MOUNTAINS, CLIMATE AND BIODIVERSITY

EDITED BY
CARINA HOORN
ALLISON PERRIGO
ALEXANDRE ANTONELLI

with website

WILEY Blackwell

Mountains, Climate and Biodiversity

Edited by

Carina Hoorn
University of Amsterdam
Amsterdam, The Netherlands

Allison Perrigo
Gothenburg Global Biodiversity Centre
Sweden
Department of Biological and Environmental Sciences,
University of Gothenburg, Sweden
Forest Cat Editing
Uppsala, Sweden

Alexandre Antonelli
Gothenburg Global Biodiversity Centre
Sweden
Department of Biological and Environmental Sciences,
University of Gothenburg, Sweden
Gothenburg Botanical Garden
Sweden

WILEY Blackwell

This edition first published 2018
© 2018 John Wiley & Sons Ltd

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, except as permitted by law. Advice on how to obtain permission to reuse material from this title is available at http://www.wiley.com/go/permissions.

The right of Carina Hoorn, Allison Perrigo and Alexandre Antonelli to be identified as the author(s) of the editorial material in this work has been asserted in accordance with law.

Registered Office(s)
John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030, USA
John Wiley & Sons Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial Office
9600 Garsington Road, Oxford, OX4 2DQ, UK

For details of our global editorial offices, customer services, and more information about Wiley products visit us at www.wiley.com.

Wiley also publishes its books in a variety of electronic formats and by print-on-demand. Some content that appears in standard print versions of this book may not be available in other formats.

Limit of Liability/Disclaimer of Warranty
While the publisher and authors have used their best efforts in preparing this work, they make no representations or warranties with respect to the accuracy or completeness of the contents of this work and specifically disclaim all warranties, including without limitation any implied warranties of merchantability or fitness for a particular purpose. No warranty may be created or extended by sales representatives, written sales materials or promotional statements for this work. The fact that an organization, website, or product is referred to in this work as a citation and/or potential source of further information does not mean that the publisher and authors endorse the information or services the organization, website, or product may provide or recommendations it may make. This work is sold with the understanding that the publisher is not engaged in rendering professional services. The advice and strategies contained herein may not be suitable for your situation. You should consult with a specialist where appropriate. Further, readers should be aware that websites listed in this work may have changed or disappeared between when this work was written and when it is read. Neither the publisher nor authors shall be liable for any loss of profit or any other commercial damages, including but not limited to special, incidental, consequential, or other damages.

Library of Congress Cataloging-in-Publication Data

Names: Hoorn, C. (Carina), editor. | Perrigo, Allison, editor. | Antonelli,
Alexandre, 1978– editor.
Title: Mountains, climate and biodiversity / edited by Dr. Carina Hoorn, Dr. Allison Perrigo,
Prof. Alexandre Antonelli.
Description: Hoboken, NJ : John Wiley & Sons, 2018. | Includes bibliographical references and index. |
Identifiers: LCCN 2017039551 (print) | LCCN 2017047780 (ebook) | ISBN 9781119159896 (pdf) |
ISBN 9781119159889 (epub) | ISBN 9781119159872 (cloth)
Subjects: LCSH: Orogeny. | Mountain biodiversity. | Climatic changes.
Classification: LCC QE621 (ebook) | LCC QE621 .M684 2018 (print) | DDC 577.5/3–dc23
LC record available at https://lccn.loc.gov/2017039551

Cover Design: Wiley
Cover Image: Courtesy of Maurico Diazgranados

The superpáramo of the Sierra Nevada del Cocuy National Park, in Colombia, with rocky slopes of Cretaceous (Albian-Aptian) sedimentary quartzitic sandstone bedrock and shales with occasional limestone inclusions. Espeletia lopezii Cuatrec. grows here in a pit at the base of the vertical slopes of the Ritacuba Blanco peak.

Set in 10/12pt Warnock by SPi Global, Pondicherry, India

10 9 8 7 6 5 4 3 2 1

27

The Alps: A Geological, Climatic and Human Perspective on Vegetation History and Modern Plant Diversity

Séverine Fauquette[1], Jean-Pierre Suc[2], Frédéric Médail[3], Serge D. Muller[1], Gonzalo Jiménez-Moreno[4], Adele Bertini[5], Edoardo Martinetto[6], Speranta-Maria Popescu[7], Zhuo Zheng[8] and Jacques-Louis de Beaulieu[3]

[1] *Institut des Sciences de l'Evolution, University of Montpellier, Montpellier, France*
[2] *Institut des Sciences de la Terre Paris, Sorbonne University, Paris, France*
[3] *Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale, Aix-Marseille University, Aix-en-Provence, France*
[4] *Departamento de Estratigrafía y Paleontología, University of Granada, Granada, Spain*
[5] *Department of Earth Sciences, University of Florence, Florence, Italy*
[6] *Department of Earth Sciences, University of Torino, Torino, Italy*
[7] *GeoBioStratData.Consulting, Rillieux la Pape, France*
[8] *Department of Earth Sciences, Sun Yat-sen University, Guangzhou, China*

Abstract

Mountain ecosystems, and in particular European Alpine ecosystems, have a rich biodiversity, as they represent complex associations controlled by elevation, soils and rocks, and climatic conditions following latitude, longitude, slope orientation and aspect. Vegetation belts are organized with respect to altitude according to a concomitant decrease in temperature and increase in precipitation, and are defined by their dominant plant elements. Plant diversity within the Alps also results from these mountains' location at the transition point between cold-temperate and warm-temperate climates, as well as from their historical biogeography. In order to explain how past environmental changes have shaped the modern plant diversity and the organization of vegetation in altitudinal belts, a temporal dimension may be provided by paleovegetation data. Abundant micro- (pollen) and macro-remains (leaves, fruits, seeds) show that European Cenozoic vegetation exhibits a similar latitudinal and altitudinal organization to the vegetation belts observed today in south-eastern China, where most of the taxa – missing in Europe since the late Neogene – now occur. Late Eocene to Pliocene pollen floras of the south-western and Eastern Alps are characterized by the presence of megatherm plants and an abundance of mega-mesotherm plants. These are typical of moist evergreen low-altitude forests, and are characterized by the presence of *Cathaya*, a conifer now restricted to subtropical China at mid to high elevations. Pollen data indicate the presence of *Abies*/*Picea* forests at high altitudes since at least the Oligocene. Since then, several thermophilous taxa have declined, and some have disappeared from the Alps due to natural or human-related processes that are responsible for the modern plant diversity pattern there. These processes include the uplift of the mountain range, which began ca. 35 Ma, late Neogene global cooling, Pleistocene glacials/interglacials and more recent human impact.

Keywords: *paleo-phytogeography, pollen, mountain uplift, paleoaltitude, Cenozoic, global cooling, climatic cycles*

27.1 Introduction

Mountain vegetation is characterized by the altitudinal stratification of plants related to temperature and precipitation. Vegetation zones change from low to high latitude or from low to high altitude in the same way (Ozenda 1989): the replacement of taxa occurs as vegetation types adapt to colder conditions.

Mountain plant ecosystems generally have high diversity, as they represent complex assemblages influenced by elevation, climatic conditions – which follow latitude and longitude – and variable amounts of rainfall. Moreover, the physiographic complexity of mountains creates environments that can vary over short distances due to, for instance, exposure to sun or slope angle and aspect.

Mountains, Climate and Biodiversity, First Edition. Edited by Carina Hoorn, Allison Perrigo and Alexandre Antonelli.

Companion website: www.wiley.com\go\hoorn\mountains,climateandbiodiversity

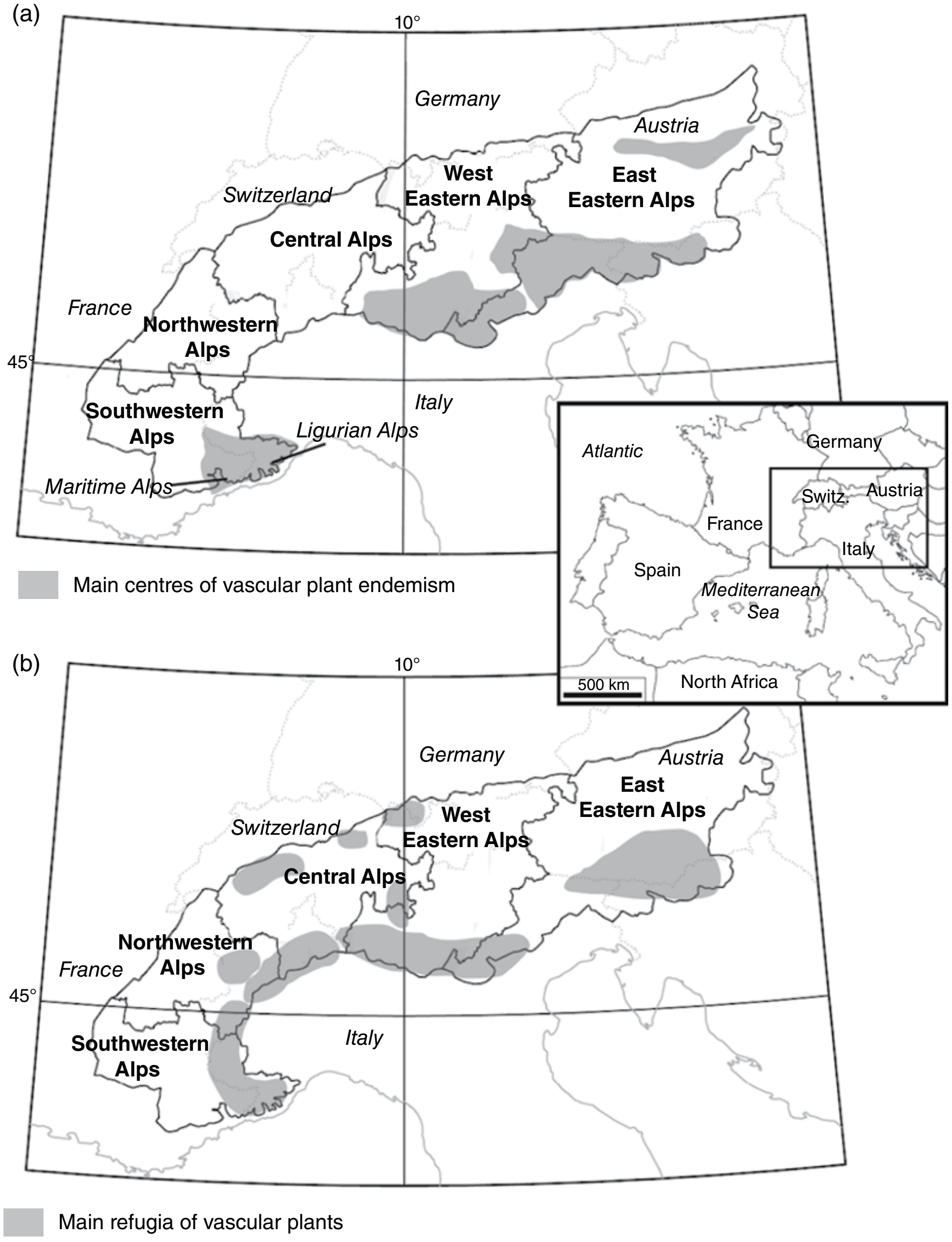

Figure 27.1 Maps of the five main phytogeographic zones of the Alps. *Source:* Adapted from Aeschimann et al. (2011). In gray: (a) The main centers of vascular plant endemism, defined by Noble & Diadema (2011), and (b) The main refugia of vascular plants in the Alps, defined by Schönswetter et al. (2005).

In the Alps, vegetation organization is also complex because of the large size of the mountains and their position at the crossroads of many floristic provinces (Ozenda 2009). Moreover, the Alpine arc is oriented north–south in France but west–east for the rest of the chain (Figure 27.1a). The French section of the chain is thus characterized by important differences between the southern and the northern parts, with the Southern European Alps being drier, as they are under Mediterranean influences.

Plant diversity within the Alps mainly results from their location at the transition point between cold-temperate and warm-temperate climates, their landscape heterogeneity, the local climate variability that arises from complex topographies and historical biogeography. A detailed knowledge of the past is thus essential to an understanding of the processes that have controlled changes in plant diversity up to the present.

This chapter, which focuses primarily on the Western Alps, starts with a description of the present flora and vegetation patterns in their physiographic and geological context. It then shows how the intense tectonic activity in this region over the last 40 My has influenced the flora and vegetation. Finally, it shows the role of Pleistocene climatic cycles and human impact on the mountains and their flora.

27.2 Present Flora and Vegetation Patterns in the Physiographic, Climatic and Geological Context of the Alps

27.2.1 Plant Distribution and Endemism Patterns

The European Alps are one of the most important hot spots of plant biodiversity in Europe (Ozenda 1985, 2002), with a high number of endemic taxa. According to Aeschimann et al. (2004), the Alps encompass 3983 indigenous taxa of vascular plants, which is more than one-third of the total European flora. The average taxonomic richness of the Alps is estimated at about 2200 taxa per 10 000 km^2, and despite their relatively restricted area, the Southwestern Alps are home to more than 70% of the entire Alpine flora. In the Alps, 501 endemic taxa are registered, making up 4% of the European flora. This corresponds to an endemism rate of 12.6% within the area's native flora.

The distribution of endemics (Figure 27.1a) is mainly concentrated in the southernmost Western Alps and the southern part of the East Eastern and West Eastern Alps (Noble & Diadema 2011). At the junction of the Mediterranean Basin and the Alps, the Maritime and Ligurian Alps constitute a zone of geographic overlap between major biotic assemblages (Comes & Kadereit 2003), an important hot spot of plant biodiversity (Médail & Quézel 1997) and also a major refugium (Figure 27.1b) (Médail & Diadema 2009). This region, with 25% of the endemic plants of the whole range, represents one of the most important biogeographical areas in Europe, due to the high concentration of paleoendemic and endemic plants (Casazza et al. 2008; Noble & Diadema 2011). Recent molecular investigations of endemic plants from the Maritime and Ligurian Alps show that vicariance events are the most important factor explaining the distribution and genetic patterns of plant populations there (Casazza et al. 2013). The Maritime Alps do not act as a strong barrier to the migration of plants, and moderate gene flow seems to create an admixture between some plant populations, even when separated by deep valleys (Diadema et al. 2005). The persistence of several endemics throughout various glacial periods appears to be linked to the capacity of mountains to provide a wide diversity of microhabitats within a reduced space.

In the Alps and Carpathian Mountains, species richness and genetic diversity do not co-vary for mountain vascular plants (Taberlet et al. 2012); rather, genetic diversity is associated with the glacial and postglacial history. In the Alps, genetic rarity (the presence of rare alleles or restricted haplotypes) is correlated with both species rarity (i.e., rare markers tend to be located in the same areas as rare species) and species endemism (i.e., rare makers in widespread species tend to be situated in the same areas as endemic species). Rare markers are often fixed in long-term isolated refugial populations, and these crucial areas correspond to distinct glacial refuges, in which the highest endemism levels also occur (Schönswetter et al. 2005).

27.2.2 Vegetation

Vegetation belts (also called altitudinal zones) in the Alps are well characterized by bioclimatic factors and their principal vegetation types, especially forests. Vegetation belts are organized altitudinally according to steep ecological gradients, with a concomitant decrease in temperature and increase in precipitation, extending from the lowlands to the nival zone. In the Central Alps, five vegetation belts are distinguished: the collinean, mountain, sub-alpine, alpine and nival belts (Table 27.1).

In the Southwestern Alps, vegetation is similarly organized in altitudinal belts on both flanks of the mountains, but with more pronounced Mediterranean influences occurring on the southern slopes, from the lowest thermo-Mediterranean to the oro-Mediterranean belt, which corresponds to the alpine belt of the Central Alps (Table 27.1). These southern mountains are heterogeneous from a biogeographical viewpoint, with the southern side clearly influenced by Mediterranean elements and the northern side composed of medio-European vegetation (Barbero & Quézel 1975). The altitudinal limits of these vegetation belts vary along a latitudinal gradient, but they are ~700 m wide in vertical elevation (Ozenda 1989). For collinean to sub-alpine species, especially trees, temperature often represents the limiting factor for survival at the upper limit and moisture at the lower limit.

These vegetation belts are well delimited by modern pollen data collected from moss polsters along two transects across the Southwestern Alps (Figure 27.2). In order to reconstruct Cenozoic vegetation and climate information from pollen data, Fauquette et al. (2015) established the relationship between modern pollen data and vegetation to serve as a baseline. To create this reference data set, pollen grains were grouped according to vegetation belts. However, *Pinus* was separated because

Table 27.1 Structure of the vegetation belts of the Alps in relation to the mean minimum temperatures of the coldest month of the year (*m*), and their correspondence with two concepts of the Mediterranean vegetation belts.

	Alpine vegetation belts		**Mediterranean vegetation belts**	
m **(°C)**	**Ozenda (1985)**	**Main vegetation types**	**Ozenda (2002)**	**Quézel & Médail (2003)**
−10				
−9	Nival Alpine	Bryophytes and lichens Grasslands with Poaceae and Cyperaceae; low heathlands with *Salix*, *Juniperus* and *Vaccinium*	Alti-Mediterranean	Oro-Mediterranean
−7				
−6	Sub-alpine	Coniferous forests with *Picea abies*, *Larix decidua*, *Pinus mugo* and *Pinus cembra*	Mountain-Mediterranean	Mountain-Mediterranean
−4				
−3	Mountain	Forests with *Fagus sylvatica* and/or *Abies alba*; mesophilous forests with *Pinus sylvestris*	Supra-Mediterranean	Supra-Mediterranean
−1				
0				
1	Collinean	Deciduous forests *with Quercus pubescens*, *Q. robur* or *Q. petraea*; xeric forests with *Pinus sylvestris*; mesophilous forests with *Tilia*, *Fraxinus*, *Acer* and *Prunus*	Medio-Mediterranean	Meso-Mediterranean
			Per-Mediterranean	Thermo-Mediterranean
9				
10		Mediterranean vegetation in the Southwestern Alps (southern slopes)		
≥10				Infra-Mediterranean

its pollen is not identifiable at the species level and may be representative of several vegetation belts. Pollen grains of *Larix* are scarce; samples containing this genus were collected within its forests or from sites immediately below such forests. Pollen grains of Cupressaceae are grouped together because infra-family identification (genus identification) is impossible, even though their species grow at different altitudes in the Southwestern Alps: *Cupressus sempervirens*, *Juniperus oxycedrus* and *J. phoenicea* in the two lowermost Mediterranean vegetation belts; *J. thurifera* in the higher supra-Mediterranean belt and in the lower part of mountain-Mediterranean belt; and *J. communis* and *J. sabina* in the mountain-Mediterranean belt. Most of the herbaceous pollen grains cannot be distinguished at the genus level, whereas such plants can inhabit different altitudes; their abundance may indicate open and/or undergrowth vegetation. Finally, alpine tundra-like plants (*Aconogonum alpinum*, *Gentiana*, *Centaurea uniflora*) were identified in only a few sites.

These west–east transects show that there is a good correlation between pollen data and observed vegetation distributions along altitudinal and longitudinal gradients, and that the vegetation distribution follows a clear asymmetric topography (Figure 27.2): replacement of pollen groups as elevation increases appears progressive on the western flank, but much more abrupt in the east.

Pollen data may therefore be used to reconstruct Paleogene to Quaternary paleovegetation. Moreover, for these periods, information from pollen may be complemented by macrofossils when they are available in the same region. However, these fossils are produced from plants that lived not more than a few kilometers from the

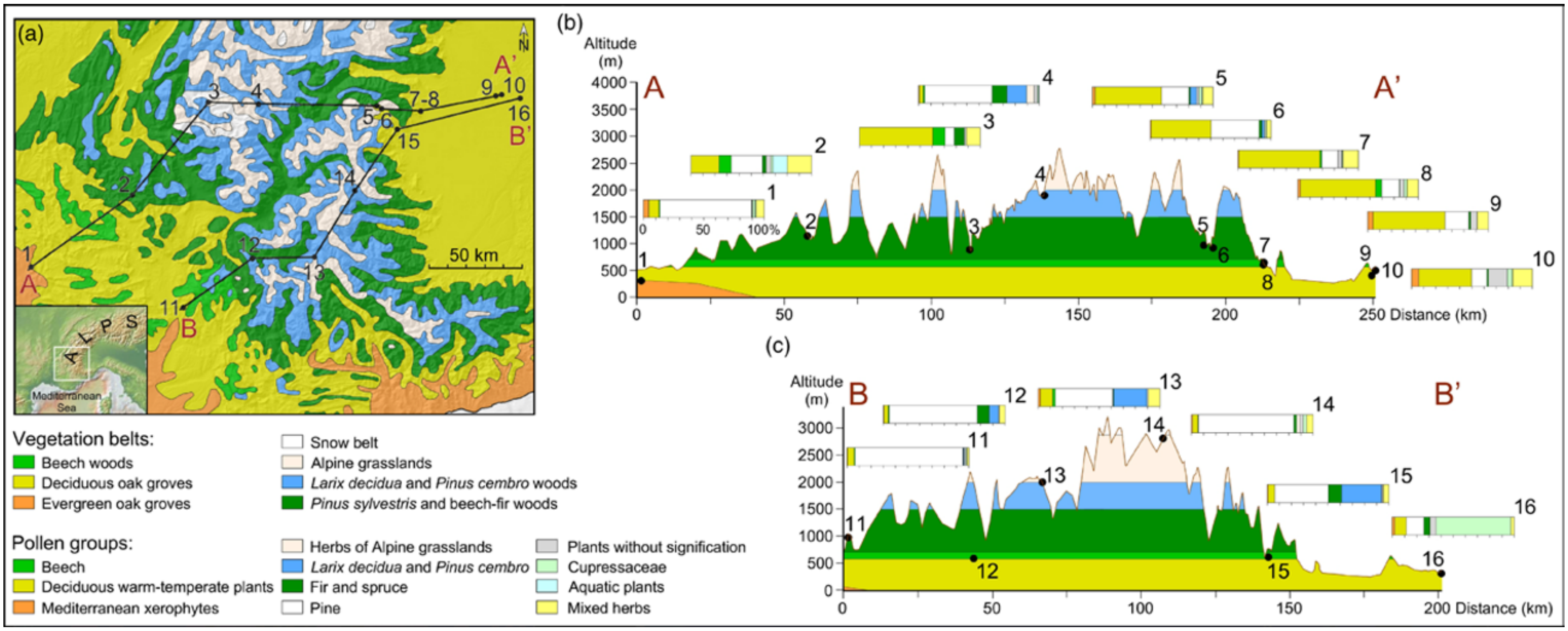

Figure 27.2 Relationship between vegetation belts positioned on a topographic profile, following studies by Noirfalise et al. (1987) and Ozenda (2002), and modern pollen data collected from moss polsters along two transects. (a) Simplified vegetation map of the Southwestern Alps (from Noirfalise et al. 1987), on which the transects are shown (dots correspond to the moss polsters). Pollen localities and altitudes are indicated below. (b) Transect AA′: 1, Nyons (300 m); 2, Luz la Croix haute (1100 m); 3, Le Freney (800 m); 4, Col du Lautaret (1850 m); 5,6, Pinerolese (Lago Villaretto di Roure and Balma di Roure, 980 and 890 m, respectively); 7,8, Cumiana Giaveno (612 and 605 m, respectively); 9,10, Baldissero Torinese (Val Samfrà and Superga road, 383 and 537 m, respectively). (c) Transect BB′: 11, Taulanne (995 m); 12, Sisteron (540 m); 13, Saint-Léger (2000 m); 14, Agnel (2800 m); 15, Pinerolese, Inverso Pinasca (560 m); 16, Moncucco Torinese, Borelli (315 m). *Source:* Adapted from Fauquette et al. (2015). See also Plate 45 in color plate section.

fossilization site, and rarely record those growing in the higher belts. To get around this problem, Bertini & Martinetto (2011) used the presence of pollen and the concomitant absence of macrofossils in several deposits of the same age to pinpoint those plants that probably grew at higher elevations (e.g., *Cedrus*, *Picea*, *Tsuga*).

27.3 Vegetation History of the Alps Since the Late Eocene

The Alps resulted from the convergence of the European and African plates, trapping the Apulian microplate between them, which led to the closure of the Tethys Ocean by the Eocene, followed by a collision between the European and Adriatic plates (e.g., Rosenbaum & Lister 2005). This complex collision history led to a nappe stack involving basement and cover rocks of the European margin, of the intervening ocean and micro-continents, and of the Adriatic margin.

The intense tectonic activity in this region over the last 40 My has influenced the vegetation and flora, with the appearance of high mountains and new marine basins, and consequent landscape fragmentation, environmental heterogeneities and new climatic patterns.

27.3.1 Vegetation History Before Human Impact

Abundant pollen records (e.g., Suc 1989; Suc et al. 1995; Jiménez-Moreno et al. 2005, 2010; Bertini 2010) show that European Neogene vegetation followed belts that were aligned similarly in latitude and altitude to the belts seen today in south-eastern China (Wang 1961), where most of the taxa that disappeared from Europe by the late Neogene are still extant.

The study by Fauquette et al. (2015) shows that in the Southwestern Alps, late Eocene to Pliocene pollen floras (Figures 27.3 and 27.4) are characterized by prevalent mega-mesotherm plants (see the definitions of these plant groups in the legend of Figure 27.4), reflecting subtropical conditions, and sometimes high frequencies of *Cathaya*, a conifer restricted today to subtropical China at mid to high elevations, below the *Abies* and/or *Picea* belts (Wang 1961). Pollen records suggest that the past representatives of *Cathaya* in Europe probably occupied a similar ecological niche (e.g., Suc 1989; Combourieu-Nebout et al. 2000, 2015; Biltekin et al. 2015). Megatherm plants supporting an interpretation of tropical conditions were present in all of the Eocene to mid-Miocene samples (Figure 27.4). The maximum frequency of such species occurred during the early Langhian (~15 Ma) (Jiménez-Moreno et al. 2005), corresponding to the mid-Miocene Climatic Optimum (MCO). The pollen record of mega-mesotherm plants decreases from the early Zanclean (ca. 5 Ma) to the Piacenzian (3.6–2.6 Ma), and major disappearance events have occurred since the earliest Pleistocene (2.6 Ma), due to the onset of northern hemisphere glaciations (Suc 1984; Bertini 2010). Climate gradients linked to the latitude, altitude and physiography of pollen sites explain the different timings of the extinctions of *Taxodium*-type, *Cathaya* and *Tsuga* species, among others (e.g., Suc et al. 1995; Bertini 2010).

On the whole, microtherm trees support the presence of boreal conditions (*Abies, Picea*) and meso-microtherm trees (particularly *Cathaya*) occur in significantly higher frequencies on the eastern side of the Southwestern Alps than on the western side (Figure 27.4). This indicates that the present-day asymmetric topography of the Southwestern Alps, with a relatively gentle western flank and steeper eastern flank, was established early, and has been in existence since at least the early Miocene, and possibly since the Oligocene or late Eocene. Therefore, the high topography and asymmetric morphology of this part of the Alps have been maintained throughout the past ~30 My.

In the East Eastern Alps, early to late Miocene pollen data (Figures 27.3 and 27.4) show a very diverse flora (Jiménez-Moreno et al. 2005, 2008). The Burdigalian and Langhian (20.4–13.6 Ma) vegetation was dominated by thermophilous elements such as evergreen trees, typical of a present-day low-altitude evergreen rainforest (e.g., south-eastern China), reflecting the MCO. During the Serravallian and Tortonian (13.6–7.2 Ma), important vegetation changes are observed: *Avicennia*, which previously populated the coastal areas up to these high latitudes, vanished, and several other megatherm elements (*Buxus bahamensis*-type, *Alchornea*, Melastomataceae), typical of broad-leaved evergreen forests, became rarer, before finally disappearing from Central Europe. These changes can be linked to cooling and correlated with global and regional climatic changes. Later, this vegetation was progressively replaced by communities rich in mesotherm plants. Percentages of mid- and high-altitude conifers increased considerably during the Langhian and, later, during the Serravallian and Tortonian, indicating their relocation to a lower altitude, nearer to the sedimentary basin, which is correlated with significant cooling phases. These coniferous belts developed again at higher altitudes during warmer phases, as signaled by their reduced frequency in younger pollen records.

Subsequently, several thermophilous plants declined in abundance, and some of them disappeared from the Alps due to global cooling and progressive amplification of the glacial–interglacial cycles (see further details in Chapter 9). The data from the Stirone site (Figure 27.4) (Bertini 2001) at the foot of the Apennines provide a good example of this phenomenon. From their onset,

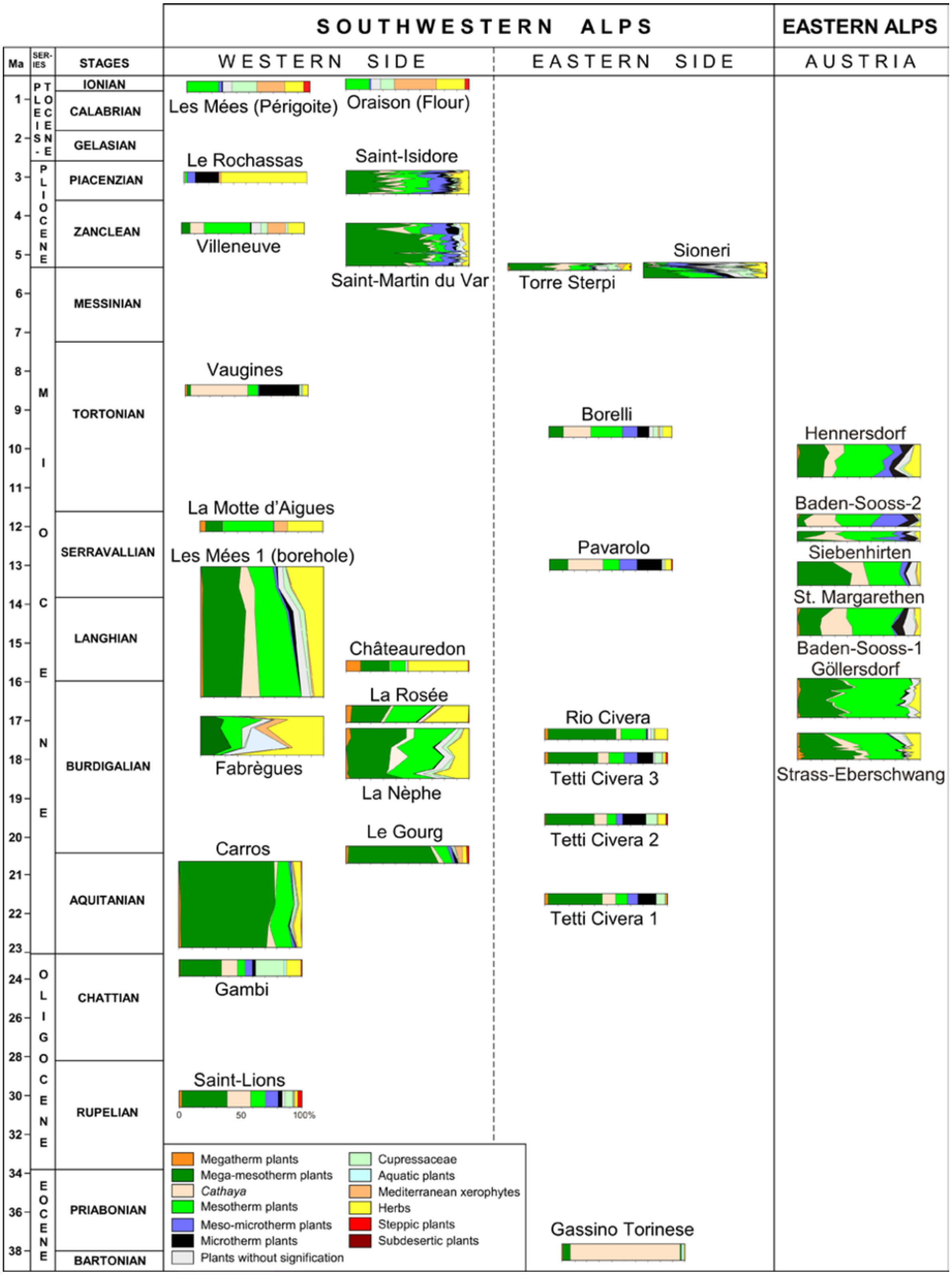

Figure 27.3 Synthetic pollen diagrams from late Eocene to Pleistocene localities of the Southwestern and Eastern Alps, and their positions in a chronostratigraphic frame. Note the change of time scale at the Paleogene–Neogene boundary. Taxa have been arranged into 13 different groups (*Pinus* excluded) based on ecological criteria to visualize the main changes in the paleovegetation cover. Plants without signification indicates families (e.g., Rosaceae, Ranunculaceae, Rutaceae) in which pollen identification is difficult at the genus level and includes cosmopolitan taxa and/or taxa with wide ecological requirements, plus unidentified pollen grains. Some groups are classified according to thermic requirements with respect to the Nix (1982) classification: equatorial and tropical forests are inhabited by megatherm plants (mean annual temperature, MAT >24 °C), subtropical forests by mega-mesotherm plants (MAT 20–24 °C), temperate deciduous forests by mesotherm plants (MAT 14–20 °C), boreal coniferous forests successively by meso-microtherm (MAT 12–14 °C) and microtherm (MAT <12 °C) plants and tundra by microtherm plants. *Source:* Adapted from Fauquette et al. (2015) and Jiménez-Moreno et al. (2008). See also Plate 46 in color plate section.

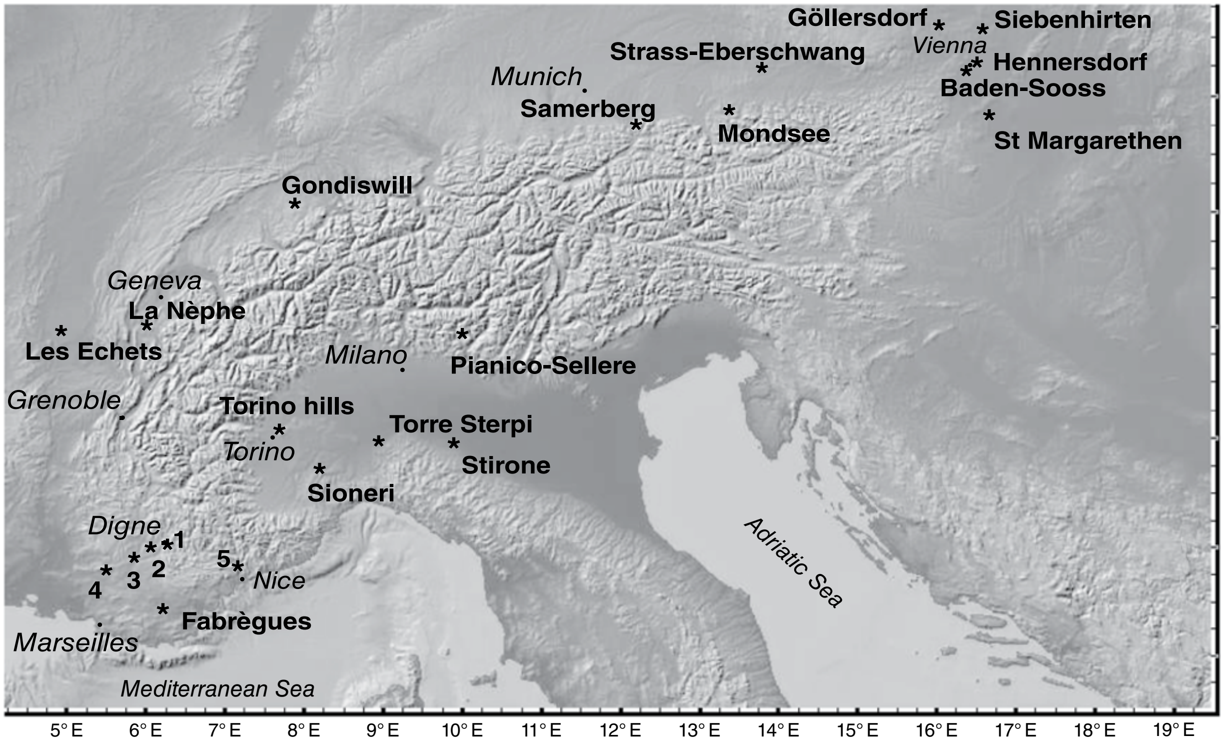

Figure 27.4 Locations of the palynological sites mentioned in the text and in Figure 27.3. The sites of the Torino Hills are: Gassino Torinese, Tetti Civera (samples 1, 2 and 3 in Figure 27.3) and Rio Civera, Pavarolo, Borelli. The numbered sites in Southern France are: 1, Saint Lions, Gambi, Châteauredon, Le Rochassas; 2, La Rosée, Les Mées 1, Les Mées-Périgoite; 3, Villeneuve, Oraison (Flour); 4, La Motte d'Aigues, Vaugines; and 5, Le Gourg, Carros, Saint Martin du Var, Saint-Isidore

glacial–interglacial cycles are marked by changes in both vegetation and reconstructed climate compared to the early Pliocene (Fauquette & Bertini 2003). During interglacials, the climate was almost as warm as in the early Pliocene, and the vegetation remained a mega-mesotherm to mesotherm plant forest. During glacials, mega-mesotherm taxa disappeared (e.g., *Distylium*, *Myrica*) or declined in abundance and distribution (*Taxodium*-type, *Sequoia*-type). Temperatures were markedly lower than during interglacials – nearly equal to modern values – and not suitable for these thermophilous taxa.

The known macrofloras mostly come from the northern and eastern borders of the Alps for the Eocene to mid-Miocene interval (Mai 1995), and from the southern Alps for the Messinian and Pliocene (Bertini & Martinetto 2011; Martinetto et al. 2015). In general, these data confirm the picture provided by pollen with respect to the flora and vegetation of the lowland Alpine fringes. The most interesting information added by macrofossils is connected with the marked climatic cooling that has occurred since ~2.6 Ma: several plants now extinct in Europe entered the macrofossil record for the first time during this period (Martinetto et al. 2015). The cones of *Picea florschuetzii*, which are very similar to a modern spruce that grows in the Himalaya (*P. smithiana*), or of *Tsuga chairugii*, whose relatives today live only in America and East Asia, are frequent in a few early Pleistocene sites of northern Italy (Ravazzi 2003). The presence of these taxa indicates either the descent of the Alpine high-vegetation belts or immigration from Northern Europe/Siberia. Reliable records of plant species typical of the modern Alpine high-altitude belt (e.g., *Larix* cf. *decidua* and *Picea abies*) are first found only in the late early Pleistocene (Ravazzi et al. 2005). Records of diagnostic species of the alpine belt are restricted to the late Pleistocene glacials and most commonly occur in the lowlands to the north of the Alps (e.g., *Salix herbacea*) (Alsos et al. 2009). This appears to be a good example of a taphonomic window, where alpine taxa are only preserved when they descend close to potential depositional environments, which are restricted to lowlands or basin floors.

Very few pollen data are available from the Pleistocene. Pollen data from Pianico-Sellere (Bergamo, Italy; Figure 27.4), attributed to early–middle Pleistocene, represent vegetation dynamics similar to those of the late Pleistocene interglacials, although "Tertiary relicts" (*Pterocarya*, *Tsuga*, *Rhododendron ponticum*) are still present (Martinetto 2009). Other pollen successions in Switzerland and Bavaria attributed to the mid-Pleistocene (Welten 1982; Grüger 1983) illustrate, as elsewhere in Europe, a moderate expansion of *Pterocarya* during the

Holstein interglacial. Several pollen records from France, Switzerland, Bavaria and Austria (respectively, Les Echets (de Beaulieu & Reille 1984), Gondiswill (Wegmüller 1992), Samerberg (Grüger 1979) and Mondsee (Drescher-Schneider 2000); Figure 27.4) document the vegetation dynamics of the last interglacial (Eemian), highlighting the significant role played by *Carpinus betulus* and the quasi-absence of *Fagus*.

27.3.2 The Onset of Modern Vegetation: An Example from the Western Alps

Numerous pollen records are available in the western Alps for the Holocene, which allow for the depiction of the general trend of vegetation changes during this period.

The Last Glacial Maximum (LGM), between 24 and 17 ka (calibrated ages), constitutes the state of maximal retreat of temperate vegetation types, to the benefit of alpine-boreal plant communities. Temperate taxa were mostly restricted to southern refuges, mainly located in the Iberian, Italian and Balkan peninsulas and around the Black Sea, but some could also have survived within cryptic northern refugia (e.g., Nieto Feliner 2011). Most of the temperate plant recolonizations occurring thereafter originated from southern regions (e.g., Brewer et al. 2002; Muller et al. 2007).

The Lateglacial period (17.0–11.3 ka) was marked by an ecological succession arising from an initial climate warming: the cold steppe vegetation dominated by *Artemisia* and Amaranthaceae was replaced by *Juniperus* scrub, then *Betula* woods and finally *Pinus* forests (de Beaulieu & Reille 1983). The Younger Dryas climatic event, which allowed a widespread expansion of steppe communities throughout Europe, led to a general lowering of the treeline to ~300 m.

The subsequent temperature increase at the beginning of the Holocene induced a second phase of successional dynamics, involving temperate tree communities that replaced *Pinus* forests. The first trees to establish were *Corylus* and deciduous *Quercus*. These communities constituted, from sea level to about 1800 m, diversified forests, including *Fraxinus*, *Ulmus* and *Tilia*. At higher altitudes, these forests were replaced by coniferous ones.

Simultaneously, around 10.1 ka, *Abies alba* penetrated into the southern French Alps, migrating from its nearest refugium in the northern Adriatic region (Muller et al. 2007). Fir forests expanded during the Atlantic period (8.9–5.4 ka), in both the southern (de Beaulieu & Reille 1983) and the northern French Alps (David 1995). This range expansion was slower in the dryer internal massifs, and ended about 6.5 ka, when fir penetrated into the extensive pine woods of the most arid region of the Alps, the Briançonnais (Muller et al. 2007). Throughout its Alpine range, this highly competitive species found suitable conditions at middle altitudes, progressively forcing pines and *Larix decidua* to migrate to higher altitudes and deciduous broad-leaved trees to migrate to lower ones.

Between 6.5 and 2.8 ka, *Pinus cembra* formed dense forests between 2000 and more than 2300 m (Muller et al. 2006). This occurred at the same time as an increase in the upper treeline, which exceeded 2900 m in the Queyras Valley (Talon et al. 1998). During the Subboreal period (5.4–2.8 ka), fir and deciduous oak declined as Neolithic human populations progressively colonized mountain territories (Walsh et al. 2014). The anthropogenic pressure was intense during the last 2.8 ka, since the beginning of the Subatlantic period, and the forest exploitation of the Bronze and Iron ages focused on some useful species, such as fir, which was intensively exploited to supply coastal shipyards (Nakagawa et al. 2000). Such human activity induced major vegetation changes from the shores to the mountains: at low altitudes, evergreen pioneer formations of *Quercus ilex* and *Pinus halepensis* replaced the deciduous forests of *Q. pubescens*, forming the anthropogenic meso-Mediterranean belt. At mid-altitudes, above the remnant deciduous oak forests of the supra-Mediterranean belt and within the mountain-Mediterranean belt, *Abies alba* forests declined to give way to *Fagus sylvatica*, while in the sub-alpine belt, *Pinus cembra* declined and *Abies* disappeared from the internal valleys (Muller et al. 2007), which allowed larch and mountain pine to disperse to lower elevations.

At the time of the Roman Empire, several cultivated trees were introduced (e.g., *Castanea*, *Juglans*), and the industrial forest exploitation (Nakagawa et al. 2000) allowed for the immigration of *Picea abies* into the newly opened vegetation zones. This species spread into the sub-alpine belt of the Northern Alps, where it found a suitably wet climate. The period between AD 500 and 1000 was marked by a forest recovery, followed by a new deforestation trend from feudal times onwards, which finally ended during the Industrial Revolution of the 19th century. Thereafter, the abandonment of agriculture in remote valleys resulted in a re-establishment of mountain forests and the significant establishment of firs and oaks in secondary pioneer forests during the 20th century.

27.4 Climate and Paleoaltitude Reconstructions of the Alps Since the Late Eocene

27.4.1 Methods Based on Pollen Data

Pollen grains offer a large number of morphological traits (such as aperture, structure and sculpture) that can be analyzed by light microscopy (Punt et al. 2007) and scanning electronic microscopy (SEM) for surface features (Halbritter et al. 2007). These features can then be used to identify the pollen to species level. The implementation of these techniques in the 1970s led to vastly improved identification rates of the Neogene pollen flora in the Mediterranean region, based on systematic comparative observations of fossil pollen grains with those of living plants (Suc 1976; Suc & Bessedik 1981). This botanical approach afforded the identification of more than 100 new taxa, including 14 robust identifications at the species level in the study area (*Avicennia officinalis*, *A. alba*, *Hamamelis mollis*, *Parrotia persica*, *Parrotiopsis jacquemontiana*, *Distylium chinense*, *Microtropis fallax*, *Juglans cathayensis*, *Nyssa sinensis*, *Rhoiptelea chiliantha*, *Carpinus orientalis*, *Rhus cotinus*, *Lygeum spartum* and *Cedrus atlantica*) (Suc et al. 2004). This achievement significantly enriched the understanding of the regional Neogene flora and contributed to reliable climate reconstructions.

The climate reconstructions assembled from the Neogene data (Fauquette et al. 1999; Jiménez-Moreno et al. 2008; Fauquette et al. 2015) are based on the "climatic amplitude method," which was developed by Fauquette et al. (1998) specifically to quantify the climate of periods with no modern analogs for the pollen spectra. In this method, the past climate is estimated by transposing the climatic requirements of the maximum number of modern taxa to the fossil data. The climatic amplitude method takes into account pollen percentages, and allows, despite some biases, for a greater refinement and precision of climatic estimates, because taxa with very low pollen percentages are not always significant. The most probable climate for a set of taxa is estimated as the climatic interval suitable for the highest number of taxa and a "most likely value" corresponding to a weighted mean.

In this method, *Pinus* pollen grains are excluded from the pollen sum, as they are generally over-represented in marine sediments due to a prolific production and overabundance resulting from long-distance air and water transport (Heusser 1988; Beaudouin et al. 2007). High-latitude/altitude taxa are also excluded from the reconstruction process to avoid a cold bias linked to pollen transport from higher elevations. The excluded taxa are defined on the basis of their occurrence in modern vegetation zones: vegetation types described for the studied time period are found today in south-eastern China. There, the vertical distribution of vegetation is characterized from the base to the top of the massifs by evergreen broad-leaved forest, mixed evergreen and deciduous broad-leaved forest, *Picea*/*Tsuga* forest, *Abies* forest and high mountain meadows (Wang 1961; Hou 1983). This stratification allows us to exclude the modern high-altitude taxa from the climatic reconstruction in order to infer the low- to middle-low-altitude climate (Fauquette et al. 1998). This procedure also allows us to discriminate between climatic variations and elevation changes.

Estimates based on this method show that the latitudinal temperature gradient in western Europe was ~0.48 °C/degree latitude during the mid-Miocene (Fauquette et al. 2007) and ~0.46 °C/degree latitude during the early Oligocene (Fauquette et al. 2015), and that a modern gradient was established during the Tortonian.

The method used to quantify paleoaltitudes, developed by Fauquette et al. (1999), is based on pollen floras, which provide a regional view of the vegetation from the lowest to the highest altitudinal belts feeding into the drainage basin from which the sediments were sourced, and the mean annual temperature (MAT) reconstructed at sea level, which is transposed into a modern latitude. The latitude difference between the Cenozoic site and the modern latitude indicates the shift in altitude of the vegetation belts; in particular, the *Abies*/*Picea* belt, which is the best indicator of elevated topography in the fossil pollen floras. This method uses a standard modern relationship established by Ozenda (1989, 2002), as the data do not allow the estimation of past terrestrial lapse rates. Ozenda's relationship assumes that, in the Alps, modern vegetation belts shift by 110 m in altitude per degree of latitude. It should be noted that terrestrial lapse rates are highly variable geographically in relation to altitude, slope aspect, prevailing wind directions, continentality and atmospheric composition, among other factors, and they are difficult to apply where the past atmospheric composition differed from the present (see Chapter 7). Meyer (1992) estimated modern terrestrial lapse rates for many areas of the world, and found that they vary between 0.36 and 0.81 °C/100 m for MAT. However, because there is no information concerning paleoterrestrial lapse rates in the Alps, Fauquette et al. (2015) hypothesized that the ratio between altitudinal and latitudinal temperature gradients was similar to the present ratio; taking into account the range of modern terrestrial lapse rates, the relationship between the latitudinal and altitudinal gradients would vary, giving different values for the shift of vegetation belts per degree of latitude (Table 27.2). If this range of values were used, the estimates of paleoaltitude would differ as well. However, Table 27.2 highlights that the estimates of the terrestrial lapse rate for each studied period based on the standard modern relationship are included in Meyer's estimated range.

Moreover, paleoelevation estimates correspond to the most probable paleoelevations based on the "most likely values" of MAT and to ranges of paleoelevation based on the minimum and maximum MAT. This partially compensates for the use of the modern altitudinal/latitudinal ratio.

In the case of sites with unknown elevation (Suc & Fauquette 2012), which were all younger than 10 Ma in Fauquette et al. (2015), the latitudinal temperature

Table 27.2 Shifts in altitude of vegetation belts in relation to different terrestrial lapse rates and to latitudinal gradients estimated for different epochs (Fauquette et al. 2015). The minimum (0.36 °C/100 m) and maximum (0.8 °C/100 m) lapse rates are those reconstructed by Meyer (1992) for many areas of the world. The lines in bold corresponds to the estimates of terrestrial lapse rate for each studied period based on the standard modern relationship.

	Latitudinal gradient (°C/°lat.)	Terrestrial lapse rate (°C/100 m)	Shift in altitude/°lat.
Standard modern	0.6	0.55	1 °lat. → 110 m
Pliocene	0.6	0.36	1 °lat. → 167 m
		0.55	**1 °lat. → 110 m**
		0.81	1 °lat. → 74 m
Middle Miocene	0.48	0.36	1 °lat. → 134 m
		0.44	**1 °lat. → 110 m**
		0.55	1 °lat. → 87 m
		0.81	1 °lat. → 60 m
Early Oligocene	0.46	0.36	1 °lat. → 128 m
		0.42	**1 °lat. → 110 m**
		0.55	1 °lat. → 84 m
		0.81	1 °lat. → 57 m

gradient was similar to the modern one, and the authors chose to keep the terrestrial lapse rate equivalent to the modern rate, taking into account that the position and continentality of the Alps were the same as today.

The record in the fossil pollen flora of microtherm trees such as *Abies* and *Picea* indicates elevated topography close to the sampled sites. Nevertheless, pollen data do not permit altitudinal range estimation for this vegetation belt, nor a determination of whether alpine herbaceous and perpetual-snow belts existed above it, due to difficulties in differentiating between the pollen of alpine herbaceous elements and that of plants growing at lower elevations. As a consequence, these pollen-based paleoelevations are minimum estimates, corresponding to the lower limit of the highest forested belt.

We must emphasize the consistency of our previous estimates: the paleoaltitude we inferred for the Mercantour Massif (Southwestern Alps) is consistent with a geomorphological reconstruction (Fauquette et al. 1999); the paleoaltitude of the Ganos Mountain in the Dardanelles Strait (Melinte-Dobrinescu et al. 2009) is in agreement with the tectonic hypothesis of Armijo et al. (1999); and the paleoaltitude of the Canigou Mount in the Eastern Pyrenees (Suc & Fauquette 2012) is supported by a paleogeographic validation (Clauzon et al. 2015).

27.4.2 Resulting Paleoaltitudes

Based on this method, the study by Fauquette et al. (2015) shows that the topography of the internal zone of the Southwestern Alps reached elevations of around 1800 m as early as the Oligocene (ca. 30 Ma). In contrast, the external massifs, including the Mercantour Massif, uplifted later, during the late Neogene, while the post-Serravallian (ca. 12–13 Ma) emplacement of the Digne thrust nappe was reinforced. Pollen data show that the present-day topographic asymmetry of the Southwestern Alps, with a relatively gentle western flank and a much steeper eastern one, dates back to at least the early Miocene, and possibly to the Oligocene or late Eocene.

In the East Eastern Alps (Jiménez-Moreno et al. 2008), paleoaltitudes during the Burdigalian were not high enough for *Abies* and *Picea* to form forests, but were sufficient to allow *Cathaya* to survive. Therefore, the relief was less than 1800 m. On the other hand, Serravallian and Tortonian pollen records, rich in conifers typical of high elevations, indicate an intense uplift during the mid-Miocene. The abundance increase in high-elevation trees is due to uplift and not to climatic changes, as the pollen records are still dominated by thermophilous plants. Paleoaltitudes were higher than 1600 m at that time.

27.5 How Do Regional Geological Evolution, Global Climatic Changes and Human Pressure Affect Alpine Plant Diversity and Vegetation?

Due to the formation of the Alps since the late Paleogene (40–35 Ma) under warm-temperate to subtropical conditions, boreal-type environments could only develop at the higher elevations. Since the Oligocene, high elevations (~1800 m) have allowed meso-microtherm (*Cedrus*, *Cathaya*) and microtherm (*Abies*, *Picea*) trees to establish.

The development of plant populations on mountains arises from two major sources (Ozenda 1985, 2009): an autochthonous (in situ) population, formed of plants already present at the beginning of the uplift, and an allochthonous component, arising from migration from other cold regions.

The autochthonous part formed from a subtropical to tropical flora. Most of these taxa, vulnerable to cold, became extinct later due to glaciations and competition, but a few, such as *Juniperus thurifera* and *Berardia subacaulis*, survived in the Western Alps (Ozenda 2009). Plants of temperate origin are represented by two groups: Holarctic and Mediterranean plants (Ozenda 1985).

The allochthonous part is made up of plants that migrated from the Mediterranean and/or central Asian mountains and Arctic regions (Ozenda 1995, 2009; Kadereit et al. 2008). Exchanges with Arctic and Northern European floras during glacials/interglacials is evidenced by the presence of "arctic-alpine" plants. However, the Alpine flora shows less pronounced affinities to the northern (Scandinavia, North America) than to the southern (Mediterranean Basin, Central and Eastern Asia) floras (Ozenda 1995, 2009; Comes & Kadereit 2003). The European Alpine system and major Central Asian mountains (Altai, Tibetan Plateau and Himalaya) are connected by a more or less continuous system of mountain ranges. This implies both a northern (boreal, sub-arctic, arctic) and a southern (southern mountains) connection between the European Alpine system and the Central Asian high mountains.

Pleistocene glaciations played a major role in the changing vegetation of the Alps: (i) the pre-existing thermophilous flora almost completely disappeared; (ii) plants of temperate origin only survived in refugia, leading to a disjunct distribution of some plants; and (iii) exchanges between the Alps and the other mountain ranges and/or northern regions were amplified. Pleistocene warming phases led to the expansion of the thermophilous floras, forcing microtherm plants to move towards colder areas to the north or to higher elevations (Ozenda 1985, 2009), which resulted in disjunct distributions of arctic-alpine plants.

The postglacial period of the French Alps is the period in which the different vegetation belts recognized today were established (Table 27.1). Around 10 ka, only two forested belts existed: a lower one, occupied by deciduous oak forest, and an upper one, characterized by coniferous forests (mainly *Pinus sylvestris* and *P. uncinata*). The boundary between these two belts was not abrupt, but formed a transition zone with mixed formations of oaks and pines. This intermediate belt only transformed into a belt in its own right with the immigration of fir, from ca. 9 ka. The fir forests, mixed with numerous deciduous trees, forced oak forests downslope and pine forests upslope. The late onset of this belt is clearly due to the migratory dynamics of firs that arrived in the French Alps from their Adriatic and Apennine refuges. Between 7.5 and 5.0 ka, the sub-alpine belt, which was made up of open woodlands of *Pinus uncinata* mixed with *Larix* and *Pinus cembra*, differed significantly from its modern physiognomy. The modern forest structure of this belt was only achieved around 5 ka, with the development of dense forests of *P. cembra* up to ~2300 m. The onset of a real forested sub-alpine belt appears to be related to a general aridification, evidenced by low lake levels (Digerfeldt et al. 1997).

The last belt to appear in the Southwestern Alps was the lower meso-Mediterranean belt, at around 5–4 ka, characterized by the establishment of typical Mediterranean plants at low altitudes, in particular *Quercus ilex* and *Pinus halepensis*. The presence of Neolithic human populations supports the anthropogenic origin of this belt, which corresponds to the replacement of deciduous forests by pioneer disturbance-adapted plant formations. Nevertheless, recent multiproxy attempts to quantify Holocene climate fluctuations have shown that a succession of dry episodes from ca. 5 ka may have also triggered the expansion of sclerophyllous Mediterranean taxa (Magny et al. 2002). Unlike the other vegetation belts, the meso-Mediterranean belt appears to be a partly human-triggered subdivision of the former (supra-)Mediterranean belt, naturally dominated by deciduous oak forests. At higher altitudes, human activity also had strong effects, such as lowering the treeline by at least 300 m (Carnetti et al. 2004) and creating sub-alpine meadows. Moreover, increased human population sizes in mountains led to the fragmentation of forest ecosystems and thus to erosion events. In the second part of the 20th century, a policy of intensive reforestation started.

27.6 Conclusion

The flora of the Alps encompasses more than one-third of the European flora. Endemic taxa, mainly concentrated in the south-westernmost Alps and the south-western part of the Eastern Alps, represent 4% of the European flora. Maritime and Ligurian Alps constitute an important hot spot of plant species richness and form a major refugium where endemic plants represent 25% of all alpine endemics.

In the Alps, vegetation belts are organized by altitude, governed by decreases in temperature and increases in precipitation at higher elevations. These vegetation belts are well recognized in modern pollen data, established on two transects along the slopes of the Southwestern Alps. The modern pollen data also reflect the asymmetric west–east elevation of the massif: the replacement of pollen groups as elevation increases appears progressive on the western flank but much more abrupt on the eastern one.

The formation of the Alps dates back to ca. 35 Ma and has influenced both the flora and the vegetation of the area, due to the appearance of high mountains and new marine basins, and consequent landscape fragmentation, environmental heterogeneities and new climatic patterns. As early as the Oligocene, high relief allowed boreal-type environments to develop at the higher elevations, and meso-microtherm (*Cedrus*, *Cathaya*) and microtherm trees (*Abies*, *Picea*) established early in the history of Alpine vegetation. During the Pleistocene, due to glaciations, the earlier, more thermophilous flora became extinct, while arctic-alpine plants developed on the massifs. Holarctic plants only survived in refugia, leading to disjunct distributions. However, warm phases also led to disjunct distributions of the arctic-alpine plants, which moved towards colder areas to the north or to higher elevations. Today, only some "Tertiary relicts," such as *Juniperus thurifera* and *Berardia subacaulis*, still survive in the Alps.

The onset of the modern vegetation patterns started in the early postglacial period, around 10 ka. The different vegetation belts recognized today gradually developed following local climate and soil conditions and the migratory dynamics of the species. The presence of human populations in the Alps since the Neolithic triggered the expansion of some vegetation types, in particular typical Mediterranean plant formations at low altitude, and the lowering of the treeline, which led to the development of the sub-alpine meadows. Finally, the recent abandonment of land cultivation has resulted in the return of mountain forests.

Acknowledgments

The authors are deeply indebted to the late Professor Pierre Quézel for his teaching, advice and unfailing support for their work on the history of the Mediterranean flora and vegetation. A part of this study has been realized in the framework of the project "Erosion and Relief Development in the Western Alps," funded by the Agence Nationale de la Recherche. The authors thank the two reviewers, R.A. Spicer and J. Carrión, who helped us to improve the chapter. This is ISEM contribution no. 2016-115.

References

Aeschimann, D., Lauber, K., Moser, D.M. & Theurillat, J.-P. (2004) *Flora Alpina*. Belin & Zanichelli: Haupt.

Aeschimann, D., Rasolofo, N. & Theurillat, J.-P. (2011) Analyse de la flore des Alpes. 1: historique et biodiversité. *Candollea* **66**, 27–55.

Alsos, I.G., Alm, T., Normand, S. & Brochmann, C. (2009) Past and future range shifts and loss of diversity in dwarf willow (*Salix herbacea* L.) inferred from genetics, fossils and modelling. *Global Ecology and Biogeography* **18**, 223–239.

Armijo, R., Meyer, B., Hubert, A. & Barka, A. (1999) Westward propagation of the North Anatolian fault into the northern Aegean: timing and kinematics. *Geology* **27**, 267–270.

Barbero, M. & Quézel, P. (1975) Végétation culminale du mont Ventoux; sa signification dans une interprétation phytogéographique des Préalpes méridionales. *Ecologia Mediterranea* **1**, 3–33.

Beaudouin, C., Suc, J.-P., Escarguel, G. et al. (2007) The significance of pollen signal in present-day marine terrigenous sediments: the example of the Gulf of Lions (western Mediterranean Sea). *Geobios* **40**, 159–172.

Bertini, A. (2001) Pliocene climatic cycles and altitudinal forest development from 2.7 Ma in the Northern Apennines (Italy): evidence from the pollen record of the Stirone section (~5.1 to ~2.2 Ma). *Geobios* **34**, 253–265.

Bertini, A. (2010) Pliocene to Pleistocene palynoflora and vegetation in Italy: state of the art. *Quaternary International* **225**, 5–24.

Bertini, A. & Martinetto, E. (2011) Reconstruction of vegetation transects for the Messinian/Piacenzian of Italy by means of comparative analysis of pollen, leaf and carpological records. *Palaeogeography, Palaeoclimatology, Palaeoecology* **304**, 230–246.

Biltekin, D., Popescu, S.-M., Suc, J.-P. et al. (2015) Anatolia: a long-time plant refuge area documented by pollen records over the last 23 million years. *Review of Palaeobotany and Palynology* **215**, 1–22.

Brewer, S., Cheddadi, R., de Beaulieu, J.-L. et al. (2002) The spread of deciduous *Quercus* throughout Europe since the last glacial period Forest. *Ecology and Management* **156**, 27–48.

Carnetti, A.L., Theurillat, J.-P., Thinon, M. et al. (2004) Past uppermost tree limit in the Central European Alps (Switzerland) based on soil and soil charcoal. *The Holocene* **14**, 393–405.

Casazza, G., Zappa, E., Mariotti, M.G. et al. (2008) Ecological and historical factors affecting distribution pattern and richness of endemic plant species: the case of Maritime and Ligurian Alps hotspot. *Diversity and Distributions* **14**, 47–58.

Casazza, G., Grassi, F., Zecca, G., et al. (2013) Phylogeography of *Primula allionii* (Primulaceae), a narrow endemic of the Maritime Alps. *Botanical Journal of the Linnean Society* **173**, 637–653.

Clauzon, G., Le Strat, P., Duvail, C. et al. (2015) The Roussillon Basin (S. France): a case-study to distinguish local and regional events between 6 and 3 Ma. *Marine and Petroleum Geology* **66**, 18–40.

Combourieu-Nebout, N., Fauquette, S. & Quézel, P. (2000) What was the late Pliocene Mediterranean climate like: a preliminary quantification from vegetation. *Bulletin de la Société géologique de France* **171**, 271–277.

Combourieu-Nebout, N., Bertini, A., Russo-Ermolli, E. et al. (2015) Climate changes in the central Mediterranean and Italian vegetation dynamics since the Pliocene. *Review of Palaeobotany and Palynology* **218**, 127–147.

Comes, H.P. & Kadereit, J.W. (2003) Spatial and temporal patterns in the evolution of the flora of the European Alpine system. *Taxon* **52**, 451–462.

David, F. (1995) Vegetation dynamics in the northern French Alps. *Historical Biology* **9**, 269–295.

de Beaulieu, J.-L. & Reille, M. (1983) Paléoenvironnement tardiglaciaire et holocène des lacs de Pelléautier et Siguret (Hautes-Alpes, France). L'histoire de la végétation d'après les analyses polliniques. *Ecologia Mediterranea* **9**, 19–36.

de Beaulieu, J.-L. & Reille, M. (1984) A long Upper Pleistocene pollen record from Les Echets, near Lyon, France. *Boreas* **13**, 111–132.

Diadema, K., Bretagnolle, F., Affre, L. et al. (2005) Geographic structure of molecular variation of *Gentiana ligustica* (Gentianaceae) in the Maritime and Ligurian regional hotspot, inferred from ITS sequences. *Taxon* **54**, 887–894.

Digerfeldt, G., de Beaulieu, J.-L., Guiot, J. & Mouthon, J. (1997) Reconstruction and paleoclimatic interpretation of Holocene lake-level changes in Lac de Saint-Léger, Haute-Provence, southeast France. *Palaeogeography, Palaeoclimatology, Palaeoecology* **136**, 231–258.

Drescher-Schneider, R. (2000) The Riss-Wurm interglacial from West to East in the Alps: an overview of the vegetational succession and climatic development. *Geologie en Mijnbouw* **79**, 233–239.

Fauquette, S. & Bertini, A. (2003) Quantification of the northern Italy Pliocene climate from pollen data – evidence for a very peculiar climate pattern. *Boreas* **32**, 361–369.

Fauquette, S., Guiot, J. & Suc, J.-P. (1998) A method for climatic reconstruction of the Mediterranean Pliocene using pollen data. *Palaeogeography, Palaeoclimatology, Palaeoecology* **144**, 183–201.

Fauquette, S., Clauzon, G., Suc, J.-P. & Zheng, Z. (1999) A new approach for paleoaltitude estimates based on pollen records: example of the Mercantour Massif (southeastern France) at the earliest Pliocene. *Earth and Planetary Science Letters* **170**, 35–47.

Fauquette, S., Suc, J.-P., Jiménez-Moreno, G. et al. (2007) Latitudinal climatic gradients in western European and Mediterranean regions from the Mid-Miocene (~15 Ma) to the Mid-Pliocene (~3.5 Ma) as quantified from pollen data. In: Williams, M., Haywood, A., Gregory, J. & Schmidt, D. (eds.) *Deep Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*. The Micropaleontological Society, Special Publications. London: The Geological Society of London, pp. 481–502.

Fauquette, S., Bernet, M., Suc, J.-P. et al. (2015) Quantifying the Eocene to Pleistocene topographic evolution of the southwestern Alps, France and Italy. *Earth and Planetary Science Letters* **412**, 220–234.

Grüger, E. (1979) Spätriß, Riß/Würm und Frühwürm am Samerberg in Oberbayern – ein vegetationsgeschichtlicher Beitrag zur Gliederung des Jungpleistozäns. *Geologica Bavarica* **80**, 5–64.

Grüger, E. (1983) Untersuchungen zur Gliederung und Vegetationsgeschichte des Mittelpleistozäns am Samerberg in Oberbayern. *Geologica Bavarica* **84**, 21–40.

Halbritter, H., Weber, M., Zetter, R. et al. (2007) *PalDat – Illustrated Handbook on Pollen Terminology*. Vienna: Springer.

Heusser, L. (1988) Pollen distribution in marine sediments on the continental margin of Northern California. *Marine Geology* **80**, 131–147.

Hou, H.-Y. (1983) Vegetation of China with reference to its geographical distribution. *Annals of Missouri Botanical Garden* **70**, 509–548.

Jiménez-Moreno, G., Rodríguez-Tovar, F.-J., Pardo-Igúzquiza, E. et al. (2005) High-resolution palynological analysis in late early-middle Miocene core from the Pannonian Basin, Hungary: climatic changes, astronomical forcing and eustatic fluctuations in the Central Paratethys. *Palaeogeography, Palaeoclimatology, Palaeoecology* **216**, 73–97.

Jiménez-Moreno, G., Fauquette, S. & Suc, J.-P. (2008) Vegetation, climate and paleoaltitude reconstructions of the Eastern Alps during the Miocene based on pollen records from Austria, Central Europe. *Journal of Biogeography* **35**, 1638–1649.

Jiménez-Moreno, G., Suc, J.-P. & Fauquette, S. (2010) Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. *Review of Palaebotany and Palynology* **162**, 403–415.

Kadereit, J.W., Licht, W. & Uhink, C.H. (2008) Asian relationships of the flora of the European Alps. *Plant Ecology and Diversity* **1**(2), 171–179.

Magny, M., Miramont, C. & Sivan, O. (2002) Assessment of the impact of climate and anthropogenic factors on Holocene Mediterranean vegetation in Europe on the basis of palaeohydrological records. *Palaeogeography, Palaeoclimatology, Palaeoecology* **186**, 47–59.

Mai, D.H. (1995) *Tertiäre Vegetationsgeschichte Europas*. Jena: Gustav Fischer.

Martinetto, E. (2009) Palaeoenvironmental significance of plant macrofossils from the Pianico Formation, Middle Pleistocene of Lombardy, North Italy. *Quaternary International* **204**, 20–30.

Martinetto, E., Monegato, G., Irace, A. et al. (2015) Pliocene and Early Pleistocene carpological records of terrestrial plants from the southern border of the Po Plain (northern Italy). *Review of Palaeobotany and Palynology* **218**, 148–166.

Médail, F. & Diadema, K. (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography* **36**, 1333–1345.

Médail, F. & Quézel, P. (1997) Hot-Spots analysis for conservation of plant biodiversity in the Mediterranean Basin. *Annals of the Missouri Botanical Garden* **84**, 112–127.

Melinte-Dobrinescu, M.C., Suc, J.-P., Clauzon, G. et al. (2009) The Messinian Salinity Crisis in the Dardanelles region: chronostratigraphic constraints. *Palaeogeography, Palaeoclimatology, Palaeoecology* **278**, 24–39.

Meyer, H.W. (1992) Lapse rates and other variables applied to estimating paleoaltitudes from fossil floras. *Palaeogeography, Palaeoclimatology, Palaeoecology* **99**, 71–99.

Muller, S.D., Nakagawa, T., de Beaulieu, J.-L. et al. (2006) Paléostructures de végétation à la limite supérieure des forêts, dans les Alpes françaises internes. *Comptes Rendus Biologies* **329**, 502–511.

Muller, S.D., Nakagawa, T., de Beaulieu, J.-L. et al. (2007) Postglacial migration of silver fir (*Abies alba* Mill.) in the southwestern Alps. *Journal of Biogeography* **34**, 876–899.

Nakagawa, T., de Beaulieu, J.-L. & Kitagawa, H. (2000) Pollen-derived history of timber exploitation from the Roman period onwards in the Romanche valley, central French Alps. *Vegetation History and Archaeobotany* **9**, 85–89.

Nieto Feliner, G. (2011) Southern European glacial refugia: a tale of tales. *Taxon* **60**, 365–372.

Nix, H. (1982) Environmental determinants of biogeography and evolution in Terra Australis. In: Barker, W.R. & Greenslade, P.J.M. (eds.) *Evolution of the Flora and fauna of Arid Australia*. Frewville: Peacock Publishing, pp. 47–66

Noble, V. & Diadema, K. (2011) *La flore des Alpes-Maritimes et de la Principauté de Monaco. Originalité et diversité.* Turriers: Conservatoire botanique national méditerranéen de Porquerolles & Naturalia Publications.

Noirfalise, A., Dahl, E., Ozenda, P. & Quézel, P. (1987) Carte de la végétation naturelle des états membres des communautés européennes et du conseil de l'Europe. Luxembourg: Office des publications officielles des Communautés européennes.

Ozenda, P. (1985) *La végétation de la chaîne alpine dans l'espace montagnard européen*. Paris: Masson.

Ozenda, P. (1989) Le déplacement vertical des étages de végétation en fonction de la latitude: un modèle simple et ses limites. *Bulletin de la Société Géologique de France* **8**, 535–540.

Ozenda, P. (1995) L'endémisme au niveau de l'ensemble du Système alpin. *Acta Botanica Gallica* **142**, 753–762.

Ozenda, P. (2002) *Perspectives pour une géobiologie des montagnes*. Lausanne: Presses polytechniques et universitaires romandes.

Ozenda, P. (2009) On the genesis of the plant population in the Alps: new or critical aspects. *Comptes Rendus Biologies* **332**, 1092–1103.

Punt, W., Hoen, P.P., Blackmore, S. et al. (2007) Glossary of pollen and spore terminology. *Review of Palaeobotany and Palynology* **143**, 1–81.

Quézel, P. & Médail, F. (2003) *Ecologie et biogéographie des forêts méditerranéennes*. Paris: Elsevier.

Ravazzi, C. (2003) *Gli antichi bacini lacustri e i fossili di Leffe, Ranica e Piànico-Sèllere (Prealpi Lombarde)*. Bergamo: CNR Special Publications Quaderni di Geodinamica Alpina e Quaternaria.

Ravazzi, C., Pini, R., Breda, M. et al. (2005) The lacustrine deposits of Fornaci di Ranica (late Early Pleistocene, Italian Pre-Alps): stratigraphy, palaeoenvironment and geological evolution. *Quaternary International* **131**, 35–58.

Rosenbaum, G. & Lister, G.S. (2005) The Western Alps from the Jurassic to Oligocene: spatio-temporal constraints and evolutionary reconstructions. *Earth-Science Reviews* **69**, 281–306.

Schönswetter, P., Stehlik, I., Holderegger, R. & Tribsch, A. (2005) Molecular evidence for glacial refugia of mountain plants in the European Alps. *Molecular Ecology* **14**, 3547–3555.

Suc, J.-P. (1976) Quelques taxons-guides dans l'étude paléoclimatique du Pliocène et du Pléistocène inférieur du Languedoc (France). *Revue de Micropaléontologie* **18**, 246–255.

Suc, J.-P. (1984) Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature* **307**, 429–432.

Suc, J.-P. (1989) Distribution latitudinale et étagement des associations végétales au Cénozoïque supérieur dans l'aire ouest-méditerranéenne. *Bulletin de la Société géologique de France* **3**, 541–550.

Suc, J.-P. & Bessedik, M. (1981) A methodology for Neogene palynostratigraphy. International Symposium on Concepts and Methods in Paleontology, Barcelona, pp. 205–208.

Suc, J.-P. & Fauquette, S. (2012) The use of pollen floras as a tool to estimate palaeoaltitude of mountains: the Eastern Pyrenees in the Late Neogene, a case study. *Palaeogeography, Palaeoclimatology, Palaeoecology* **321–322**, 41–54.

Suc, J.-P., Bertini, A., Combourieu-Nebout, N. et al. (1995) Structure of West Mediterranean and climate since 5.3 Ma. *Acta Zoologica Cracovia* **38**, 3–16.

Suc, J.-P., Fauquette, S. & Popescu, S.-M. (2004) L'investigation palynologique du Cénozoïque passe par les herbiers. In: Aupic, C., Labat, J. & Pignal, M. (eds.) *Les herbiers: un outil d'avenir. Tradition et modernité.* Nancy: Association française pour la Conservation des Espèces Végétales, pp. 67–87.

Taberlet, P., Zimmermann, N.E., Englisch, T. et al. (2012) Genetic diversity in widespread species is not congruent with species richness in alpine plant communities. *Ecology Letters* **15**, 1439–1448.

Talon, B., Carcaillet, C. & Thinon, M. (1998) Etudes pédoanthracologiques des variations de la limite supérieure des arbres au cours de l'Holocène dans les Alpes françaises. *Géographie physique et Quaternaire* **52**, 195–208.

Walsh, K., Court-Picon, M., de Beaulieu, J.-L. et al. (2014) A historical ecology of the Ecrins (Southern French Alps): archaeology and palaeoecology of the Mesolithic to the Medieval period. *Quaternary International* **353**, 52–73.

Wang, C.W. (1961) *The Forests of China with a Survey of Grassland and Desert Vegetation*. Maria Moors Cabot Foundation 5. Cambridge, MA: Harvard University Press.

Wegmüller, S. (1992) *Vegetationsgeschichtliche und stratigraphische Untersuchungen am Schieferkohlen des nördlichen Alpenvorlandes*, vol. **102**. Basel: Birkhauser.

Welten, M. (1982) Stand der palynologischen Quartörforschung am schweizerischen Nordalpenrand. *Geographica Helvetica* **2**, 75–83.