be consistently or easily  
296 distinguished palynologically, and this limits the environmental significance of the combined  
297 *Pinus* clusters; however, the associated taxa (the constant, frequent and common types) can  
298 assist in understanding the nature of the vegetation communities represented in these  
299 samples. Cluster 5.2 (pine steppe) is dominated by a combination of pine, grass and sedge  
300 with similar values for each, whereas cluster 7.0 is a distinctive fir cluster group, which also  
301 includes a mixture of other deciduous and coniferous woodland types. *Abies* and *Picea* have  
302 been separated from *Pinus* in the dataset and Pinaceae is mainly composed of *Pinus*, but as  
303 other genera such as *Cedrus* are in the same family, the name used here to describe this group  
304 is Pinaceae.

305

306 *Deciduous and mixed forests/woodlands*

307 This "super group" includes clusters 6.1 (deciduous oak woods), 6.2 (deciduous oak  
308 parkland), 8.1 (alder woods), 8.2 (coniferous forest), 8.3 (beech woods) and 8.4 (mesic forest)  
309 (see Table 1 for a list of the dominant taxa in these groups). Cluster 6.1 is a distinct deciduous  
310 oak class whereas grass and pine are also key taxa in cluster 6.2. Cluster 8.1 includes samples  
311 with a high, but wide, IQR for alder, with frequent but lower values of a selection of other  
312 deciduous woodland types, pine, sedge and grass. Cluster 8.3 has high average values for  
313 beech (*Fagus*) and other taxa that occur frequently in the dataset, and cluster 8.2 represents a

314 combination of spruce, pine and fir. Cluster 8.4 is distinct from the other clusters in this broad  
315 group and described as ‘mesic forest’ with high average values for elm, hazel and oak,  
316 although, pine, grass, birch, alder and sedge also frequently occur in samples in this group  
317 and all taxa have fairly wide IQR, indicating that this is a varied woodland group.

318

### 319 **Deciphering patterns of vegetation change**

320

321 The overall patterns of Holocene vegetation change (Fig. 4) reveal that pine forest (4.0), pine  
322 woods (5.1) and deciduous oak woods (6.1) dominated the early Holocene period prior to  
323 8000 BP. These were then partly replaced by other cluster groups, especially wooded  
324 parkland (e.g. cluster 6.2: deciduous oak parkland and 1.1: sclerophyllous parkland) into the  
325 mid-Holocene (i.e. 8000-4500 BP). Some vegetation clusters increased in abundance during  
326 the latter part of the record after ~4500 BP (e.g. 3.0 (pasture/wetland) and 1.4  
327 (parkland/grassland). A number of clusters also only appear in the second half of the  
328 Holocene, such as 8.3 (beech woods), 8.1 (alder woods) and 1.2 (evergreen shrubland:  
329 Oleaceae). The declining nMDS scores and varied ratio of change in the early Holocene  
330 appears to reflect shifts in vegetation patterns as a result of natural processes, notably  
331 adaptation to the onset of interglacial climatic conditions. This was followed a period of  
332 greater vegetation stability between ~9000 and 6000 BP with more consistent nMDS scores  
333 and steadily increasing diversity. Since the mid to late Holocene there has been an increasing  
334 ratio of change in the pollen-inferred vegetation clusters (since ~5000 BP) and nMDS scores  
335 (since ~2000 BP), while the Simpson’s diversity index steadily increased throughout the  
336 entire Holocene. The nMDS patterns (Fig. 3) indicate that the open vegetation types that have  
337 prevailed during the later Holocene are more diverse taxonomically. Overall, the ratio of  
338 change and analysis of ecosystem trajectories (Fyfe et al., 2018) indicate continual turnover

339 during the Holocene, rather than any clearly identifiable stable baseline state for  
340 Mediterranean vegetation.

341

342 Grouping sites according to elevation has revealed that needle-leaf forests (4.0, 5.1 and 5.2)  
343 and deciduous oak woods/parkland (6.1 and 6.2) were abundant in the early Holocene at the  
344 lowest elevation (below 500 m) (Fig. 5). Parkland/grassland (1.4), sclerophyllous  
345 steppe/parkland (1.3) and pasture/wetland (3.0) then become more abundant from the mid-  
346 Holocene, and in the most recent 5000 years evergreen shrubland (Oleaceae) (1.2) and alder  
347 woods (8.1) increase. Evergreen shrubland (1.2) is most abundant in this lowest elevation  
348 group. At mid-elevation levels (between 500-1200 m) in addition to pine forest types, mesic  
349 forest (8.4) has high values in the early Holocene, while beech woods (8.3) become  
350 significant after ~3500 BP. Conifer trees are most common at the highest elevation level  
351 (above 1200 m), with pine forest/woods types (4, 5.1 and 5.2) having very high values in the  
352 early Holocene (greater than 80% when pine clusters are combined), which are then partly  
353 replaced by fir, conifer and pine steppe (7.0, 8.2 and 5.2).

354

355 There are cluster groups in the fossil record that are not represented in the modern dataset; for  
356 example, mesic forest (8.4), which may represent a non-analogue community, as it is also  
357 absent in the most recent fossil pollen time window (200 BP - present). However, there are no  
358 groups that are present in the modern dataset that are not also present in the fossil dataset,  
359 although some clusters appear rarely, for example, 2.0 (evergreen shrubland: *Quercus*) and  
360 1.2 (evergreen shrubland: Oleaceae). The modern surface samples cover a much larger  
361 geographical area, as there are around ten times more site locations than in the fossil dataset,  
362 and greater diversity of landscape types may be therefore expected in the modern dataset. On



363 the other hand, the fossil dataset is much larger than the surface pollen dataset in terms of the  
364 number of samples included and encompasses landscape types that have changed over time.

365

## 366 **DISCUSSION**

367

368 The pollen-based results indicate that modern/recent vegetation in the Mediterranean basin is  
369 spatially diverse, in accord with vegetation mapping using remote sensing and ground-level  
370 field survey, as reflected by the Corine remote sensed land cover map (Fig. 6). The similarity  
371 between pollen clusters and the Corine maps is best in areas with homogeneous land cover,  
372 whereas more heterogeneous landscapes lead to poorer matches (Woodbridge et al., 2014).

373 The Corine map and pollen-inferred vegetation clusters show good overall similarities, for  
374 example, parkland/grassland (1.4) and sclerophyllous parkland (1.1) are similarly reflected by  
375 both datasets in north central Spain while the evergreen shrubland (Oleaceae) (1.2) cluster is  
376 located in areas of olive groves in south central Spain shown on Corine maps. However, there  
377 are also dissimilarities, which relate to the difference in these two data types in sensing  
378 vegetation patterns (Woodbridge et al., 2014). This partly results from the amalgamation of  
379 pollen types reaching a site in a mosaic landscape and the difficulty in identifying some  
380 landscape types palynologically. Differential pollen productivity and dispersal may lead to  
381 over-representation of pine forests and under-representation of some herbaceous taxa and  
382 thus open vegetation types.

383

384 Plotting pollen samples in nMDS space according to cluster group (Fig. 3) provides an  
385 independent assessment of the major patterns within the dataset, although the full range of  
386 variability is not captured by two dimensions. Similar vegetation types identified according to  
387 the cluster analysis approach occupy similar areas of nMDS ordination space, such as all pine

388 dominated forest types (4.0, 5.1 and 5.2) while the two evergreen shrubland types (1.2 and  
389 2.0) also occupy similar nMDS space.

390

### 391 **Temporal dynamics in vegetation patterns**

392

393 The cluster analysis-based approach and datasets presented here and in a companion paper  
394 (Fyfe et al., 2018) focussing on exploring trajectories of change, permit a more detailed  
395 description of Mediterranean vegetation change through the Holocene than some previous  
396 studies. Prentice et al. (1996), for example, identified only four key vegetation types in the  
397 Mediterranean: xerophytic woods/scrub, temperate deciduous forest, broad-leaved  
398 evergreen/warm mixed forest, and steppe. These vegetation types are reflected by the limited  
399 array of pollen clusters shown in Fig. 6. Within the ‘BIOME 6000’ mapping project (Prentice  
400 et al., 1996), the Mediterranean was dominated by “temperate deciduous broad-leaf forest” at  
401 6000 BP and by “xerophytic woods/scrub” and “warm-temperate evergreen broad-leaf and  
402 mixed forest” at 0 BP. The vegetation clusters presented in our new analysis reveal a much  
403 wider range of forest types, which appear to shift northwards between 6000 BP and the  
404 present day. For example, they include 6.2 (deciduous oak parkland), 4.0 (pine forest) and 5.1  
405 (pine woods) in northern Spain at 6000 BP, while 1.1 and 1.3 (sclerophyllous clusters) were  
406 restricted to southern Spain. The forest types in northern Spain were then replaced by clusters  
407 1.1 and 1.3 and other open vegetation types (e.g. 1.4 (parkland/grassland) and 3.0  
408 (pasture/wetland) while some forests persisted, primarily in upland regions, with the  
409 appearance of others such as 8.3 (beech woods). This matches the BIOME 6000 analysis of  
410 vegetation change in Iberia and Greece between the mid-Holocene and modern presented in  
411 Roberts et al (2004; plate 7).

412

413 In a cluster analysis-based approach, Huntley (1990) identified key taxa associations using  
414 percentage data for 44 pollen taxa, which were placed on a six-point smoothed scale, and  
415 mapped these across Europe for specific time slices. According to Huntley (1990), at 6000  
416 BP the Mediterranean was represented by three vegetation types (described in Table 2). The  
417 pollen cluster results presented for the current study provide a more detailed reconstruction of  
418 vegetation assemblages and greater representation of open landscapes (Fig. 6). For example,  
419 cluster 1.4 (parkland/grassland) and 1.1 (sclerophyllous parkland) are the main open  
420 landscapes in Italy, while 1.3 (sclerophyllous steppe/parkland) and 1.2 (evergreen shrubland:  
421 Oleaceae) are more widely represented in Spain.

422

423 Differences between the cluster results for the modern and most recent fossil datasets (Fig. 4)  
424 may be partly influenced by differences in the spatial distribution of sites. Coniferous, fir and  
425 alder woods (clusters 8.2, 7.0 and 8.1) are poorly represented in the surface pollen dataset,  
426 but are present in the fossil data, including the most recent time window (200 BP - present).  
427 The modern samples are not always co-located with the fossil datasets and thus sample  
428 different parts of the landscape. Differences between modern and most recent fossil pollen  
429 vegetation types are also due to real changes in land cover that have occurred in recent  
430 decades, and are linked to both direct and indirect anthropogenic intervention. This has been  
431 demonstrated by Colombaroli et al. (2007) with the disappearance of *Abies alba* at low  
432 altitudes in the Mediterranean since the Neolithic. It is clearly reflected in the cluster results  
433 (Fig. 5) when sites are separated by elevation groups, as fir forest (7.0) is well represented  
434 above 500 m, but does not appear in the dataset below this altitude.

435

436 Various factors lead to the existence of non-analogue vegetation assemblages (Williams &  
437 Jackson, 2007), such as rates of postglacial migration (Médail & Diadema, 2009), climate

438 change, human disturbance (Jalut et al., 2009) and altitudinal changes; for example, Geri et  
439 al. (2010) found that loss of Mediterranean forest has mostly been confined to low altitude  
440 areas. The altitudinal differences in the dataset reflect the ecotone boundaries of vegetation  
441 types and land use differences. For example, the only open vegetation type present >1200 m  
442 is 1.4 (parkland/grassland) and the only forest types represented at low elevation are 6.1 and  
443 6.2 (deciduous oak parkland/woods). In a comparison of Holocene vegetation diversity across  
444 a transect from central Europe to the Mediterranean, Colombaroli & Tinner (2013) identified  
445 how diverse open-land ecosystems increase when human disturbance intensifies while forest  
446 becomes less diverse, highlighting the important role of anthropogenic fire and other  
447 disturbance related activities. Pollen taxa diversity appears to increase with the development  
448 of cultural landscapes and not just as a by-product of deforestation (Colombaroli & Tinner,  
449 2013).

450

451 The patterns of change in different plant species and communities may sometimes be missed  
452 in the broad scale synthesis presented here. For example, evergreen *Quercus ilex*  
453 communities, which are recognised as more fire resistant than broad-leaf oak forests,  
454 developed before the emergence of Neolithic farming and were heavily impacted by land use  
455 strategies (e.g. Calò et al., 2012), but this pattern is not clearly shown in the changing  
456 abundance of the evergreen shrubland (dominated by *Quercus*) cluster (2.0). This suggests  
457 that regional patterns may become hidden within the broad scale synthesis, and that smaller  
458 spatial scale analyses would be required to investigate sub-regional patterns of vegetation  
459 change in more detail.

460

461 **Potential and actual natural vegetation**

462

463 There has been recent debate about potential natural vegetation (PNV) and the disconnect  
464 between PNV, actual vegetation and the role that palaeoecological evidence of past  
465 vegetation might play in determining or assessing PNV (e.g. Carrión & Fernandez, 2009;  
466 Chiarucci et al., 2010; Loidi et al., 2010; Jackson, 2013). Jackson (2013) sees PNV as a  
467 ‘useful fiction’, but one that might be better informed through use of data such as those  
468 presented here, which can be used to develop understanding of the processes that controlled  
469 historical vegetation character and change. PNV, when applied to the Iberian Peninsula, has  
470 modelled vegetation with a single dominant tree taxon at broad spatial scales (Carrión &  
471 Fernandez, 2009). This is not the case for the clusters generated in this analysis, which  
472 indicates frequent co-dominant species, even taking into account differential pollen  
473 productivity between taxa (Broström et al., 2008). Whilst it is recognised that the PNV  
474 concept encapsulates vegetation that would develop in the absence (or cessation of) human  
475 activity (Loidi et al., 2010), it is clear from palynological records that vegetation turnover  
476 rather than stability has been the norm in the Mediterranean, even in the absence of human  
477 impacts associated with agriculture and pastoralism.

478

479 Several long, continuous pollen records from the Mediterranean (e.g. Sadori et al., 2013)  
480 have demonstrated continuous vegetation change during past interglacial periods. These  
481 suggest that the character of ‘natural’ vegetation succession in the Mediterranean has been  
482 predictable and comparable during different interglacials (Tzedakis, 2007). Open woodland  
483 develops first, followed by expansion of deciduous oak, sclerophyll scrub, elm, hazel and  
484 lime, then by fir, beech and spruce, followed by reversion to open woodland. The fact that  
485 the early Holocene vegetation clusters presented here show similar patterns implies that  
486 predominantly natural processes were driving vegetation succession at least until ~8000 BP.  
487 Magri (1995) suggested that the Holocene interglacial may currently be experiencing a later

488 phase that matches previous interglacials during which natural openings in forests and the  
489 development of grasslands produced environments suitable for agriculture and pastoralism in  
490 the current interglacial. However, the complexity of land cover types and frequency of  
491 vegetation cluster change during the second half of the Holocene is likely to have been  
492 amplified by intensifying human impacts, a pattern also identified by Carrión and Fernandez  
493 (2009). In the pollen-based synthesis presented here, for example, total non-arboreal pollen  
494 across the Mediterranean increased from ~35% to ~47% between 3500 BP and recent times  
495 (Fig. 4). Looking to the future, dynamic vegetation models driven by future climate change  
496 scenarios predict a shift from mesic forest (the current PNV) to more open shrubland and  
497 eventually steppe as a result of reduced water availability (Hickler et al., 2012).  
498 Transformation of the vegetation by human agency has already begun this process over the  
499 past millennia.

500

## 501 **CONCLUSIONS**

502

503 We have demonstrated a method that allows exploration of vegetation dynamics in time and  
504 space and potentially the detection of non-analogue communities. A high degree of spatio-  
505 temporal heterogeneity is recognised in Mediterranean vegetation patterns (Shoshany, 2000)  
506 and this is evident within the results presented here. In comparison with some previous  
507 classification studies, such as the BIOME mapping vegetation classification (Prentice et al.,  
508 1996; Roberts et al., 2004), which often focussed on discrete time windows, our results show  
509 almost continuous turnover of most plant communities during the last 11,000 years, as  
510 demonstrated by the rate of vegetation cluster change (Fig. 4). This indicates that stable  
511 baseline vegetation communities cannot be easily identified, at least not at a pan-  
512 Mediterranean scale. Our transformation and synthesis of multiple modern and fossil pollen

513 records has revealed key vegetation types that existed in the past and are rare or absent in the  
514 modern landscape (e.g. mesic forest) and vice versa (e.g. evergreen shrub dominated by  
515 Oleaceae). The pollen cluster results highlight the potential of this approach to explore  
516 complex vegetation patterns and provide detailed information about vegetation assemblages  
517 not previously identified, which is open to future development with the availability of  
518 additional datasets.

519

520 While it can be difficult to establish precise causes for changes in vegetation, stochastic  
521 characteristics, associated with a range of disturbance factors, such as natural fire, climate  
522 fluctuations and human impacts, will have resulted in what are often considered to represent  
523 ‘subclimax’ vegetation communities. There is long-standing evidence of the complex  
524 interaction between plant assemblages, disturbance and climate (Colombaroli et al., 2007;  
525 Guiot & Kaniewski). If stable natural vegetation communities never existed when viewed on  
526 a Holocene timescale, then attempts to use them as targets for environmental restoration may  
527 be misplaced. Understanding land cover types in an area of the world with a long-standing  
528 (multi-millennial) history of human transformation has potential value in informing  
529 palaeoecologists, conservationists, and climate modellers, among other groups concerned  
530 with vegetation change and has potential to help identify biogeographic regions that are more  
531 resilient or susceptible to future disturbance.

532

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534

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540 coordinated by Marie-José Gaillard (Linnaeus University, Kalmar, Sweden). Thanks are also  
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542 helpful comments.

543

#### 544 **DATA AVAILABILITY STATEMENT**

545

546 The datasets underpinning this study are publically available from the European Pollen  
547 Database (<http://www.europeanpollendatabase.net/>). The results of the analyses carried out  
548 are available from the authors upon request.

549

#### 550 **REFERENCES**

551

552 Allen, H. (2009) Vegetation and Ecosystem Dynamics. In: Woodward, J. (Ed.) *The Physical*  
553 *Geography of the Mediterranean*. Oxford University Press, New York.

554 Blasi, C., Capotorti, G., Copiz, R., Guida, D., Mollo, B., Smiraglia, D. & Zattero, L. (2014)  
555 Classification and mapping of the ecoregions of Italy. *Plant Biosystems*, **148**, 1255-  
556 1345.

557 Blondel, J. (2006) The 'Design' of Mediterranean Landscapes: A Millennial Story of Humans  
558 and Ecological Systems during the Historic Period. *Human Ecology: An*  
559 *Interdisciplinary Journal*, **34**, 713-729.

560 Bossard, M., Feranec, J. & Otahel, J. (2000) Corine land cover technical guide: addendum  
561 2000. Technical report 40. European Environment Agency, Copenhagen.



- 562 Brewer, S., Giesecke, T., Davis, B.A.S., Finsinger, W., Wolters, S., Binney, H., de Beaulieu,  
563 J-L., Fyfe, R., Gil-Romera, G., Köhl, N., Kuneš, P., Leydet, M. & Bradshaw, R.H.  
564 (2017) Late-glacial and Holocene European pollen data. *Journal of Maps*, **13**, 921-  
565 928.
- 566 Broström, A., Nielsen, A.B., Gaillard, M.J., Hjelle, K., Mazier, F., Binney, H., Bunting, M.J.,  
567 Fyfe, R.M., Meltsov, V., Poska, A., Räsänen, S., Soepboer, W., Stedingk, H., Suutari,  
568 H. & Sugita, S. (2008) Pollen productivity estimates: the key to landscape  
569 reconstructions. *Vegetation History and Archaeobotany*, **17**, 461-478.
- 570 Calò, C., Henne, P.D., Curry, B., Magny, M., Vescovi, E., La Mantia, T., Pasta, S., Vannièr,  
571 B. & Tinner, W. (2012) A Spatio-temporal patterns of Holocene environmental  
572 change in southern Sicily. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 323-  
573 325, 110-122.
- 574 Carrión, J.S. & Fernández, S. (2009) The survival of the ‘natural potential vegetation’  
575 concept (or the power of tradition). *Journal of Biogeography*, **36**, 2202-2203.
- 576 Chiarucci, A., Bacaro, G. & Scheiner, S.M. (2011) Old and new challenges in using species  
577 diversity for assessing biodiversity. *Phil. Trans. R. Soc. B*, 366, 2426-2437.
- 578 Chiarucci, A., Araújo, M.B., Decocq, G., Beierkuhnlein, C. & Fernández-Palacios, J.M.  
579 (2010) The concept of potential natural vegetation: an epitaph? *Journal of Vegetation*  
580 *Science*, **21**, 1172-1178.
- 581 Collins, P.M., Davis, B.A.S. & Kaplan, J.O. (2012) The mid-Holocene vegetation of the  
582 Mediterranean region and southern Europe, and comparison with the present day.  
583 *Journal of Biogeography*, **39**, 1848-1861.
- 584 Colombaroli, D & Tinner, W. (2013) Determining the long-term changes in biodiversity and  
585 provisioning services along a transect from Central Europe to the Mediterranean.  
586 *Holocene*, **23**, 1625-1634.

- 587 Colombaroli, D., Marchetto, A & Tinner, W. (2007) Long-term interactions between  
588 Mediterranean climate, vegetation and fire regime at Lago di Massaciuccoli (Tuscany,  
589 Italy). *Journal of Ecology*, **95**, 755-770.
- 590 Davis, B.A.S., Zanon, M., Collins, P. et al. (2013) The European modern pollen database  
591 (EMPD) project. *Vegetation History and Archaeobotany*, **22**, 521-530.
- 592 Edwards, K.J., Fyfe, R.M. & Jackson, S.T. (2017) The first 100 years of pollen analysis.  
593 *Nature Plants*, **3**, doi:10.1038/nplants.2017.1
- 594 Ellis, E. (2015) Ecology in an anthropogenic biosphere. *Ecological Monographs*, **85**, 287-  
595 331.
- 596 European Environment Agency (EAA) (2016) *Corine Land-cover 2006 raster data*. Online:  
597 <http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster-3>  
598 Accessed: 6/9/16.
- 599 Felde, V.A., Hooghiemstra, H., Torres-Torres, V. & Birks, H.J.B (2016) Detecting patterns of  
600 change in a long pollen-stratigraphical sequence from Funza, Colombia – A  
601 comparison of new and traditional numerical approaches. *Review of Palaeobotany*  
602 *and Palynology*, **234**, 94–109.
- 603 Felde, V.A., Bjune, A.E., Grytnes, J.A. & Birks, H.J.B. (2014) A comparison of novel and  
604 traditional numerical methods for the analysis of modern pollen assemblages from  
605 major vegetation–landform types. *Review of Palaeobotany and Palynology*, **210**, 22-  
606 36.
- 607 Fyfe, R.M., Woodbridge, J. & Roberts, N. (2018) Trajectories of change in Mediterranean  
608 Holocene vegetation through classification of pollen data. *Vegetation History and*  
609 *Archaeobotany*, **27**, 351-364.
- 610 Fyfe, R.M., de Beaulieu, J.L., Binney, H., Bradshaw, R.H., Brewer, S., Le Flao, A.,  
611 Finsinger, W., Gaillard, M.J., Giesecke, T., Gil-Romera, G. & Grimm, E.C. (2009)

- 612 The European Pollen Database: past efforts and current activities. *Vegetation History*  
613 *and Archaeobotany*, **18**, 417-424.
- 614 García-Madrid, A.S., Molina, J.A. & Cantó, P. (2014) Classification of habitats highlights  
615 priorities for conservation policies: The case of Spanish Mediterranean tall humid  
616 herb grasslands. *Journal for Nature Conservation*, **22**, 142-156.
- 617 García-Valdés, R., Gotelli, N.J., Zavala, M.A., Purves, D.W. & Araújo, M.B. (2015) Effects  
618 of climate, species interactions, and dispersal on decadal colonization and extinction  
619 rates of Iberian tree species. *Ecological Modelling*, 309-310, 118-127.
- 620 Geri, F., Amici, V. & Rocchini, D. (2010) Human activity impact on the heterogeneity of a  
621 Mediterranean landscape. *Applied Geography*, **30**, 370-379.
- 622 Giesecke, T., Davis, B.A.S., Brewer, S., et al. (2013) Towards mapping the late Quaternary  
623 vegetation change of Europe. *Vegetation History and Archaeobotany*, **23**, 75-86.
- 624 Guiot, J. & Kaniewski, D. (2015) The Mediterranean Basin and Southern Europe in a warmer  
625 world: what can we learn from the past? *Front. Earth Sci.*, 3, 1-16.
- 626 Hickler, T., Vohland, K., Feehan, J., Miller, P. A., Smith, B., Costa, L., Giesecke, T.,  
627 Fronzek, S., Carter, T.R., Cramer, W., Kühn, I. & Sykes, M.T. (2012) Projecting the  
628 future distribution of European potential natural vegetation zones with a generalized,  
629 tree species-based dynamic vegetation model. *Global Ecology and Biogeography*, **21**,  
630 50–63.
- 631 Huntley, B. (1990) Dissimilarity Mapping between Fossil and Contemporary Pollen Spectra  
632 in Europe for the Past 13,000 Years. *Quaternary Research*, **33**, 360-376.
- 633 Izdebski, A., Holmgren, K., Weiberg, E., et al. (2015) Realising consilience: How better  
634 communication between archaeologists, historians and natural scientists can transform  
635 the study of past climate change in the Mediterranean. *Quaternary Science Reviews*,  
636 **136**, 5–22.

- 637 Jalut, G. Dedoubat, J.J., Fontugne, M. & Otto, T. (2009) A Holocene circum-Mediterranean  
638 vegetation changes: Climate forcing and human impact. *Quaternary International*,  
639 **200**, 4-18.
- 640 Jackson, S.T. & Blois, J.L. (2014) Community ecology in a changing environment:  
641 *Perspectives from the Quaternary*, **112**, 4915-4921.
- 642 Jackson, S.T. (2013) Natural, potential and actual vegetation in North America. *Journal of*  
643 *Vegetation Science*, **24**, 772-776.
- 644 Juggins, S. (2015) 'Rioja': *Analysis of Quaternary Science Data*, R package version (0.9-9).  
645 (<http://cran.r-project.org/package=rioja>).
- 646 Langgut, D., Almogi-Labin, A., Bar-Matthews, M. & Weinstein-Evron, M. (2011) Vegetation  
647 and climate changes in the South Eastern Mediterranean during the Last Glacial-  
648 Interglacial cycle (86 ka): new marine pollen record. *Quaternary Science Reviews*, **30**,  
649 3960-3972.
- 650 Leydet, M. (2007-2017) The European Pollen Database. (online:  
651 <http://www.europeanpollendatabase.net/>). Accessed: May 2016.
- 652 Loidi, J., Del Arco, M., Pérez de Paz, P.L., Asensi, A., Díez Garretas, B., Costa, M., Díaz  
653 González, T., Fernández-González, F., Izco, J., Penas, Á. & Rivas-Martínez, S. (2010)  
654 Understanding properly the 'potential natural vegetation' concept. *Journal of*  
655 *Biogeography*, **37**, 2209-2211.
- 656 Magri, D. (1995) Some questions on the late-Holocene vegetation of Europe. *The Holocene*,  
657 **5**, 354-360.
- 658 Marinova, E., Harrison, S.P. & Bragg, F. et al. (2017) Pollen-derived biomes in the Eastern  
659 Mediterranean–Black Sea–Caspian–Corridor, *Journal of Biogeography*. 1-16. DOI:  
660 10.1111/jbi.13128.

- 661 Mauri, A., Davis, B.A.S., Collins, P.M. & Kaplan, J.O. (2015) The climate of Europe during  
662 the Holocene: a gridded pollen-based reconstruction and its multi-proxy evaluation.  
663 *Quaternary Science Reviews*, 112, 109-127.
- 664 Médail, F. & Diadema, K. (2009) Glacial refugia influence plant diversity patterns in the  
665 Mediterranean Basin. *Journal of Biogeography*, **36**, 1333-1345.
- 666 Morris, E.K., Caruso, T., Buscot, F., et al. (2014) Choosing and using diversity indices:  
667 insights for ecological applications from the German Biodiversity Exploratories.  
668 *Ecology and Evolution*, 4, 3514-3524.
- 669 Murtagh, F. & Legendre, P. (2014). Ward's hierarchical agglomerative clustering method:  
670 which algorithms implement Ward's criterion? *Journal of Classification*, **31**, 274-295.
- 671 Oksanen, J., Guillaume Blanchet, F., Friendly, M., et al. (2016). 'vegan' (Community  
672 Ecology Package), R package version 2.4-1. [https://CRAN.R-](https://CRAN.R-project.org/package=vegan)  
673 [project.org/package=vegan](https://CRAN.R-project.org/package=vegan).
- 674 StatSoft Inc. (2003) STATISTICA (data analysis software system), version 6.1. StatSoft, Inc.,  
675 Tulsa, OK.
- 676 Ozenda, P. & Borela, J.L. (2000) An ecological map of Europe: why and how? *Ecology*, **323**,  
677 983–994.
- 678 Pausas, J.G. (1999) Mediterranean vegetation dynamics: modelling problems and functional  
679 types. *Plant Ecology*, **140**, 27-39.
- 680 Perez, M., Fyfe, R.M., Charman, D.J. & Gehrels, R. (2015) Later Holocene vegetation  
681 history of the Isles of Scilly, UK: coastal influence and human land use in a small  
682 island context. *Journal of Quaternary Science*, **30**, 764-778.
- 683 Peyron, O., Guiot, J., Cheddadi, R., Tarasov, P., Reille, M., De Beaulieu, J.L., Bottema, S. &  
684 Andrieu, V. (1998) Climatic reconstruction in Europe for 18,000 year BP. from pollen  
685 data. *Quaternary Research*, **49**, 183-196.

- 686 Prentice, I.C. & Webb, T. (1998) BIOME 6000: Reconstructing Global Mid-Holocene  
687 Vegetation Patterns from Palaeoecological Records. *Journal of Biogeography*, **25**,  
688 997-1005.
- 689 Prentice, I. C., Guiot, J., Huntley, B., Jolly, D. & Cheddadi, R. (1996). Reconstructing  
690 biomes from palaeoecological data: a general method and its application to European  
691 pollen data at 0 and 6 ka. *Climate Dynamics*, **12**, 185-194.
- 692 Preston, C.D., Hill, M.O., Harrower, C.A. & Dines, T.D. (2013) Biogeographical patterns in  
693 the British and Irish flora. *New Journal of Botany*, **3**, 96-117.
- 694 Roberts, N., Stevenson, A.C., Davis, B., Cheddadi, R., Brewer, S. & Rosen, A. (2004)  
695 Holocene climate, environment and cultural change in the circum-Mediterranean  
696 region. In: *Past climate variability through Europe and Africa*, Battarbee, R.W.,  
697 Gasse, F. & Stickley, C. (eds). Kluwer, Dordrecht, pp. 343-362.
- 698 Rundel, P.W., Montenegro, G. & Jaksic, F.M. eds. (1998) *Landscape Disturbance and*  
699 *Biodiversity in Mediterranean-Type Ecosystems*. Springer, Germany.
- 700 Sadori, L., Bertini, A., Combourieu-Nebout, N., Kouli, K., Mariotti Lippi, M., Roberts, N. &  
701 Mercuri, A.M. (2013) Palynology and Mediterranean vegetation history. *Flora*  
702 *Mediterranea*, **23**, 141-156.
- 703 Shoshany, M. (2000) Satellite remote sensing of natural Mediterranean vegetation: a review  
704 within an ecological context. *Progress in Physical Geography*, **24**, 153-178.
- 705 Simpson, E.H. (1949) Measurement of diversity. *Nature*, **163**, 688.
- 706 Tzedakis, P.C (2007) Seven ambiguities in the Mediterranean palaeoenvironmental narrative.  
707 *Quaternary Science Reviews*, **26**, 2042-2066.
- 708 Küchler, A.W. & Zonneveld, I.S. (1988) The UNESCO Classification of Vegetation. In:  
709 Küchler, A.W. & Zonneveld, I.S. (Eds.) *Vegetation mapping. Handbook of vegetation*  
710 *science: vol 10*. Springer, Dordrecht.

- 711 Vogiatzakis, I.N., Mannion, A.M. & Griffiths, G.H. (2006) Mediterranean ecosystems:  
712 problems and tools for conservation. *Progress in Physical Geography*, **30**, 175-200.
- 713 Ward, J.H. (1963) Hierarchical grouping to optimize an objective function. *Journal of the*  
714 *American Statistical Association*, **58**, 236-244.
- 715 Williams, J.W. & Jackson, S.T. (2007) Novel climates, no-analogue communities, and  
716 ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475-482.
- 717 Woodbridge, J., Fyfe, R.M. & Roberts, C.N. (2014) A comparison of remotely sensed and  
718 pollen-based approaches to mapping Europe's land cover. *Journal of Biogeography*.  
719 **41**, 2080-2092.

720

## 721 **BIOSKETCHES**

722

723 Jessie Woodbridge is a Post-Doctoral Research Fellow at Plymouth University (UK) and is  
724 conducting research that aims to reconstruct changes in European land cover throughout the  
725 Holocene using pollen data. Her research background is based on palaeoenvironmental  
726 reconstruction, specifically in relation to understanding human impacts and past climate  
727 trends.

728

729 Ralph Fyfe is Professor of Geospatial Information at Plymouth University. His research  
730 focuses on developing innovative methodological approaches to reconstruct patterns of  
731 vegetation cover at local to European scales, and deciphering the processes that led to these  
732 patterns with an emphasis on human agency.

733

734 Neil Roberts is Professor of Geography at Plymouth University. His research emphasises past  
735 climatic and environmental change since the last glacial maximum, specifically using lake-

736 sediment archives from eastern Africa, the Mediterranean and West Asia. Professor Roberts  
737 is a fellow of the Royal Geographical Society, and has served on national and international  
738 committees concerning past global changes.

739

## 740 **TABLES**

741

742 Table 1 Comparison of pollen-inferred vegetation groups within the modern and fossil  
743 datasets using Ward's hierarchical clustering method. Towards the left of the table, the  
744 groups combine at lower levels of clustering and to the right cluster groups separate as  
745 different pollen taxa assemblages are detected at a higher clustering level. The inter-quartile  
746 range of the dominant taxa (appearing in 81-100% of samples in the cluster) are provided.

747

748 Table 2 Pollen-inferred vegetation clusters compared with Corine remote sensed land cover  
749 maps (EEA, 2016) and vegetation types defined by previous studies (Huntley, 1990; Prentice  
750 et al., 1996; Peyron et al., 1998).

751

## 752 **FIGURES**

753

754 Fig 1 Modern and fossil pollen site locations colour coded according to elevation group. The  
755 white area represents the Mediterranean region for which results are presented in this study.  
756 Pollen samples in the Rhone Valley of southern France are also shown on the map as these  
757 sites contributed to the generation of vegetation cluster groups.

758

759 Fig 2 Box plots for pollen taxa within each vegetation cluster group for the combined fossil  
760 and modern pollen datasets. The middle vertical bar for each taxon represents the median, the



761 lower and upper boundaries of the boxes show the interquartile range, and the dashed  
762 horizontal lines show the minimum and maximum occurrence of the taxon in the cluster. The  
763 bars representing taxa that are frequent or abundant in a specific cluster group are coloured  
764 black and those that are not frequent or abundant are grey (a version of this diagrams has  
765 been published in Fyfe et al., 2018).

766

767 Fig 3 Modern and fossil pollen samples: non-metric multidimensional scaling (nMDS) kernel  
768 density plots for 16 cluster analysis derived vegetation groups. Darker colours indicate  
769 greater density of samples and lighter colours indicate fewer samples.

770

771 Fig 4 Percentage of pollen samples statistically assigned to each cluster group throughout the  
772 Holocene for the entire Mediterranean combined fossil and modern dataset with ratio of  
773 vegetation cluster group change, average non-metric multidimensional scaling (nMDS)  
774 scores, average Simpson's diversity index and average non-arboreal pollen sum (% NAP)  
775 (scale: 28-48%) (11,000 BP to modern).

776

777 Fig 5 Percentage of pollen samples statistically assigned to each cluster group throughout the  
778 Holocene separated by elevation group: a) <500 m (415 modern and 47 fossil pollen sites), b)  
779 500-1200 m (643 modern and 28 fossil pollen sites), and c) >1200 m (498 modern and 30  
780 fossil pollen sites) (11,000 BP to modern).

781

782 Fig 6 Pollen-inferred vegetation clusters (6200-6000 BP and modern surface samples)  
783 compared with the results of BIOME 6000 vegetation maps (Prentice et al., 1996) for modern  
784 pollen (0 BP) and 6000 BP and the Corine remotely-sensed (EEA, 2006) land cover map.

785

786 Fig 7 Frequency of vegetation types according to the pollen cluster results and the BIOME  
787 6000 vegetation maps for 0 BP and 6000 BP maps (Prentice et al., 1996). Similar vegetation  
788 types are shown alongside one another.

789

790 Supplementary Information 1: EPD fossil pollen site metadata for the records used in these  
791 analyses (for details of the modern pollen sites see Davis et al., 2013).

792

793 Supplementary Information 2: Pollen-inferred vegetation classification tables: land-cover  
794 types (clusters) and pollen taxa percentage (inter-quartile range) in the combined modern and  
795 fossil pollen datasets (all taxa presented are in the higher frequency class for each cluster)  
796 (Lactuceae: synonym Cichorieae). V represents a taxon occurring in 81-100% of all samples  
797 in a cluster and IV = 61-80%.

Fig. 1

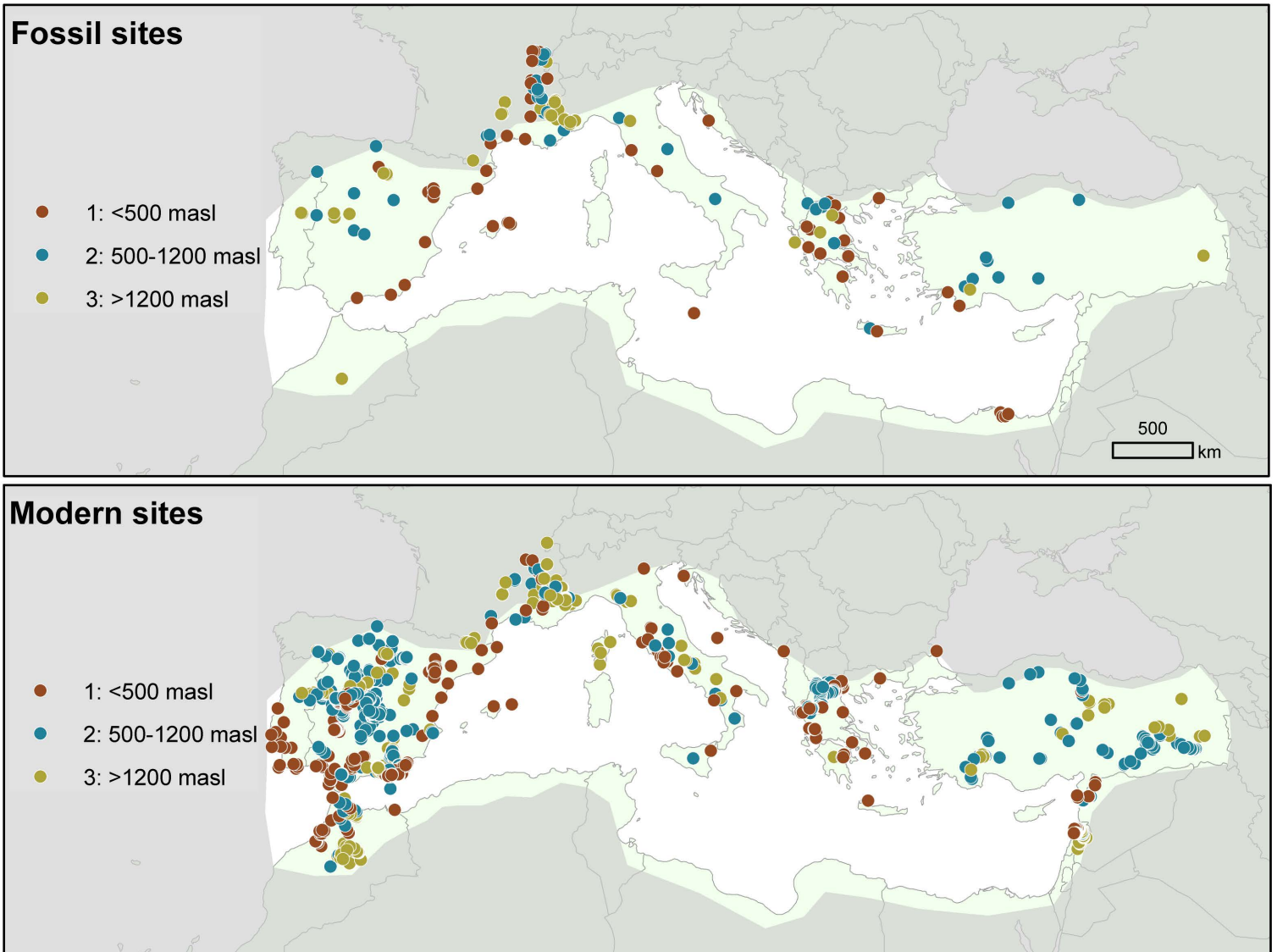
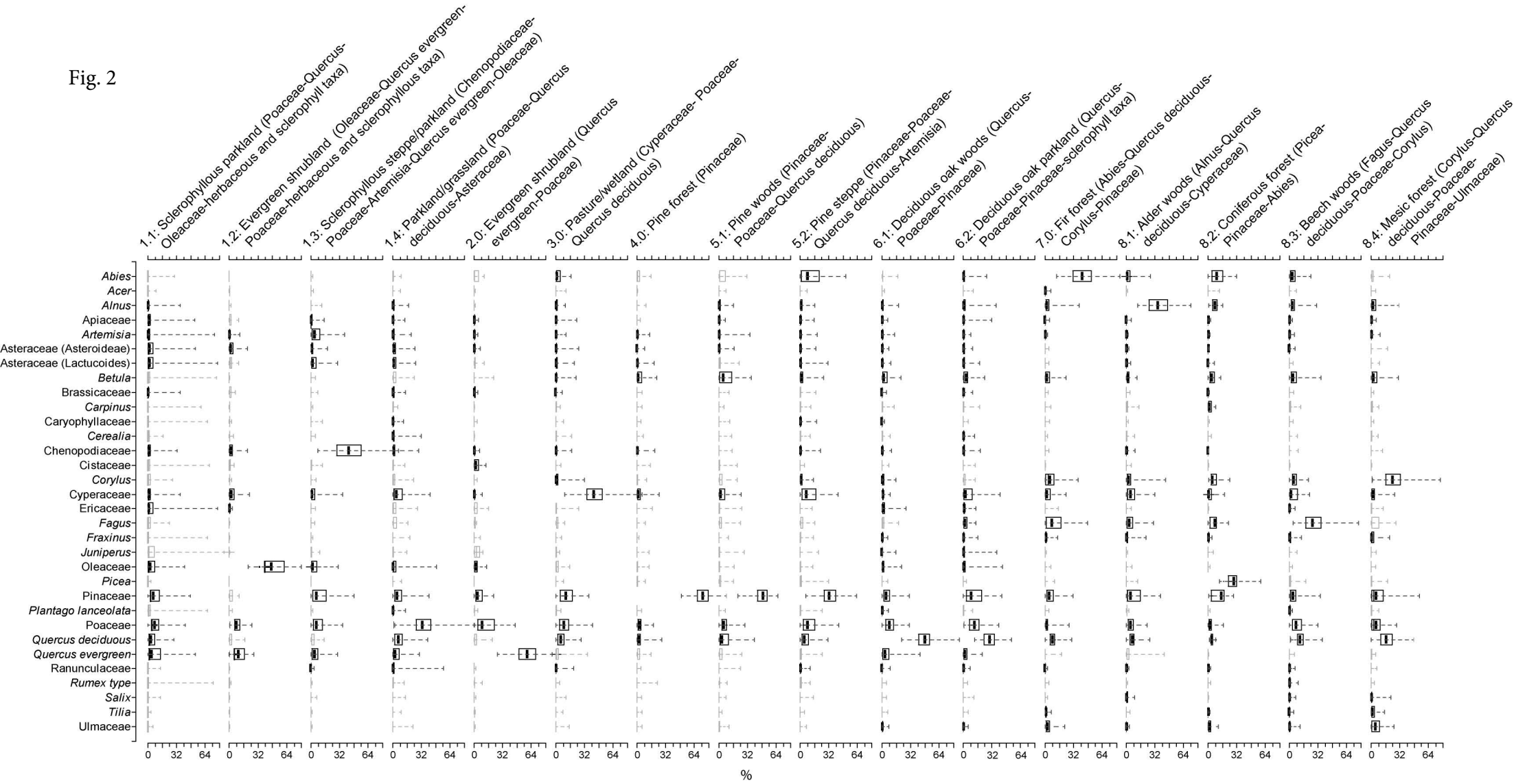


Fig. 2



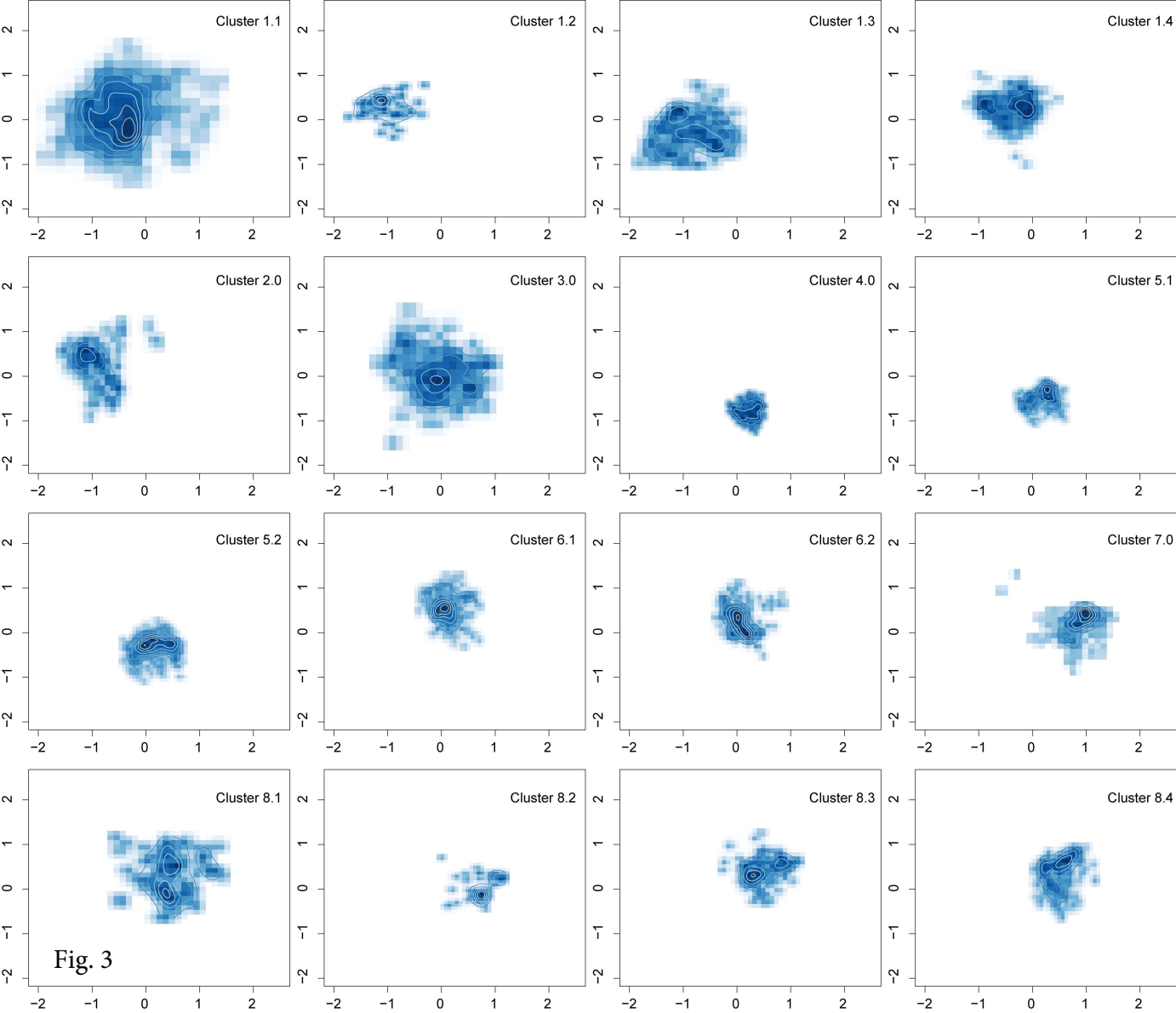


Fig. 4

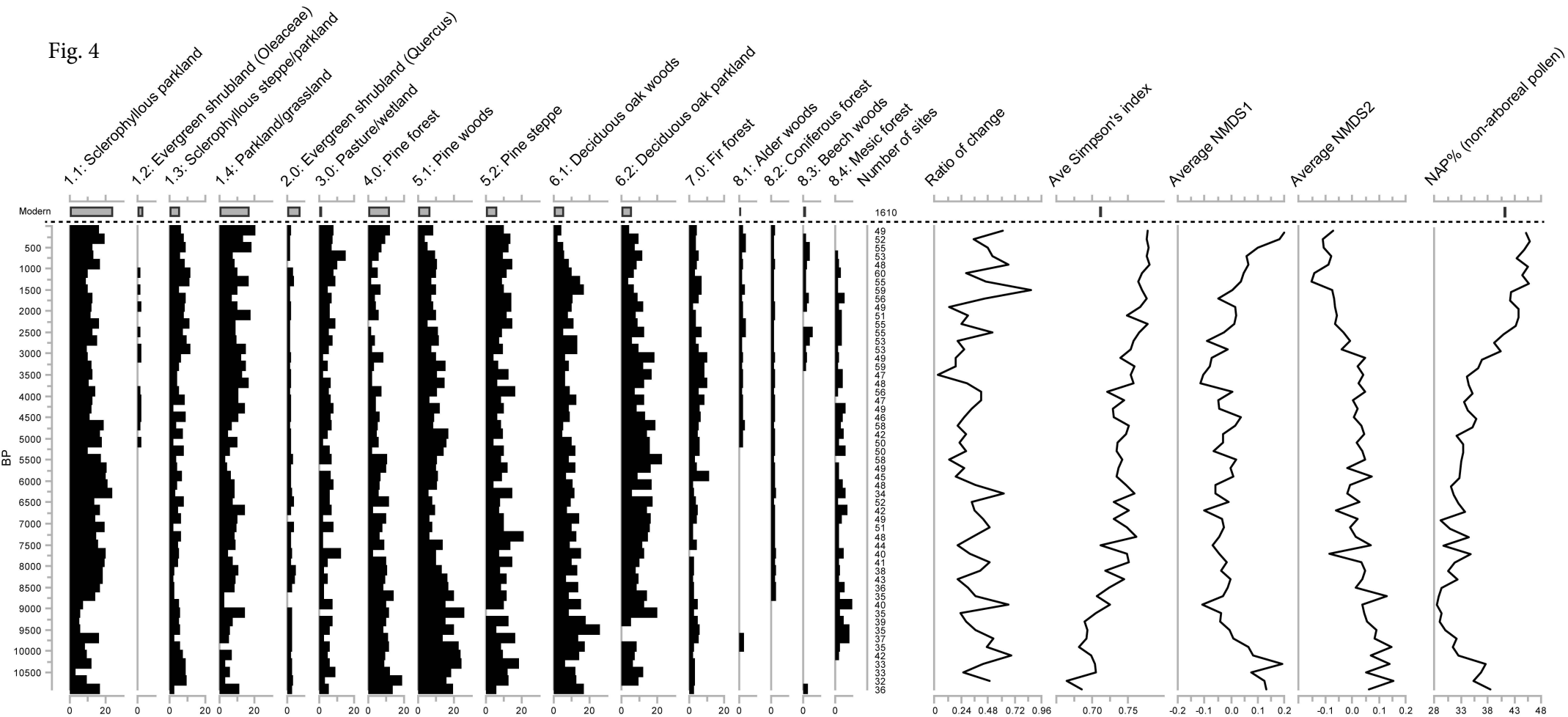


Fig. 5

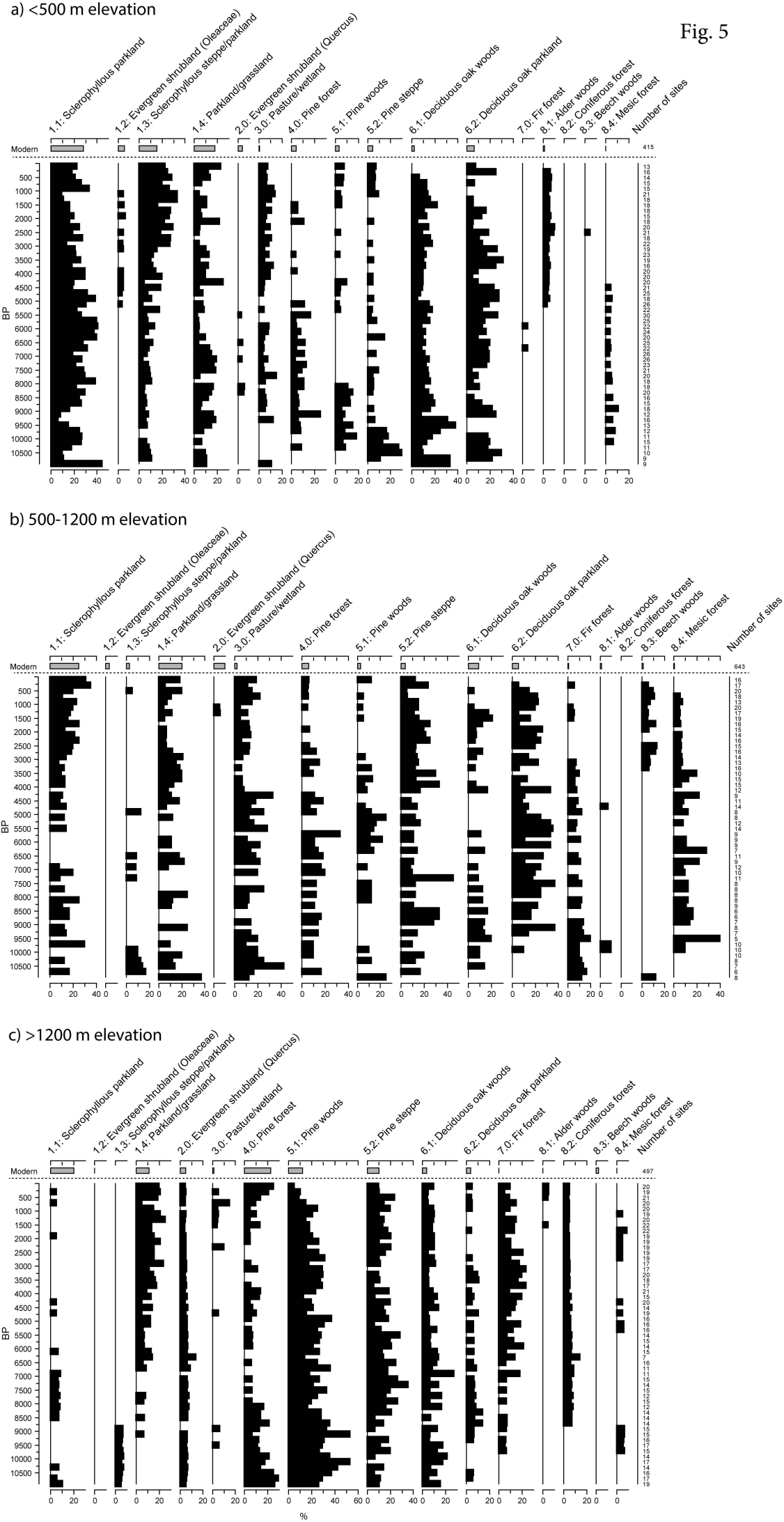
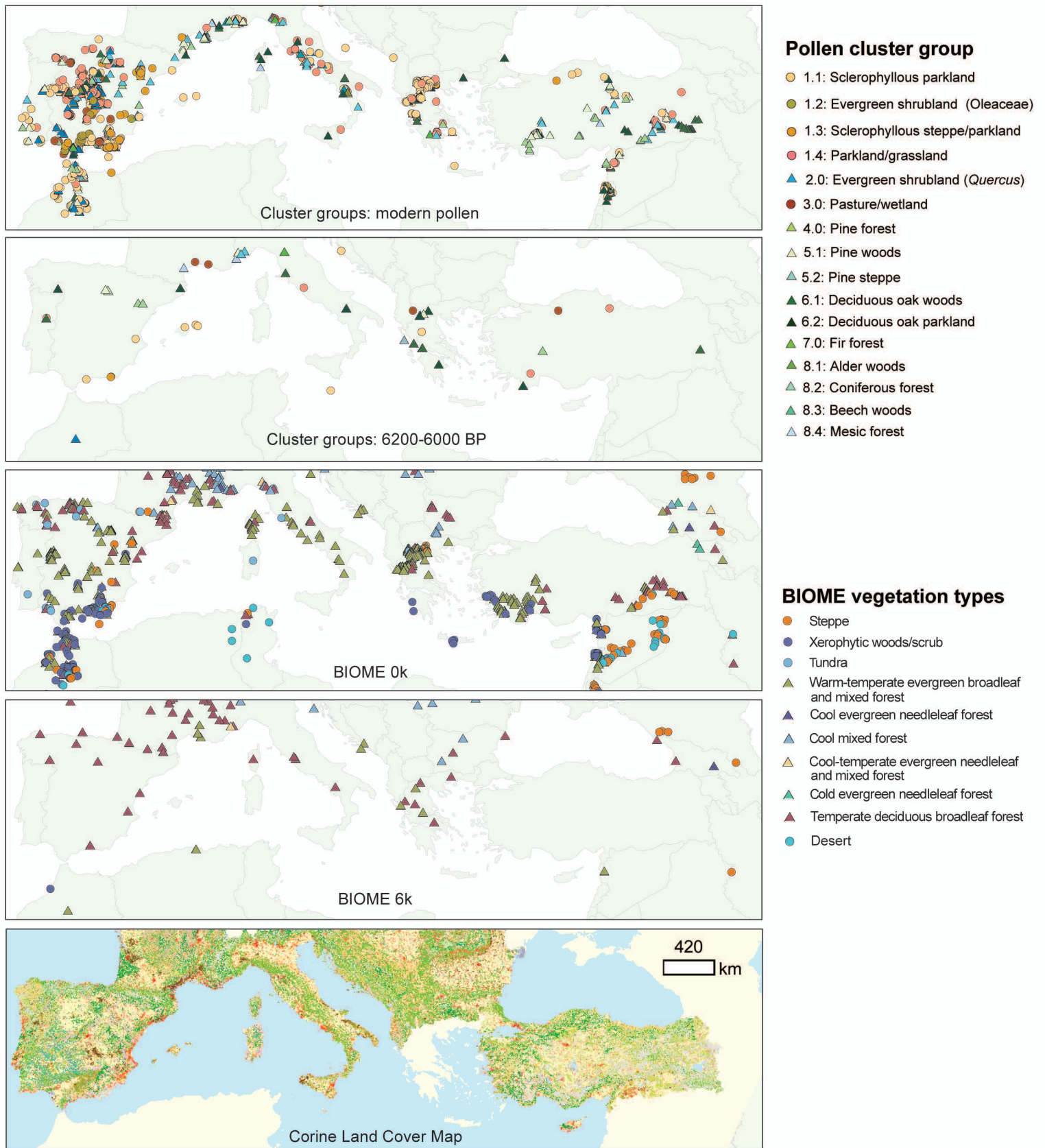


Fig. 6



**Corine Land Cover Class**





Fig. 7

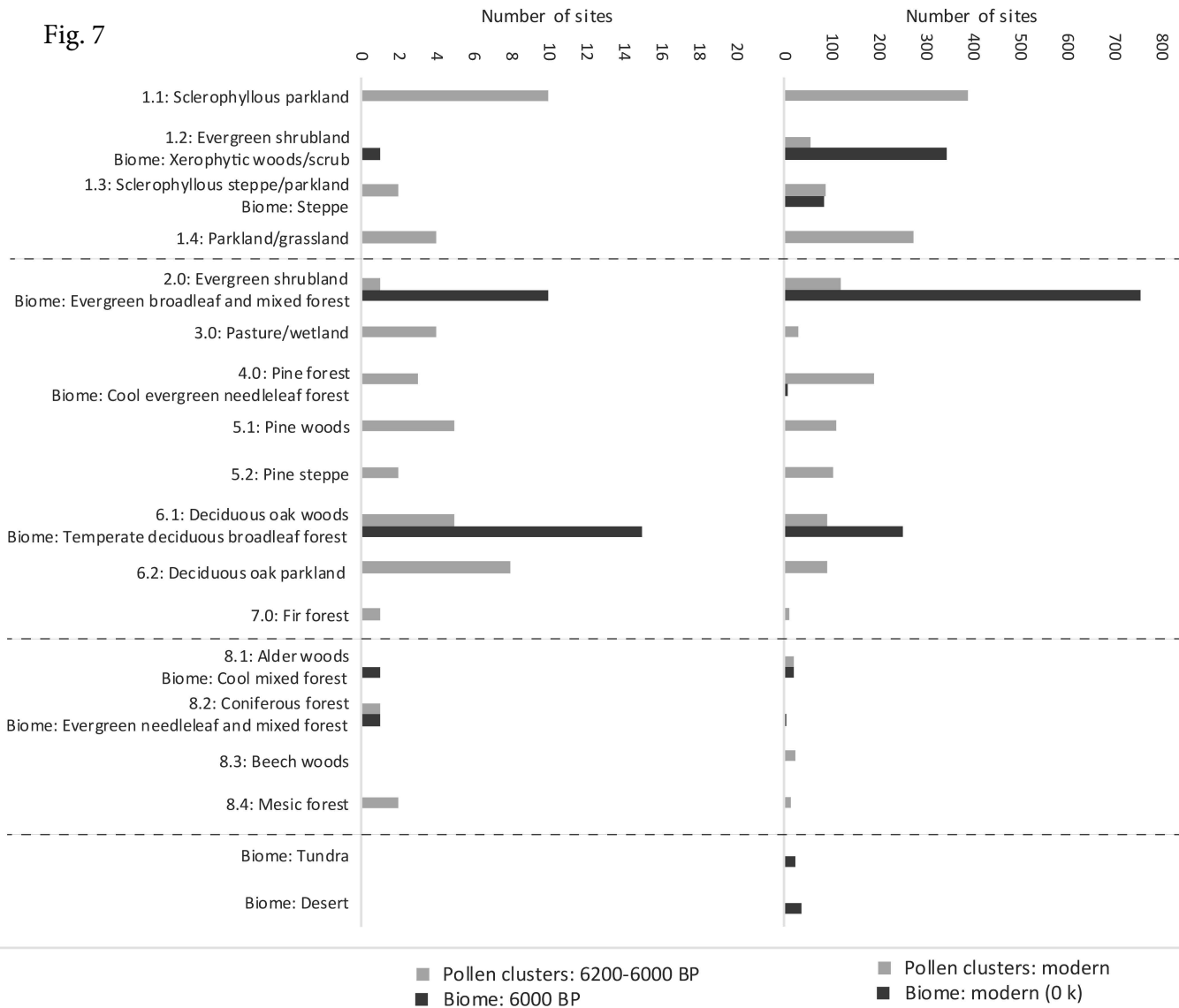


Table 1 Comparison of pollen-inferred vegetation groups within the modern and fossil datasets using Ward's hierarchical clustering method. Towards the left of the table, the groups combine at lower levels of clustering and to the right cluster groups separate as different pollen taxa assemblages are detected at a higher clustering level. The inter-quartile range of the dominant taxa (appearing in 81-100% of samples in the cluster) are provided.

3 clusters	8 clusters	12 clusters	13 clusters	15 clusters	16 clusters	Dominant taxa (most frequently occurring taxa within the cluster)		
<b>1: open vegetation</b>	<b>1: Open vegetation/shrubland</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1.1:</b> Sclerophyllous parkland	Poaceae (4-12.5), Pinaceae (2.8-13.3), <i>Quercus</i> deciduous (1.4-8.6), Asteraceae: <i>Asteroidae</i> (0.9-6.4), <i>Quercus</i> evergreen (11.2-14.9), Oleaceae (10.7-8.6), Asteraceae: <i>Lactuceae</i> (10.8-6.2), Ericaceae (10.5-6.2)		
				<b>9</b>	<b>1.2:</b> Evergreen shrubland (Oleaceae)	Oleaceae (39-61.8), <i>Quercus</i> evergreen (5.4-17.8), Poaceae (6-12.9), Asteraceae: <i>Asteroidae</i> (1.1-5.2), Chenopodiaceae (0.7-4.4), Cyperaceae (10.8-6.1)		
		<b>3</b>	<b>3</b>	<b>3</b>	<b>1.3:</b> Sclerophyllous steppe/parkland	Chenopodiaceae (29.1-56.7), Pinaceae (2.4-18), Poaceae (2.9-13.4), Artemisia (1.1-10.9), <i>Quercus</i> evergreen (1.5-8.3), Oleaceae (0.7-7.3)		
		<b>7</b>	<b>8</b>	<b>8</b>	<b>1.4:</b> Parkland/grassland	Poaceae (26.2-43), <i>Quercus</i> deciduous (2.3-11.3), Pinaceae (2.4-10.3), Asteraceae: <i>Lactuceae</i> (0.5-4.4), Asteraceae: <i>Asteroidae</i> (0.6-3.3), Cyperaceae (11.5-11.3)		
	<b>2: Evergreen shrubland</b>	<b>5</b>	<b>5</b>	<b>7</b>	<b>2.0:</b> Evergreen shrubland ( <i>Quercus</i> )	<i>Quercus</i> evergreen (50.6-69.4), Poaceae (4.2-23.7), Brassicaceae (0.5-2), Chenopodiaceae (0.4-1), Pinaceae (12-10)		
	<b>3: Pasture/wetland</b>	<b>11</b>	<b>12</b>	<b>14</b>	<b>3.0:</b> Pasture/wetland	Cyperaceae (34.6-52.2), Pinaceae (5.2-18.8), Poaceae (4.4-15.2), <i>Quercus</i> deciduous (2.1-10.1)		
<b>2: Pine forests</b>	<b>4: Pine forest</b>	<b>2</b>	<b>2</b>	<b>2</b>	<b>4.0:</b> Pine forest	Pinaceae (67-82.1), Poaceae (1.5-4.8), <i>Quercus</i> deciduous (0.6-4.2), Betula (10.4-5.7)		
	<b>5: Pine woods/steppe</b>	<b>4</b>	<b>4</b>	<b>4</b>	<b>5.1:</b> Pine woods	Pinaceae (43.3-54.5), Poaceae (3.5-8.9), <i>Quercus</i> deciduous (1.1-11.2)		
			<b>6</b>	<b>6</b>	<b>5.2:</b> Pine steppe	Pinaceae (26.9-40.5), Poaceae (3.4-16.9), Cyperaceae (2-18.3), <i>Quercus</i> deciduous (1.9-9.7), Artemisia (0.4-1.7)		
<b>3: Deciduous and mixed forests</b>	<b>6: Deciduous (broad-leaved)</b>	<b>6</b>	<b>7</b>	<b>7</b>	<b>6.1:</b> Deciduous oak woods	<i>Quercus</i> deciduous (40.8-53.5), Poaceae (4.2-13.8), Pinaceae (2.3-8.9)		
				<b>10</b>	<b>6.2:</b> Deciduous oak parkland	<i>Quercus</i> deciduous (23.1-35.4), Poaceae (7.1-18.3), Pinaceae (3.7-21.5)		
	<b>7: Fir forest</b>	<b>8</b>	<b>9</b>	<b>11</b>	<b>7.0:</b> Fir forest	<i>Abies</i> (31.4-52.3), <i>Quercus</i> deciduous (5.7-11.6), <i>Corylus</i> (3.2-10.5), Pinaceae (2-10.2)		
	<b>8: Mixed woods</b>	<b>9</b>	<b>10</b>	<b>12</b>	<b>8.1:</b> Alder woods	<i>Alnus</i> (25.8-46.7), <i>Quercus</i> deciduous (4.2-9.4), Cyperaceae (1.8-9.6)		
				<b>10</b>	<b>11</b>	<b>13</b>	<b>8.2:</b> Coniferous forest	Picea (22.6-32.7), Pinaceae (3.6-18.2), <i>Abies</i> (4.3-17.2)
				<b>12</b>	<b>13</b>	<b>15</b>	<b>8.3:</b> Beech woods	Fagus (18.7-36.3), <i>Quercus</i> deciduous (9.2-16), Poaceae (3.7-14.1), <i>Corylus</i> (3.5-8.4)
					<b>8.4:</b> Mesic forest			



Table 2 Pollen-inferred vegetation clusters compared with Corine remote sensed land cover maps (EEA, 2016) and vegetation types defined by previous studies (Huntley, 1990; Prentice et al., 1996; Peyron et al., 1998).

Cluster name descriptor	Corine Land Cover Classes	Comparison with previous studies	
		Prentice et al. (1996) Peyron et al. (1998)	Huntley (1990)
<b>1.1:</b> Sclerophyllous parkland (Poaceae- <i>Quercus</i> -Oleaceae-herbaceous and sclerophyll taxa)	Sclerophyllous vegetation	Grass / heath	<i>Quercus-Pinus-sclerophyll</i> taxa  <i>Quercus-Chenopodiaceae-</i> <i>Pistacia</i>
<b>1.2:</b> Evergreen shrubland (Oleaceae- <i>Quercus</i> evergreen-Poaceae- herbaceous and sclerophyllous taxa)	Transitional woodland-shrub / broad-leaved forest / sclerophyllous	Warm-temperate sclerophyll trees/shrub	<i>Quercus-Chenopodiaceae-</i> <i>Pistacia</i>
<b>1.3:</b> Sclerophyllous steppe/parkland (Chenopodiaceae-Poaceae- <i>Artemisia-</i> <i>Quercus</i> evergreen-Oleaceae)	Sclerophyllous vegetation	Steppe forb / shrub	Chenopodiaceae  <i>Quercus-Pinus-Ericales-</i> Chenopodiaceae
<b>1.4:</b> Parkland/grassland (Poaceae, <i>Quercus</i> deciduous, Asteraceae)	Natural grasslands / pastures / agriculture	Grass	No similar group
<b>2.0:</b> Evergreen shrubland ( <i>Quercus</i> evergreen, Poaceae)	Transitional woodland-shrub / broad-leaved forest / sclerophyllous	Warm temperate broad-leaved evergreen	<i>Quercus-Chenopodiaceae-</i> <i>Pistacia</i>
<b>3.0:</b> Pasture/wetland (Cyperaceae, Poaceae, <i>Quercus</i> deciduous)	Moors and heathland	Cyperaceae	<i>Quercus-Pinus-sclerophyll</i> taxa
<b>4.0:</b> Pine forest (Pinaceae)	Coniferous forest / mixed forest	Boreal evergreen conifer	Pinus-Betula
<b>5.1:</b> Pine woods (Pinaceae-Poaceae- <i>Quercus</i> deciduous)	Coniferous forest / mixed forest	Boreal evergreen conifer	Pinus-Betula
<b>5.2:</b> Pine steppe (Pinaceae-Poaceae- <i>Quercus</i> deciduous- <i>Artemisia</i> )	Coniferous forest / mixed forest	No similar group	Pine-Betula-Chenopodiaceae- <i>Quercus</i>
<b>6.1:</b> Deciduous oak woods ( <i>Quercus-</i> Poaceae-Pinaceae)	Broad-leaved forest	Temperate summer green	<i>Quercus-Pinus-sclerophyll</i> taxa
<b>6.2:</b> Deciduous oak parkland ( <i>Quercus-</i> Poaceae-Pinaceae-sclerophyll taxa)	Broad-leaved forest	Temperate summer green	<i>Quercus-Pinus-sclerophyll</i> taxa
<b>7.0:</b> Fir forest ( <i>Abies-Quercus</i> deciduous- <i>Corylus</i> -Pinaceae)	Coniferous forest / mixed forest	Boreal evergreen conifer	No similar group

<b>8.1:</b> Alder woods ( <i>Alnus-Quercus</i> deciduous-Cyperaceae)	Broad-leaved forest	Temperate summer green	<i>Corylus-Quercus-Alnus</i>
<b>8.2:</b> Coniferous forest ( <i>Picea-Pinaceae-Abies</i> )	Coniferous forest / mixed forest	Boreal evergreen conifer	<i>Picea-Pinus-Betula</i>
<b>8.3:</b> Beech woods ( <i>Fagus-Quercus</i> deciduous-Poaceae- <i>Corylus</i> )	Broad-leaved forest	Cool temperate summer green	<i>Fagus-Picea-Carpinus</i>
<b>8.4:</b> Mesic forest ( <i>Corylus-Quercus</i> deciduous-Poaceae-Pinaceae-Ulmaceae)	Broad-leaved forest	Cool temperate summer green	<i>Corylus-Quercus-Alnus</i>