

## The historical origins of aridity and vegetation degradation in south-eastern Spain

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### Abstract

The complex relationships within modern landscapes cannot be understood without the benefit of retrospective studies. We review palaeoenvironmental data for southeastern Spain, a landscape vulnerable to desertification and with antiquity of human pressure on the landscape. A xerophytic component is discernible in the pollen diagrams of the southeastern peninsula ever since the Middle Miocene. During glacial stages of the Pleistocene, mountain grasslands and lowland steppes expanded, but tree vegetation, although episodically contracted, was ever present across the region, explaining part of the modern plant-species diversity. The magnitude of human impacts on vegetation during the Holocene has been highly variable, starting earlier (e.g. after c. 5000 cal yr BP) in low-elevation areas and river basins. Forest degradation of the mountains started rather late during the Argaric period, and reached its maximum during the Roman occupation. Over the last millennia, natural and/or human-set fires, combined with overgrazing, probably have pushed forests over a threshold leading to the spread of grassland,

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4 thorny scrub, junipers, and nitrophilous communities. The high degree of xerophytization  
5 observed today in southeastern Spain results from the long-term determinism of the mid-late  
6 Holocene climate aridification, and the contingency of historical factors like fire events and  
7 changes in prehistoric local economies involving resource exhaustion.  
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15 **Key words**  
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17 Palaeoecology, historical biogeography, Spain, Tertiary, Quaternary, Holocene  
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23 **Introduction**  
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25 This paper deals with the ecological history of a semi-desert region, the Murcian-Almerian  
26 bioprovince, extending over 13,000 km<sup>2</sup> in the southeast of the Iberian Peninsula (Peinado et al.,  
27 1992) (Fig.1). We review available evidence of past vegetation and climate-human-vegetation  
28 interactions in the study area with the goal of establishing a temporal framework incorporating the  
29 vegetation patterns and the natural processes observed today in an area that has witnessed one  
30 of the highest rates of long-term land degradation within the European continent (Puigdefábregas  
31 and Mendizábal, 1998). Specific issues to be addressed relate to (i) whether the arid belt with  
32 xerothermic Mediterranean, and Saharo-Irano-Turanian elements in the Mediterranean coast of  
33 southeastern Iberia is a recent feature or originates during or prior to the Quaternary, (ii) whether  
34 the region served as glacial refugium for woody species during the Pleistocene, (iii) whether this  
35 generally treeless region was forested any time during the Holocene, and, if so, which arboreal  
36 species were involved, (iv) which factor(s) gave rise to the high degree of xerophytization  
37 observed in the region today, and (v) whether the palaeo-record of biotic changes, fire  
38 occurrence, and anthropogenic disturbance can shed light on the characteristics of modern  
39 vegetation. This last issue includes the consideration of causal links with prehistoric patterns of  
40 human settlement.  
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6 **Present-day climate and vegetation**  
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9 Although essentially Mediterranean, with summer drought and average annual temperatures of  
10 16-17°C in the lowlands, the climate of the Murcian-Almerian bioprovince is characterised by  
11 greater aridity than other Mediterranean areas. Extreme summer temperatures are common, with  
12 daily maxima of up to 46 °C. The region is bounded by the Mediterranean Sea and surrounded by  
13 mountain ranges acting as a natural barrier to precipitation (IGME, 1999) (Fig. 1). Yearly rainfall  
14 ranges from 250 to 330 mm, though in mountainous areas it may exceed 400 mm and in some  
15 coastal areas it falls below 190 mm (Lázaro et al., 2001). Precipitation is irregular and often  
16 causes devastating floods of great erosive power, and evapotranspiration is greater than  
17 anywhere else in the Iberian Peninsula (Cantón et al., 2001).

18 Interestingly, while being one of the most arid regions on the European continent, it is  
19 among the richest floristically, perhaps due to the region's extensive bioclimatic gradients and  
20 geological diversity (Mota et al., 2004). More than half of the c. 7500 vascular plants found in  
21 Iberia (Devesa and Ortega, 2004) occur within the limited territory of this province, a majority of  
22 which are Mediterranean species (65%), including Iberian, Murcian-Almerian, Ibero-North African  
23 and Ibero-Irano-Turanian endemics (Mota et al., 2003). In the most arid environments, namely  
24 coastal mountains and littoral depressions, sclerophyllous brushwoods prevail, dominated by one  
25 or more of the following species: *Maytenus senegalensis* subsp. *europaea*, *Periploca angustifolia*,  
26 *Withania frutescens*, *Ziziphus lotus*, *Calicotome intermedia*, *Launaea arborescens*, and several  
27 species of *Genista*. Other abundant species include *Lycium intricatum*, *Rhamnus oleoides*,  
28 *Pistacia lentiscus*, *Olea europaea* var. *sylvestris*, *Stipa tenacissima*, *Ephedra fragilis*, as well as a  
29 diversity of Cistaceae, Lamiaceae, and Asteraceae species. Open forests with *Pinus halepensis*  
30 and *Quercus rotundifolia*, and *Quercus coccifera* scrub occur in the more continental depressions  
31 and less dry conditions of the mountainous hinterland. Saline depressions, as well as intermittent  
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4 watercourses, are colonised by *Artemisia*, Chenopodiaceae, *Nerium oleander*, *Tamarix*,  
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6 *Limonium*, and Poaceae species.  
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11 **Aridity was already present in the late Tertiary**  
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13 Little is known about the Tertiary (65-1.8 Ma) evolution of Iberian floras. Available data suggest  
14 that aridity is a feature of the southeastern peninsula ever since the middle Miocene, about 16  
15 million years ago. It is also possible that Mediterranean-type climates had appeared intermittently  
16 during the Miocene (23-5.3 Ma), as Tzedakis (2007) has recently suggested. Pollen spectra in  
17 records from Alborán A1 (36° 38'N 4° 13'E), Andalucía A1 (36° 35'N 2° 43'E) and Gor (37° 22'N  
18 2° 59'W) (Fig. 1), include minor subdesertic elements since the Langhian (16-13.6 Ma) such as  
19 *Nitraria*, *Neurada*, *Prosopis*, *Lygeum*, *Ephedra*, Caesalpiniaceae, *Acacia* and *Calligonum*, while  
20 non-arboreal elements (Poaceae, Chenopodiaceae-Amaranthaceae, Plumbaginaceae,  
21 Caryophyllaceae) prevail in the pollen spectra (Jiménez-Moreno, 2005) (Fig. 2). These elements  
22 are but a part of a complex assemblage involving tropical and subtropical components  
23 (Taxodium-Glyptostrobus, *Bombax*, *Engelhardia*, Sapotaceae, *Myrica*, *Buxus bahamensis*,  
24 *Croton*, *Alcornea*, *Mussaenda*), mangrove species (*Avicennia*), and mesothermic (deciduous  
25 *Quercus*, *Carya*, and *Zelkova*), mid-altitude (*Cedrus*, *Tsuga*) and high-altitude (*Abies*, *Picea*)  
26 trees (Jiménez-Moreno and Suc, 2007). Physiographic heterogeneity must have been important  
27 at this time, as the rainfall requirements of these taxa vary greatly. Doubtless, the arid conditions  
28 were not widespread in the southeastern peninsula but there must have been sub-desertic areas  
29 because the *Neurada-Nitraria* assemblages are typical of the northern fringes of the Sahara today  
30 (Fauquette et al., 2006), and the Middle Miocene (c. 16-11 Ma) pollen sequences from the  
31 southeast contain a greater herbaceous component than northeastern records (Jiménez-Moreno  
32 and Suc, 2007).

The pollen sequence of the Andalucía G1 borehole (Fig.1) follows the erosional phase corresponding to the deep Mediterranean salinity crisis (Clauzon et al. 1990), and has been dated from c. 5.32 to 2.4 Ma (Suc et al. 1995). This sequence includes abundant herbs (Poaceae, Asteraceae, Chenopodiaceae-Amaranthaceae, *Artemisia*), deciduous *Quercus*, and subdesertic elements such as *Lygeum*, *Nitraria*, and *Calligonum*, indicating dry and hot conditions (Fauquette et al., 1998). These elements are, however, also present in the Tarragona E2 borehole, offshore northeastern Spain (Bessais and Cravatte, 1988) (Fig. 1), suggesting that an arid thermomediterranean belt with Saharo-Irano-Turanian elements continued to occur during the Pliocene along the Mediterranean coast of Iberia from Andalucía to southern Cataluña. Fauquette et al. (1999) quantified climatic conditions for this site through a pollen-derived method based on the mutual climatic range of plant taxa. Apart from the record of two major coolings that took place at 4.5 and 3.5 Ma (Suc and Zagwijn, 1983), annual temperatures remained equivalent to 6°C higher than today, and annual precipitation was eventually lower than today (if the Pliocene climate is calculated excluding deciduous *Quercus*, on the assumption that the species occupied mountainous areas adjacent to the study site (Fauquette et al., 1999)). The Pliocene at Andalucía G1 strongly contrasts with the site of Rio Maior in Portugal where Ericaceae dominates the non-arboreal pollen spectra and the subtropical component (*Cathaya*, *Engelhardia*, *Sequoia*, *Myrica*, *Taxodium*...) dominates the arboreal (Diniz, 1984). Using the former method of climatic estimation, their pollen data, and the plant functional types established by Prentice et al. (1992), Fauquette et al. (1999) reconstructed Pliocene biomes between 5.32 and 5 Ma for the West Mediterranean area. Hot desert, semi desert, xerophytic scrub, and warm grass/shrub biomes were reconstructed for southeastern Spain (Fig. 3).

#### Glacial refugium for tree taxa

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4 Early to Mid-Pleistocene palaeobotanical records of the study region are lacking. If we take into  
5 account the biogeochemistry and ecomorphology of the large mammal assemblage, we can infer  
6 early Pleistocene landscapes characterised by the presence of shallow lakes with swampy  
7 marginal zones and extensive areas of savanna with tall grass and shrubs (Palmqvist et al.,  
8 2003). For the better documented Upper Pleistocene, the region can be broadly characterized by  
9 a diversity of landscapes including mountain grasslands and lowland steppes, *Pinus* woods at  
10 mid-altitudes, and the occurrence of a number of woody plants in the present-day meso and  
11 thermomediterranean belts along coastal shelves and intramontane valleys (Carrión et al., 2008).  
12 Glacial stages are characterized by the expansion of desert-like communities of Poaceae,  
13 *Artemisia*, Chenopodiaceae, Asteraceae, *Ephedra*, and Lamiaceae, among others (Finlayson and  
14 Carrión, 2007). However, mesothermophilous taxa occur along the coastal shelves such as in the  
15 Neanderthal sites of Cueva Perneras ( $37^{\circ} 31' N$ ,  $1^{\circ} 25' W$ ) (Carrión et al., 1995) and Sima de las  
16 Palomas ( $37^{\circ} 47' N$ ,  $0^{\circ} 53' W$ ) (Carrión et al., 2003b) (Fig. 1). These sites have provided  
17 abundant pollen of *Pinus*, *Quercus* and Oleaceae, and continuous or frequent occurrence of  
18 broad-leaved trees (*Fraxinus*, *Alnus*, *Corylus*, *Juglans*, *Ulmus*, *Salix*) and thermophytes (*Myrtus*,  
19 *Erica arborea*, *Pistacia*, *Buxus*, *Periploca*, *Maytenus*, *Osyris*, *Withania*, *Lycium*, *Calicotome*,  
20 *Ephedra fragilis*). At San Rafael marshland there is continuous occurrence of evergreen and  
21 deciduous *Quercus* and *Olea* from c. 16000 to 10000 BP (Pantaleón-Cano et al., 2003).  
22 Anthracological studies on charcoal fragments, *Pinus* cone remains, and *Pinus* kernel shells in  
23 Nerja Cave, Málaga, document the occurrence of three species of *Pinus* between c. 24000 and  
24 17500 yr BP: *Pinus pinea*, *Pinus nigra* and *Pinus halepensis* (Badal, 1998). Charcoal of *Pinus*,  
25 *Quercus*, *Juniperus*, *Cistus*, *Rhamnus-Phillyrea*, *Prunus*, and *Sorbus-Crataegus* have been found  
26 (Badal, 1998).

27 In general, the inland areas of south-eastern Spain fail to show continuous presence of  
28 mesothermophilous taxa during the last glacial stage. The pollen sequences from Beneito Cave  
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(38° 48' N, 0° 28' W) (Carrión and Munuera, 1997), Navarrés peatbog (39° 06' N, 0° 41' W) (Carrión and van Geel, 1999), and Villena peatbog (38°39' N, 0°52' W) (Yll et al., 2003) show episodic occurrences of *Quercus* and other woody taxa during OIS3, like Padul peatbog (37°N, 3° 40'W) (Pons and Reille, 1988) and Carihuella Cave (37° 26' N, 3° 25' W) (Carrión et al., 1999) during OIS4, OIS3 and OIS2. Lateglacial (after c. 15000 years BP) *Quercus* invasions (Pons and Reille, 1988; Fernández et al., 2007) suggest the proximity of refugia of evergreen and deciduous *Quercus*.

Refugia for woody taxa developed not only along the thermomediterranean belt in the coast, but also along intramontane valleys where sufficient precipitation may have provided enough moisture to support trees within a generally arid environment. Here, the lacustrine pollen site of Siles (Carrión, 2002) (38° 24' N, 2° 30' W), dating from upper pleniglacial times (c. 17030 yr BP), includes *Pinus pinaster*, deciduous *Quercus*, evergreen *Quercus*, Ericaceae, *Corylus*, *Betula*, and *Fraxinus*, in pollen percentages always above 2%, and also frequently with *Acer*, *Taxus*, *Arbutus*, *Buxus*, *Salix*, *Ulmus*, *Phillyrea*, *Pistacia*, and *Olea*.

### Mid to late Holocene xerophytization

The Holocene is a time of great environmental variability in Mediterranean Spain. Several pollen sequences show an early-Holocene dominance by *Quercus* (Pons & Reille, 1988; González-Sampériz, 1998; Fernández et al., 2007), but in others *Pinus* continues to be dominant until the mid Holocene (Carrión & van Geel, 1999; Carrión et al. 2001b) or long thereafter (Stevenson, 2000; Franco et al., 2005). Overall, the period from c. 7500-5000 cal yr BP represents the mesophytic optimum, the xerophytic minimum, the period of lowest fire activity, and locally, a phase of relatively high lake levels (Carrión et al., 2001c, Carrión, 2002). During this period, the mountainous areas were forested with several species of *Pinus*, *Quercus faginea*, *Q. pyrenaica*, *Q. ilex*, *Q. suber*, broad-leaf trees (*Corylus*, *Alnus*, *Betula*, *Acer*, *Fraxinus*, *Ulmus*, *Juglans*,

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4 *Arbutus*, *Salix*, *Castanea*) and other woody taxa (*Juniperus*, *Taxus*, *Olea*, *Phillyrea*, *Pistacia*,  
5 *Buxus*, *Prunus*, *Ephedra fragilis*) (Carrión et al., 2007, 2008).

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7 A relevant question is when did the arid southeast attain its present status? In addition,  
8 what was the ultimate factor that provided the high degree of xerophytization observed today  
9 (Calmel-Avila, 2000)? A comparative analysis of palaeobotanical data from the Murcian-Almerian  
10 province and surroundings (Fig. 1) sheds light onto these questions. The pollen sequences of  
11 Sierras de Gádor (2° 55'W, 36° 54'N, 1530 m a.s.l.) and Baza (37° 14'N, 2° 42'W, 1900 m a.s.l.)  
12 are particularly useful in this respect.

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22 Holocene ecological change in Sierra de Gádor has been constant, and at times, rapid  
23 (Carrión et al., 2003a). After c. 3940 cal yr BP, frequent alternation of dominance of *Pinus* and  
24 evergreen *Quercus* at the expense of deciduous *Quercus*, is observed. This change is preceded  
25 by increases of microcharcoal particles at c. 4200 cal yr BP, suggesting enhanced fire (Fig. 4).  
26 Fire events along the Gádor sequence are correlative of xerophyte pollen (*Lygeum*,  
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65 evergreen *Quercus* at the expense of deciduous *Quercus*, is observed. This change is preceded by increases of microcharcoal particles at c. 4200 cal yr BP, suggesting enhanced fire (Fig. 4). Fire events along the Gádor sequence are correlative of xerophyte pollen (*Lygeum*, *Chenopodiaceae*, *Artemisia*, *Lamiaceae*, *Ephedra fragilis*), but the change towards sclerophyllous vegetation is also contemporaneous with the Argaric settlement, which, according palaeoanthracological analyses (Rodríguez-Ariza, 1992), would have intensified pastoralism, forest destruction and matorralization. A Poaceae increase after c. 1760 cal yr BP is preceded by rising percentages of Sordariaceae, *Polygonum aviculare*, *Riccia* and Genisteae, indicating heavy grazing in the lake catchment (Carrión et al., 2003a). The first pollen records of *Vitis* are dated at c. 1600 cal yr BP (Fig. 4). Pastoralism and agriculture are further supported by charcoal and seed remains of *Olea*, *Vitis*, and heliophytic taxa in the excavation sites of the slopes (Rodríguez-Ariza, 1995; Buxó, 1997), and archaeological evidence suggests great demographic pressure during Roman times (Cámalich and Martín, 1999). Sierra de Gádor today is a treeless mountain, but one millennium ago, several taxa were found that are now extinct in the Sierra, such as *Taxus baccata*, *Corylus avellana*, *Betula celtiberica*, *Alnus glutinosa*, and *Myrtus communis* (Carrión et

al., 2003a). Others, like *Arbutus unedo*, *Buxus sempervirens*, *B. balearica*, and *Acer granatense*, have become extremely rare. In addition, historical records and toponymic information suggest there was extensive brush and *Pinus* and *Quercus* forest cover in several mountain systems of Almería only three centuries ago (García-Latorre and García-Latorre, 1996). These most recent changes could have resulted from impact of lead extraction, beginning in 1822 (Grove and Rackham, 2001). The current treeless condition of Sierra de Gádor is, therefore, a relatively recent phenomenon. Under the long-term influence of increased dryness and burning, opening of the landscape may have started patchily after c. 3940 cal yr BP, but the definitive loss of forest is a human-induced case.

Like Gádor, the history of the vegetation in Sierra de Baza appears clearly influenced by changes in local economy, with emphasis on the highly-populated Argaric period, in a context of increased dryness over the last 5000 years (Carrión et al., 2007). The replacement of mesophytic by more xeric Mediterranean vegetation around 3800 cal yr BP is preceded by greater fire activity at c. 4100 cal yr BP. Grassland scrub and thorny matorral spread after c. 2560 cal yr BP (Fig. 4). Sierra de Baza is today partially forested due to recent afforestations, but deforestation became strong over the last two millennia, when anthropogenic disturbance (agriculture, mining, pastoralism) reached its maximum.

Anthropogenic landscapes have their origins later in more continental territories, like the Segura Mountains (Fig. 1). Yet, spatial complexity prevailed. *Plantago* and other indicators of agriculture and arboriculture, and indicators of forest degradation, occur first in the pollen record of the mesomediterranean Villaverde (c. 2200-1600 cal yr BP) (Fig. 4), then in Siles (c. 1400 cal yr BP) and El Sabinar (c. 1353 cal yr BP), and finally in the high-elevation Cañada de la Cruz (c. 670 cal yr BP) (Carrión, 2002b) (Fig. 1). Archaeological data from the Neolithic to the Bronze Age suggest that settlement was sparse in these mountains, and that agriculture was not important before Roman times (Jordán, 1992). Documentary evidence suggests that only in the last

centuries has population growth and the improvement of agricultural technologies caused transformation of forests into croplands at low- and mid-altitudes, although many areas were left uncultivated or reverted to grazing until the present-day, and much of the forested territory was managed exclusively for timber (Sánchez-Gómez et al., 1995).

Important forest losses are detected earlier in thermomediterranean areas than in the mountains and most continental territories. The San Rafael marshland pollen record, in the littoral ( $36^{\circ} 46' N$ ,  $2^{\circ} 36' W$ ), shows the development of shrublands (with expansion of communities of *Artemisia* and *Chenopodiaceae*) since the mid Holocene c. 5000 cal BP (Pantaleón-Cano et al., 2003) (Fig. 4). A similar sequence occurs at Roquetas (Pantaleón-Cano et al., 2003), Gata (Burjachs et al., 2000, Jalut et al., 2000), Antas (Pantaleón-Cano et al., 2003), and Caldereros (Fuentes et al., 2006) (Fig. 1). Geomorphological studies confirm a gradual erosive down cutting of many river catchments in the south-east from the Chalcolithic (Calmel-Avila, 2000). Anthracological studies also suggest that the anthropic impact in the thermomediterranean began earlier, since the Neolithic. This lead to the progressive expansion of garrigues, depending on the locality, to the detriment of *Pinus* and arboreal *Quercus* (Badal et al., 1994, Rodríguez-Ariza, 2000). During and after the Chalcolithic, the well-developed riparian vegetation became progressively denuded in the lowland river valleys and their immediate surroundings (Rodríguez-Ariza, 1992).

Modern vegetation in southeastern Spain cannot be adequately understood in the absence of the palaeorecord. It is worth emphasizing that *Pinus* forests are natural in the region while evergreen *Quercus*-dominated formations are not systematically the pre-anthropic stage of vegetation (Carrión et al., 2004). Mixed conifer-*Quercus* forests including deciduous *Quercus* are a common feature in the middle Holocene (Fig. 4). Several species such as *Corylus avellana*, *Betula celtiberica*, *Acer granatense*, *Taxus baccata*, and *Arbutus unedo* are relicts of the mid-Holocene mesic forests (Carrión et al., 2003a). The pollen sequences are also pertinent to

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4 discern the ecological affinities of several species such as *Maytenus europaeus*, *Chamaerops*  
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6 *humilis*, *Myrtus communis*, *Asparagus*, *Phillyrea* (cf. *P. media*), and *Buxus*  
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8 *sempervirens/balearica*, which behaved as mesophytes by reaching a maximum during the mid  
9 Holocene (Carrión et al., 2003a). These taxa have declined since c. 4000 yr BP, and their  
10 variation does not correlate with that of the xerothermic scrub of *Ziziphus*, *Withania*, *Periploca*,  
11 and *Calicotome*, which have been phytosociologically related with (Peinado et al., 1992).  
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## Conclusions

21 Aridity is a feature of southeastern Spain ever since the Middle Miocene, 16 million years ago,  
22 which is characterized by complex palynological assemblages including a subdesertic  
23 component with *Nitraria*, *Neurada*, *Prosopis*, *Lygeum*, *Ephedra*, Caesalpiniaceae, *Acacia* and  
24 *Calligonum*. For the Pliocene (5.3-1.8 Ma), pollen records also reflect the occurrence of episodes  
25 with abundant herbs (Poaceae, Asteraceae, Chenopodiaceae-Amaranthaceae, *Artemisia*), and  
26 subdesert elements such as *Lygeum*, *Nitraria*, and *Calligonum* which indicate dry and hot  
27 conditions. During the Pleistocene (1.8-0.1 Ma), southeastern Iberia can be characterized by a  
28 diversity of landscapes including mountain grasslands and lowland steppes, *Pinus* woods in mid-  
29 altitudes and a number of woody plants in the present-day meso and thermomediterranean belts  
30 along coastal shelves and intramontane valleys. Forest cover was less extensive but ever present  
31 across the region during glacial stages, with the occurrence of *Pinus*, *Quercus*, *Juniperus*, *Abies*,  
32 *Corylus*, *Betula*, *Alnus*, *Ulmus*, *Salix*, *Castanea*, *Fraxinus*, *Juglans*, *Acer*, *Sorbus*, *Taxus*, *Olea*,  
33 *Pistacia*, *Phillyrea*, *Arbutus*, and *Myrtus*, among others.  
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Complicating the effects of climate on vegetation during the Holocene is the impact of  
humans, which has been highly variable over southeastern Spain, starting earlier in low-elevation  
areas and river basins. Forest degradation of the mountains started late during the Argaric period  
(4300-3600 cal yr BP), and reached its maximum during the Roman occupation, c. 2000 cal yr

BP. Over the last two millennia, natural and/or human-set fires, combined with overgrazing, would have pushed mountain forests over a threshold leading to the spread of grassland, thorny scrub, junipers, and nitrophilous communities. Specifically-orientated projects could be directed towards the investigation of whether ancient forests would be able to recover if anthropogenic pressures ceased, but the picture would remain speculative because demographic pressure is becoming greater over the last years. It can be concluded that the high degree of xerophytization observed today in southeastern Spain is not an unicausal process, but rather it is spatially heterogeneous, and resulting from a combination of anthropogenic disturbance, and resource exhaust under enhanced aridity.

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40 **FIGURE LEGENDS**  
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45 Figure 1. Palaeobotanical sites of south-eastern Spain discussed in this paper. Alborán A-1,  
46 Andalucía A-1, Andalucía G-1, Tarragona E2 and Gor (Jiménez-Moreno and Suc, 2007),  
47 Navarrés (Carrión and van Geel, 1999), Beneito (Carrión and Munuera, 1997), Villaverde  
48 (Carrión et al. 2001b), Siles (Carrión 2002a), Sabinar (Carrión et al., 2004), Cañada de la Cruz  
49 (Carrión et al., 2001a), Carihuera (Carrión et al., 1999, Fernández et al., 2007), Padul (Pons and  
50 Reille, 1988), Nerja (Badal, 1998), Gádor (Carrión et al., 2003a), Baza (Carrión et al., 2007), Las  
51 Palomas (Carrión et al., 2003b), Caldereros (Fuentes et al., 2005), Perneras (Carrión et al., 1995),  
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4 Antas, San Rafael, Roquetas de Mar (Pantaleón-Cano et al., 2003), Gata (Jalut et al, 2000).  
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6 Asterisks refer to sites with evidences of tree pollen during glacial stages of the Pleistocene.  
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11 Figure 2. Synthetic pollen diagrams of the Middle Miocene sites Alborán-A1 and Andalucía-A1 in  
12 southeastern Spain. Subdesertic elements include *Nitraria*, *Calligonum*, *Lygeum*, *Neurada*, and  
13  
14 *Prosopis*, among others. Mediterranean xerophytes include *Olea*, *Phillyrea*, *Ceratonia* and  
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16 *Quercus ilex-coccifera*. Palaeogeography on palinspastic map of Harzhausser and Piller (2007).  
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18 Redrawn from Jiménez-Moreno and Suc (2007).  
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24 Figure 3. Biomes of the Iberian Peninsula at 5.32-5 Ma using the typology established by Prentice  
25 et al. (1992), and climatic estimations. Redrawn from Fauquette et al. (1999).  
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31 Figure 4. Comparative chart of vegetational developments during the Holocene in four important  
32 pollen sequences from southeastern Spain, from the high-elevation Baza to the littoral San Rafael  
33 marshland. A climatically-induced mesophytic optimum is observed during the middle Holocene.  
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35 Xerophytization starts from c. 5000-4500 cal yr BP, but it is modulated by changes in fire  
36 occurrence, and human activities. Deforested landscapes occur first in the  
37 thermomediterranean San Rafael.  
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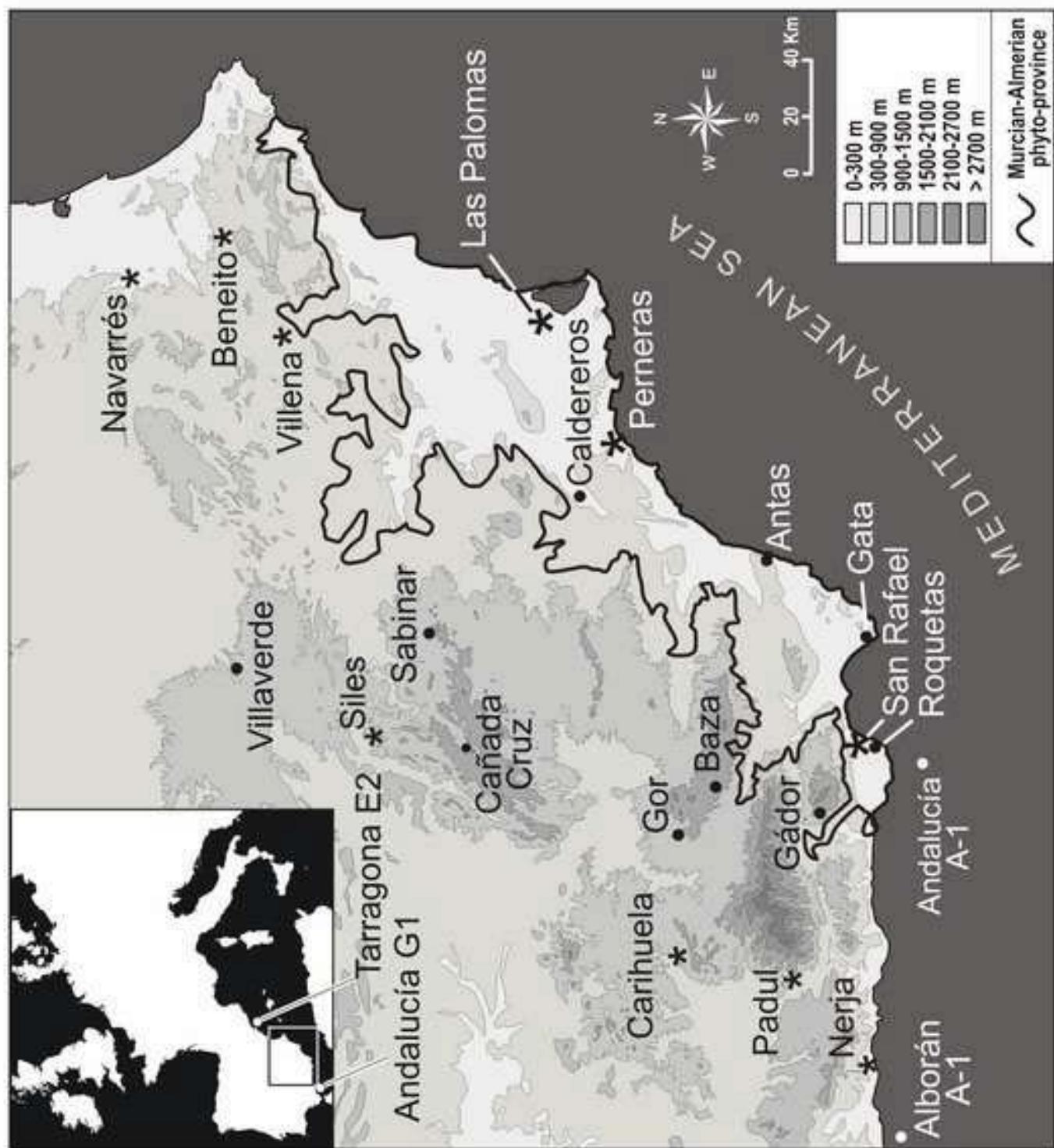
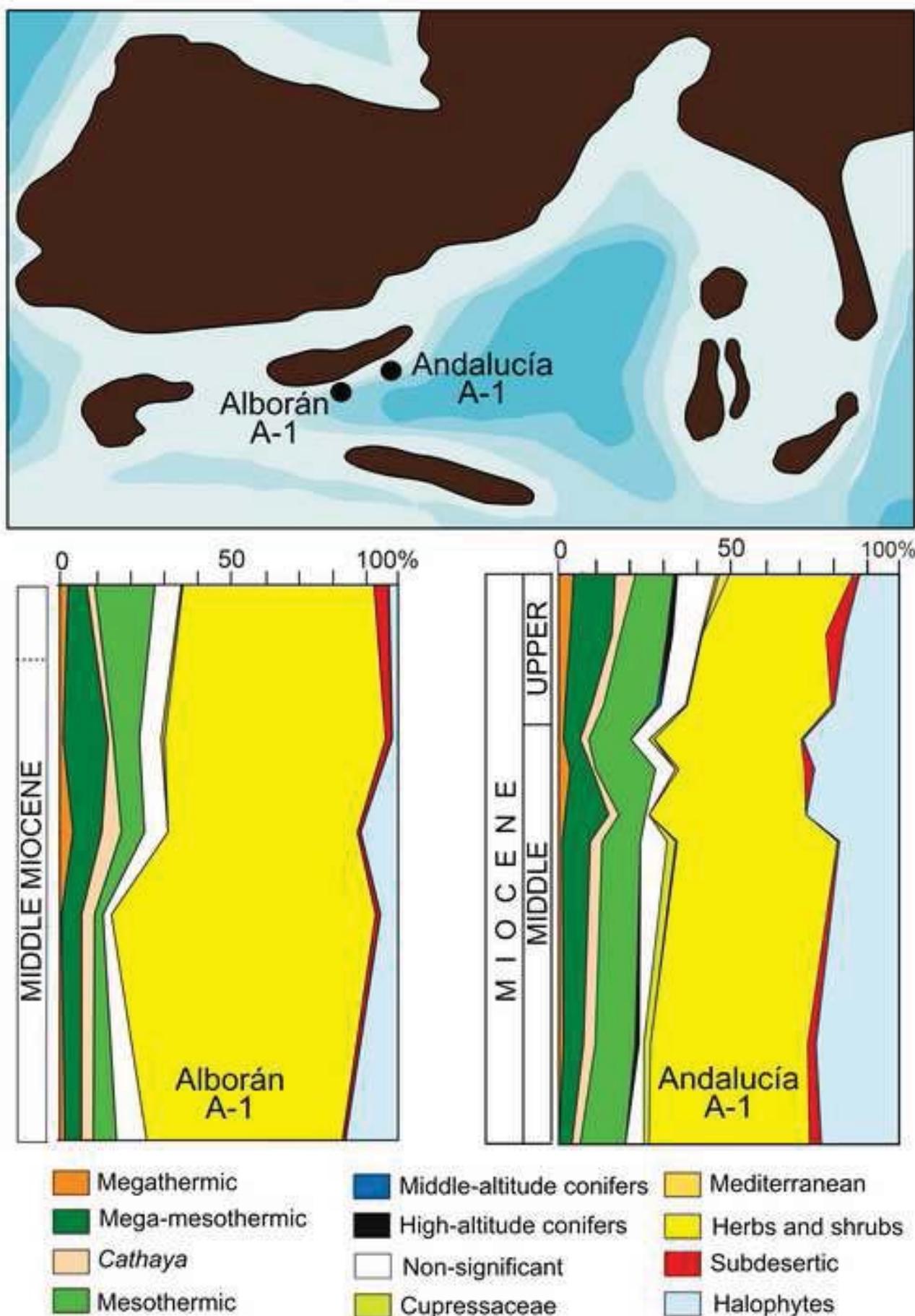


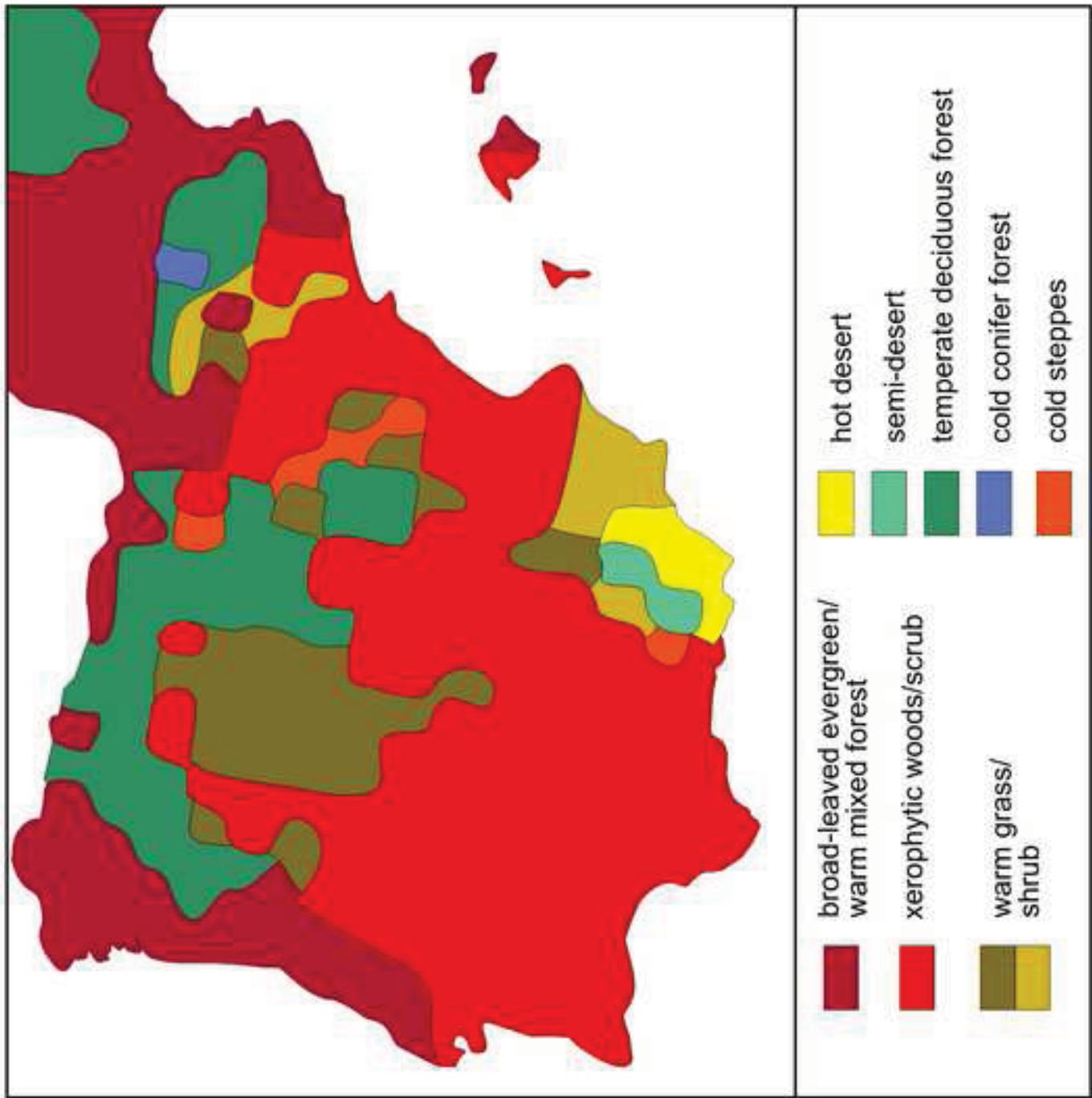
Figure 1  
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**Figure 2**

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**Figure 4**

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