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Research article

# *Buxus* in Europe: Late Quaternary dynamics and modern vulnerability

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ABSTRACT

The suggested location of broadleaved evergreen trees in Europe during the last full-glacial has traditionally favoured a southerly refugial model, which proposes survival in the Mediterranean peninsulas and recolonization of central and northern Europe during the Holocene. This hypothesis is not always substantiated by thorough reviews of original past and modern occurrence data, or considered in the light of plant traits and autoecology. Our approach focuses on the genus *Buxus* with the aim of exploring (i) the relationship between the location of refugia and post-glacial population dynamics, (ii) past processes determining density, fragmentation and local extinctions of modern populations, and (iii) the vulnerability of *Buxus* in the context of the undergoing environmental changes. We compiled a database of over 3600 modern occurrences and 676 fossil sites to reconstruct the distribution of *Buxus* in Europe since 30 ka cal BP. The location of fossil finds and the plant traits of *Buxus* indicate that it persisted widely across its modern distribution through the last glacial period with modes varying from region to region. The E Pyrenees, W Alps, and Jura Mts hosted dense populations, which expanded exponentially during the whole Holocene, and resulted in a modern continuous distribution area. In contrast, the Mediterranean Peninsulas hosted sparse populations, which increased exponentially only during the first half of the Holocene, clearly decreased in the last 4.5 ka BP and resulted in a highly fragmented modern distribution area, most likely in relation to the climate trends towards dry conditions of the last few millennia. These results challenge the common view that the Mediterranean regions are the exclusive and most important refuge areas for evergreen broadleaved trees and stress the importance of considering long-term population dynamics based on fossil data to evaluate the vulnerability of modern fragmented plant populations in view of conservation actions.



## Introduction

The suggested location of broadleaved evergreen trees in Europe during the last full-glacial has traditionally favoured a southerly refugial model, which proposes survival in the three Mediterranean peninsulas and recolonization of central and northern Europe during the Holocene. Modern studies involving fossil and genetic data (Magri et al., 2006; Willis and Van Andel, 2004) indicate that some broadleaved deciduous (e.g. *Fagus sylvatica* L., *Corylus avellana* L.) and needleleaved evergreen (e.g. *Taxus baccata* L., *Pinus sylvestris* L., *Juniperus communis* L.) trees may have survived in central Europe. No reports for northerly persistence of evergreen broadleaved woody taxa (e.g. *Ilex aquifolium* L., *Hedera helix* L., *Buxus sempervirens* L.) are known, and in the common view such species were confined to the Mediterranean Peninsulas during the last glacial period (Bennett et al., 1991; Bhagwat and Willis, 2008).

Recently, some authors showed that biogeographical plant traits of woody species play an important role in determining the chances of local persistence through the last glacial period in central and northern Europe (Bhagwat and Willis, 2008). In particular, it was shown that species with a full-glacial distribution including northerly locations were wind-dispersed, habitat-generalist trees with the ability to reproduce vegetatively.

On these premises, we decided to study the history of *Buxus* L., a genus with two shrub/tree (up to 15 m) species in Europe, *B. sempervirens* L. and *B. balearica* Lam. The genus has a long history in Europe, as witnessed by a continuous fossil record since the Miocene, through the Pliocene and Early Pleistocene (Kvaček et al., 1982; Leroy and Roiron, 1996). A few studies deal with its Holocene history (Lang, 1992; Wegmüller, 1984; Yll et al., 1997; Di Domenico et al., 2011), but they are either limited in time and/or space or require updating with the large amount of data published in the last 20 years.

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In this paper, a reconstruction of the late-glacial and Holocene history of *Buxus* in Europe is presented using modern and past distribution data and interpreted in the light of the ecological features, with the aim of answering the following questions:

- is the modern distribution of *Buxus* the result of a post-glacial migration from limited glacial refugia? *Buxus* is often considered a thermophilous (sub-)mediterranean woody taxon. From the refugia in the Mediterranean regions and in the southern and western Alps *Buxus* would have recolonized the northern parts of its modern distribution area (Lang, 1992; Wegmüller, 1984). The wealth of recently published modern and fossil data of *Buxus* may contribute defining times and modes of its postglacial expansion.
- are there regional differences in the Holocene dynamics of *Buxus* populations in Europe? *Buxus* is presently distributed in both central and southern Europe. The combined use of modern and past distribution data may highlight and explain similarities and dissimilarities in the behaviour of populations located in different bioclimatic areas.
- which are the different roles played by natural population dynamics, climate change and human impact in shaping the European distribution of *Buxus* in the last 15,000 years? Considering that the modern distribution of plant species is the result of a combination of factors, including location of glacial refugia and ecological responses to post-glacial climate changes and human activities, it may be of interest to evaluate which factor was especially influential on *Buxus*.
- is *Buxus* a vulnerable genus in Europe? While *B. balearica* is considered vulnerable in some parts of its distribution range (Blanca, 1999), no conservation actions focus on *B. sempervirens*, apart from weak regulations at local or regional levels in central Europe. The post-glacial history of *Buxus* may help distinguish areas where the populations are vigorous and do not require any specific conservation action from areas where they are weak and demand special attention in the context of the ongoing climate change and increasing human impact.

The combined analyses of modern distribution and fossil records may concur to define where *Buxus* is “natural” in Europe and serve as a scientific basis on which to base conservation actions in areas where *Buxus* populations are at risk. In this sense, they contribute to the practical application of palaeoecological studies to long-term biodiversity maintenance, ecosystem naturalness, conservation evaluation, habitat alteration, and changing disturbance regimes (Willis and Birks, 2006).

## Materials and methods

A thorough survey of the modern distribution data of *Buxus* has been carried out, including more than 3600 occurrences. Online Vegetation Databases were queried for the distribution of *Buxus* in Portugal, Spain, France, Germany, Switzerland, and Austria (Appendix S1). A number of sites (0.7%) that appeared incorrectly georeferenced were checked with the original source. The distribution of *Buxus* in Italy follows Di Domenico et al. (2011). For all the other European countries, the distribution was reconstructed using (i) original field data, (ii) national and regional floras, and (iii) papers reporting the natural occurrence of *Buxus* (Appendix S1). The distributions of *B. sempervirens* and *B. balearica* are represented in Fig. 1 by green and orange squares, respectively.

To reconstruct the Holocene history of *Buxus*, we compiled a pollen database consisting of 650 sites throughout Europe (Fig. 1 and Appendix S2). The characteristics of *Buxus* pollen are unmistakable (Beug, 2004; Wegmüller, 1984), so misidentifications in the reviewed palynological studies are unlikely. Considering the low frequency of *Buxus* pollen and its short dispersal distances (Cañellas-Boltà et al., 2009), we assumed that the occurrence of *Buxus* pollen indicates its presence in the surrounding vegetation.

Records of *Buxus* pollen were extracted from published diagrams, and ages were determined with the associated depth-age model, when available, or by linear interpolation between radiocarbon ages. All dates were calibrated to calendar years before present (cal BP) using the online program Calib 6.0 (http://calib.qub.ac.uk/calib/calib.html). Since many published diagrams show only selected pollen taxa, the full list of species was checked in the European Pollen Database (www.europeanpollendatabase.net), when available. The complete list and references of the reviewed pollen sites are reported in Appendix S2. The presence or absence of *Buxus* pollen is represented in Fig. 2 by red or yellow dots, respectively.

In addition to pollen data, the past distribution of *Buxus* was enhanced by a macrofossil dataset (wood and leaves) derived from the published literature (26 sites). The complete list and references of the macrofossil sites are presented in Appendix S3. The chronological setting of the macrofossils is based on radiocarbon measurements at all the sites. The macrofossil sites of *Buxus* are represented in Fig. 2 by red triangles.

Modern and past distribution data were processed in GIS environment using the Mollweide Equal-Area Projection (Figs. 1 and 2). The Bioclimatic Map of Europe (Rivas-Martínez et al., 2004; http://www.globalbioclimatics.org/) was used to assign each site to a Macro-Bioclimatic zone (Fig. 1).

## Distribution, ecology and plant traits of *Buxus* in Europe

### *Distribution and ecology*

*B. sempervirens* L. has a gregarious and locally abundant distribution but it is also absent in vast areas where suitable habitats are present (Tutin et al., 1968). It shows a centre of continuity, abundance and frequency in the Pyrenees, Southern France, French Prealps and all around the Jura Mts (Fig. 1). Fragmented populations are found in the southern European Peninsulas (Iberian, Italian, and Balkan) and in central France. Exiguous stands are located in Britain, Belgium, Luxembourg, Germany, Sardinia, Montenegro, and Kosovo. *B. sempervirens* also occurs, outside the studied area, in Morocco, Algeria, Turkey, Georgia, Iran and Kazakhstan. *B. sempervirens* is a species with a wide ecological niche, being generally found between sea-level and 2000 m (e.g. Pyrenees, Mount Olympus, Pindos). It mainly lives on limestone, but it may also be found on ophiolite and volcanic tuff. *B. sempervirens* is often found along slopes, river valleys, canyons, gorges, ravines, and thermal springs, which provide suitable sub-humid conditions. It is present in a wide range of vegetation types, such as deciduous and evergreen broadleaved forests, evergreen needled woodlands, garigues, and calcareous grasslands. Calcareous grasslands with *B. sempervirens* on rock slopes (*Berberidion* p.p.) are a natural habitat type of community interest which requires the designation of special areas of conservation (Natura 2000 code 5110).

*B. balearica* Lam. shows a distribution restricted to the Balearic Islands and to southern Spain, with a single population located in Sardinia (Tutin et al., 1968). Besides, it occurs in Morocco, Algeria and Turkey. It is found on limestone (Balearic Islands, Sardinia) and on the metamorphic crystalline rocks with ultramafic inclusions of the Alboran Block (southern Spain). Despite its restricted distribution, *B. balearica* occurs in both deciduous and evergreen broadleaved forests (Balearic Islands, Sardinia) as well as in evergreen needled woodlands with *Pinus halepensis* Mill. (southern