Chapter 7
Endemism in Mainland Regions – Case Studies

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7.1 Endemism in an Ecotone: From Chaparral to Desert in Baja California, Mexico

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7.1.1 Introduction

Vegetation patterns on a global scale are primarily determined by climate. The Mediterranean climate of coastal California and the first true desert conditions in western North America are thought to have originated during the late Miocene and the Pliocene, 5–10 million years ago, with modern warm-desert vegetation becoming extensive approximately 12,000 years ago, after the end of the last glacial period (Axelrod 1978; Frenzel 2005; Raven and Axelrod 1978). Regional geography also has a significant impact on plant distributions; when the Baja California peninsula broke away from mainland Mexico new barriers to plant migrations were formed. The peninsula is recognized as a center of unique biodiversity, largely due to its isolation from the mainland (Garcillán et al. 2010). The northwestern region of the peninsula has a Mediterranean climate and chaparral vegetation, but to the south and east lies the Sonoran Desert, with vegetation adapted to some of the hottest conditions in the Americas.

This case-study is focused in the region between parallels 30 and 33 in Baja California, Mexico and SW California (see Fig. 7.1). The size of the region is approximately 14,000 km^2. Along the Pacific Coast of North America a Mediterranean climate prevails, resulting in a phytogeographic region known as the California Floristic Province (CFP) stretching from southern Oregon to northern Baja California. The Mediterranean climate is characterized by hot dry summers and cool wet winters. Differences in the air temperatures in the Tropozone cause jet stream winds to sweep down along the Pacific Coast. In North America, the Coriolis effect causes the jet stream to hit the Pacific Coast, and water precipitates out as the moisture-laden jet stream passes over land. The strength of the jet stream has a positive correlation with the latitudinal temperature gradient (i.e., a greater temperature difference between the North Pole and the equator results in a stronger jet stream). A rainfall gradient from winter to summer precipitation is

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Fig. 7.1 California Floristic Province (*red shape*), Baja California and region of case study (*red shape* south of latitude 33° N)

clearly observed as one moves southward along the peninsula of Baja California (Aschmann 1959; Caso et al. 2007; Hastings and Turner 1965; Shreve 1936). Mean monthly temperatures vary little across northwestern Baja California (13 °C, or 55 °F, in winter and 23 °C, or 73 °F, in summer in the north at Tijuana, and

14 °C, or 57 °F, in winter and 24 °C, or 75 °F, in summer to the south at El Rosario). However, rainfall is not exactly predictable in the ecotone and the evapotranspirative balance varies significantly between seasons and between years. The massive 3,000-m tall Sierra San Pedro Mártir forms the spine of the peninsular ranges that act as a barrier to westerly winds and cause a rainshadow effect in the east. The southern end of the Sierra San Pedro Mártir meets the relatively low relief of the desert plain and that region coincides with the shift from Mediterranean climate to desert near the 30th parallel. That break in the topography allows north-westerly winds to blow across the peninsula moving moisture quickly across the landscape into the Gulf of California and the Mexican mainland, resulting in reduced precipitation in the peninsula.

The California Floristic Province (CFP) has been designated as a global biodiversity hotspot, an area of high endemism, that has been heavily impacted by human activity (Myers et al. 2000). The CFP, home to 2,125 endemic vascular plants, originally occupied 324,000 km^2; however, today only 80,000 km^2 – less than 25 %, remain naturally vegetated (Myers et al. 2000). The Baja California portion of the CFP is home to around 1,800 native vascular plant species, with almost half being rare, threatened, or locally endemic in the region. O'Brien et al. (in prep.) evaluated all plant taxa within the CFP of Baja California, scoring them for rarity and endemism, and documenting 172 plant taxa entirely endemic to the region (ca. 10 % of the native flora) and an additional 67 near-endemic species. These 239 species represent more than 11 % of total endemism for the entire CFP in an area that is less than 5 % of the size of the total province.

There has been debate concerning the southern limit of the CFP in Baja California, with some authors excluding the Maritime Succulent Scrub. The debate is partly due to the difficulty of classifying the vegetation as an increasing number of succulent plants are seen southward and more mesic plants become increasing scarce. However, the botanical community generally recognizes the southern limit of the CFP reaching the 30th parallel near El Rosario (Garcillán et al. 2010; Minnich and Franco-Vizcaíno 1998; Thorne 1993). Studies on the flora of San Quintín and Colonet also highlight the predominant contingent of the CFP flora in this region (Harper et al. 2010; Vanderplank 2011a, b).

Cowling et al. (1996) looked at the flora of California and other Mediterranean regions and found speciation from disruptive selection to be strongly driven by fire and climate change. Fire suppression is much less frequent in Baja California than in California, and studies comparing areas on either side of the border have shown dramatic changes in fire dynamics as a result of fire suppression in California (Minnich 1985, 2006). As a result of reduced fire suppression (stable fire interval and more frequent disturbance regime), the chaparral plants of Baja California may be more actively undergoing speciation processes, and perhaps more resistant to extinction. Within northwest Baja California there are two primary areas of high plant endemism: the mountain ranges and the coastal plain between Ensenada and El Rosario (Riemann and Ezcurra 2007). The influence of the relatively cold California current along the coast results in a heavy marine layer of low coastal fog that is highly stable and may sit over the land for days at a time (Vanderplank 2011a).

The effect of the cold current is strongest inland during the warmer months of the year and therefore fogs are most prevalent during those months, buffering the evapotranspiration balance until the winter months. Unique habitats have been identified within this region – namely the Maritime Succulent Scrub, noted for its high numbers of rosette-forming taxa that harvest moisture from the heavy coastal fogs (Rundel et al. 1972; Martorell and Ezcurra 2002). There are also small areas of Maritime Chaparral that favor non-sprouting chaparral species adapted to longer intervals between fire cycles and increased moisture from fog than inland areas.

The low relief coastal plain between Ensenada and El Rosario is an area of exceptionally high endemism in the state of Baja California (Garcillán et al. 2010; Riemann and Ezcurra 2007). As an area with a relatively strong climate gradient, this region may be key to species migrations under changing climate regimes. The area seems to be a hotbed of speciation and an important species refugium since the coastal fog mitigates some of the changing precipitation and temperature patterns (Minnich 2007). El Niño events typically favor higher winter rainfall and dense spring flowering events; but many years are very dry. The flora responds rapidly to local weather, which in turn affects all higher trophic levels, causing pulses in the availability of resources (Minnich 1985). The coastal plain has relatively little variation in elevation, but minor topographical features and underlying edaphic conditions have a strong effect on floristic composition. A rich patchwork of species assemblages (within the same broad vegetation belt) is also observed along the California coast. Microclimatic conditions appear to have a strong influence on plant distributions and putatively relict vegetation associations are fragmented throughout the Californias, and in particular in northwestern Baja California (Minnich and Franco-Vizcaíno 1998; Peinado et al. 1994; Delgadillo 1998; Raven and Axelrod 1978). The occurrence of micro-endemics in northwest Baja California suggests that plant distributions are not homogeneous and thus unlikely to be entirely controlled by broad climatic and latitudinal effects.

Most endemics inhabit succulent scrub and chaparral, at higher elevations also rocky habitats. There are very few endemics of riparian habitats because almost all riparian areas are arroyos that are dry most of the year (with underground water) and therefore the sandy soil tends to attract (semi-)desert plants. Some endemics like the blue palm (*Brahea armata*) are associated with permanent oases but they are few (Photos 7.1 and 7.2).

7.1.2 Primary Hypothesis

The coastal area between Ensenada and El Rosario appears to have been a plant species refugium with a more stable climate than the adjacent regions to the north and south. As an area that sits between two climate regimes, it presently has a more variable climate than either of the adjacent areas. Historically, however, climatic change was probably greater either side of this transitional area than within it. This hypothesis assumes that the area has had a climatic transition near the 30th parallel

Photo 7.1 Pristine Succulent Maritime Scrub, near Cerro Solo, on the coast of northwestern Baja California (Photographed by Sean Lahmeyer)

for most of the Quaternary, which seems reasonable in light of the Coriolis Effect on the jet stream. These weather patterns have resulted in a flora that is rich in both paleotaxa (maintained by the relatively stable climate through time) and neo-endemic taxa that appear to have radiated in response to changing climate not severe enough to cause extinction. The most significant refugium is seen along the coast where fog buffers variation in radiant loadings from the sun.

7.1.3 How Has Water Availability Shaped the Plant Communities?

Northwestern Baja California currently experiences relatively extreme short-term weather variation, ranging from severe droughts to major flooding events that may cause bridges to collapse and scour the arroyos of vegetation. Heavy rainfall events also create vernal pools, and snowmelt from winter storms in nearby mountains can augment water resources in the aquifer for long periods of time. Historical data indicate that in this region the moist glacial (Pleistocene) climates gradually transitioned into moist Holocene climates, with shifts in the source of precipitation

Photo 7.2 Endemic palm *Brahea armata* (Arecaceae) in the southern Sierra San Pedro Martir of Baja California. This area experiences light grazing and fires are occasionally started to keep mountain lions away from cattle and mules (Photographed by Sula E. Vanderplank)

and the radiant loadings (Bartlein et al. 1998). The predominant rainfall regimes north and south of the 30th parallel varied in intensity with the ecotone receiving some precipitation from each regime.

The degree of endemism in northwestern Baja California suggests that the amplitude of historic climatic change has not been as large as that in the adjacent regions. The plant communities of northwest Baja California are dynamic and, while some species have migrated, others have remained in situ and evolved in a locally changed climate regime. Ability to respond to climatic change is probably more limited in long-lived slow-growing species such as certain tree species as compared to shorter-lived herbaceous species due to generation times. The impact of climate on phenology may be the actual driver of plant evolution and migration in many cases (i.e., in short growing seasons flowering times are strongly correlated to temperatures and day lengths).

There are numerous putatively ancient paleoendemic taxa in northwestern Baja California (Raven and Axelrod 1978). The putative paleotaxa are often assumed to have undergone niche conservatism through time, suggesting that they occupy microclimates that are remnants of historical weather patterns. The southern side of the transverse range just south of Ensenada houses many of these species.

Small-scale topography and microclimates have a significant effect on species distributions. For example, conditions in a canyon (e.g., one about 20 m deep) will greatly alter the vegetation found on either side of the canyon walls and exposed ridges (which also differs from the wetter areas at the canyon bottom). Such canyons often support populations of narrow endemics and disjunct taxa. This distributional pattern suggests that this diversity of microhabitats and niches offers greater opportunity for refuge to the micro-endemic species of the region, hence the paleo-nature of many of the plants in the ecotone. Similarly, the large islands of Guadalupe and Cedros, offshore west Baja California, have altered evapotranspirative potentials from the fog that allow relict populations of pines (*Pinus*; Axelrod 1980) and cypress (*Cupressus*) to persist. The relative absence of fossil packrat middens (due to a humid climate; see Betancourt et al. 1990) in the region makes the reliable identification of paleoendemics challenging. However, the absence of close relatives suggests a long lineage in taxa such as *Adenothamnus*, and less obviously in monotypic genera such as *Xylococcus* and *Ornithostaphylos* (Francisco 2001).

In the same region there are also several genera with relatively numerous closely related species occupying small, often allopatric, ranges (e.g., *Arctostaphylos, Astragalus, Ceanothus, Dudleya*), which might be considered neoendemics or species undergoing adaptive radiations. Several species of *Hazardia* in northwest Baja California form a “patchwork quilt” when their ranges are mapped. Although largely not sympatric, each species borders the other, occupying a small geographic region. This pattern alludes to a common origin and perhaps an adaptive radiation event in their evolutionary history. These occurrences provide supportive evidence that the ecotone has been a refugium through times of global climate change, fostering both ancient lineages and more recent species diversifications. The buffering effect of the fog may have been a significant factor in the provision of climatic refugia for plants under changing climate.

7.1.4 Drought-Avoidance Strategies and Plant Physiognomies

Throughout the peninsula of Baja California there is great variation in rainfall both spatially and temporally (e.g., Hastings and Turner 1965). Studies by Franco-Vizcaíno (1994) show that even within the arid desert province to the south, floristic composition continues to vary southward along the gradient from winter to summer rainfall. The frequency and intensity of rainfall events affects soil properties and plant species composition (Shreve 1951). The unpredictability of water in this region has resulted in a suite of different drought-adaptations in the flora. Throughout this precipitation gradient a variety of life-strategies are observed.

Forrest Shreve (1936) published a seminal paper observing the precipitation gradient and the transition in the vegetation of the ecotone region between Ensenada and El Rosario in NW Baja California. In particular he noted the increased number of succulent species as one moves south, combined with decreasing numbers of chaparral species, and the increase in locally endemic taxa that are adapted to this small area with its unique climate. Shreve also commented on the nature of this ecotone and the increased heterogeneity of vegetation and life-forms, and therefore of the landscape.

Many of the drought-tolerant physiognomies of the northwest Baja California ecotonal plants have phenological phases that correlate directly to precipitation, with varied responses depending on the timing, intensity and duration of rainfall events. The phenological plasticity of the ecotone plants correlates with rainfall and fog moisture, often producing pulses that vary in magnitude with the availability of water.

Annual plants: This strategy represents the ultimate in opportunism for plants in an area of uncertain rainfall. After sufficient rainfall these species germinate rapidly, often flowering and fruiting very quickly without necessarily becoming large (Felger 2000). In northwestern Baja California these species are often showy with flowers and/or reproductive organs that may be larger than the vegetative structures. In areas of summer rainfall a contingent of C4 summer annuals appear that are well adapted to a very rapid growth and high temperatures following rains (Mulroy and Rundel 1977), however, the ecotone region has mostly winter annuals given the stochasticity of summer rainfall in modern times.

Deep-rooted trees: Several broad-leaved deciduous tree species in northwestern Baja California survive the dry warm late-summer–early fall weather by forming roots deep into perennial water sources. During Pleistocene times these trees species were generally more widespread in what is now arid North America. Currently they are largely restricted to permanent streams, and areas where bedrock pushes the aquifer into the reach of the roots. The role of mycorrhizal fungi also enables some of these species to survive in bedrock that roots cannot penetrate but does not prevent the fungal hyphae reaching the water table (Allen 2009). These tree species are generally wind pollinated and dispersed, with predictable flowering times. Only putative paleo-endemics, such as *Brahea armata*, and *Pinus muricata*, fall into this category in northwestern Baja California.

Evergreen chaparral: The evergreen sclerophyllous shrubs of California's chaparral exhibit a suite of characteristics that make them highly tolerant of seasonal (late summer and early fall) drought. Small, tough, leaves with short internodes have strong stomatal controls and high cuticular resistance to reduce water-loss (Minnich 1985). Their evergreen habit allows them to respond quickly after rainfall events and flower/fruit profusely. The large amounts of organic matter that these plants accumulate make them highly fire-prone in dry weather. Eventually the evapotranspirative ratio is so high that fire weather results in regular burns. As such, the distribution of the chaparral and its evolutionary history are tightly linked to the history of fire (Minnich 2006). Chaparral ecotone endemics include various parapatric species of *Arctostaphylos* and *Ceanothus*, genera which appear to still have high potential for future speciation. There are also several of the putatively paleo-endemic large woody shrubs (e.g., *Ornithostaphylos, Xylococcus*, and *Arctostaphylos* species such as *A. australis*).

Succulent plants: Succulence is a well-known strategy for dealing with the pressures of increasingly arid conditions and drought. In combination with CAM (crassulacean acid metabolism) photosynthesis, this strategy is particularly effective for resisting high radiant loadings and irregular precipitation. There are an increasing number of species in the Cactaceae and Crassulaceae at the southern end of the CFP, many of which are locally endemic (e.g., *Ferocactus fordii, Echinocereus maritimus, Mammillaria louisae*). Special adaptations are seen in *Mammillaria brandegeei*, a locally endemic species that actually has its vegetative body underground, exposing on the top of the plant at the soil surface. During drought it actually shrinks down into the soil, where the microclimate is much more equitable.

Drought deciduousness: Particularly common in the coastal scrub is a drought-deciduous habit, which is the condition of many narrowly endemic habitat dominants (e.g., *Ambrosia chenopodifolia, Aesculus parryi, Bahiopsis laciniata*). The number of months a plant is without leaves varies depending on local weather conditions. Drought deciduousness is often combined with other drought-tolerant strategies, e.g., succulent stems with drought-deciduous leaves (*Euphorbia misera*).

Rosettes and clumping: The Maritime Succulent Scrub has a dominant element of rosette-forming plants, e.g., the near-endemic *Agave shawii* subsp. *shawii* and various locally endemic *Dudleya* species. In Spanish it is known as the 'Matorral Costero Rosetofilo' or rosetophyllous coastal scrub. These rosette-forming plants have been shown to be efficient fog harvesters (Martorell and Ezcurra 2002).

Geophytes/underground storage organs (culms, bulbs, tubers, etc.): Although there are few true bulbs in the region (excepting a few species of wild onion (*Allium*) and mariposa lily (*Calochortus*)), there are several species that have some kind of under-ground storage organ (e.g., *Dichelostemma pulchellum, Marah macrocarpa, Jepsonia parryi*). These species avoid hot dry spells, remaining underground until soil moisture reaches levels appropriate to stimulate growth, yet there a very few, if any, endemic taxa with underground storage organs as their primary drought adaptation.

Some taxa have combined multiples of the above strategies. Of particular note are some of the most narrowly restricted taxa – three *Dudleya* species that grow in areas with different lithologies on Colonet mesa (Harper et al. 2010). All three are *Hasseanthus*-complex *Dudleya* species that are drought-deciduous with underground storage organs (rhizomes), and above-ground leaves are succulent and pseudo-rosetophyllous.

7.1.5 Plant Distributions: Rarity and Endemism

In reviewing the work of Grime (1977), Kruckeberg and Rabinowitz (1985) note that many plants that are adapted to come with an environmental extreme (e.g., serpentine endemism, halophytes) appear to be restricted to these extreme habitats only by competition from other species in more favorable habitats (i.e., many halophytes can grow in non-saline conditions, but appear to be out-competed in natural habitats). These processes highlight the role that repeated disturbances (e.g., fire) or stress (e.g., basic soils) will have on selecting for the composition of a vegetation type. There is evidence that species in the lower stages of plant succession are much less likely to go extinct; however, endemic species in climax communities are much more susceptible to catastrophic events and human activities (Kruckeberg and Rabinowitz 1985).

Vanderplank (2011a, b) found no correlation between the local and global abundance of taxa in the ecotone (i.e., a plant that was globally scarce was equally likely to be rare, frequent or abundant locally, as was a cosmopolitan species). This puts most of the endemics of this region in the 'locally abundant but restricted geographically' or 'constantly spare and geographically restricted' categories (Rabinowitz 1981). Stebbins (1980) states that the primary cause of localized endemism is adaptation to localized ecological factors. Kruckeberg and Rabinowitz (1985) note that narrow endemics are most often members of distinctive communities or singular habitats, but this statement is difficult to verify globally. The number of narrow or micro-endemics in the ecotone that are seemingly not restricted to a harsh environment or highly specific micro-habitat is noteworthy.

Qian (1998) showed that globally, along the latitudinal gradient, generic richness (in terms of the number of genera) shows a striking increase with decreasing latitude. However, recent research from Jansson (2003) indicates that global patterns in locally endemic taxa are caused by the amplitude of climatic change during peaks of Milankovitch oscillations (every 10,000–100,000 years). Smaller climatic shifts allow the survival of paleoendemics and diverging gene pools (neoendemics) are able to persist. Using change in mean annual temperature since the last glacial maximum Jansson showed that areas that have experienced higher temperature changes have lower endemism in mammals, birds, reptiles, amphibians and vascular plants (robust to area, latitude, extent of former glaciation and oceanic island syndrome). This research suggests that Rapoport's rule (species range increases with latitude) is a product of the increase in the amplitude of climatic oscillations towards the poles.

Consistent with the patterns seen in northwest Baja California, Sorrie and Weakley (2010) show that topography may be a minor consideration in endemism; for example, the coastal plain of Florida is flat (less than 250 m (800 ft) change in relief in the whole coastal plain) yet the state is second in endemism only to California. They suggest that this may be partially the result of the climatic transition between ecotones but also involves edaphic factors. Endemism in ecotones is not well-studied but often a peak in endemism is seen in ecotones. The forest-savannah ecotone in Africa has been shown to be important to divergence and speciation (Smith et al. 1997, 2005). If one compares the ecoregions of Baja California with the hotspots of endemism and species richness for the peninsula (Garcillán et al. 2010; Riemann and Ezcurra 2007), we see that where each ecotone occurs there is almost always a peak in species richness (presumably from the overlapping ranges of many species from two distinct biomes). In contrast; however, only sometimes is a peak in local endemism also seen in these ecotones, suggesting that the presence of an ecotone alone is not responsible for the elevated levels of endemism.

Recent research on the biotic interactions between desert plants has revealed that facilitation as a mutualism evolved between taxa from the Quaternary (nurse plants) and taxa from the Tertiary that were adapted to wetter conditions, but persist as a result of the nursing effects of more recently derived lineages (Valiente-Banuet et al. 2006). This facilitation saved many species from extinction during times of climatic change at the end of the Tertiary, and facilitation is often facilitated by a few key-stone 'nurse' species (Verdú and Valiente-Banuet 2008). Surprisingly the generalist nurses are often the most abundant species in the community, providing strong resistance to extinction for the dependent species. This facilitation also allows niche conservatism in ancient lineages and increases phylogenetic diversity in plant communities (Valiente-Banuet and Verdú 2007). However, in closely related species, these facilitative mutualisms can turn into competition in times of stress of changing climate (Valiente-Banuet and Verdú 2007; Verdú et al. 2003).

The amount of literature on the flora of California far exceeds that available for Baja California, yet it gives some insight into the origins of the present endemism and diversity (Stebbins and Major 1965; Richerson and Lum 2008; Thorne and Viers 2009; Vandergast et al. 2008; Viers et al. 2006). Most recently, Kraft et al. (2010) looked at the distribution of neoendemics in California, which correlated poorly to climate and topography. They found the endemics of the western edge of deserts to be very young, with most endemism in habitats that have undergone post-Pleistocene isolation or climatic change; with sky islands having wetter climates and the greatest temporal diversity of endemics.

Jansson (2009) stresses the relevance of emerging information on historical climate change that can be used to study microrefugia of the Pleistocene climate oscillations. The heterogeneous environment of the ecotone in Baja California lends itself to the concept of microrefugia and studies of the likelihood of microrefugia in this zone should be pursued. Médail and Diadema (2009) found that glacial refugia are climatically stable areas that are determined by complex historical and environmental factors. Refugia are priorities for the long-term conservation of species and genetic diversity, representing 'phylogeographical hotspots' especially under changing climate regimes.

Ackerly (2009) reviews the factors affecting the age and origin of California and Mediterranean vegetation. He introduces the concepts of synclimatic (with climate) migration, resulting in niche conservatism (as documented by Kelly and Goulden 2008); and anticlimatic (not following climate) migration which often results in adaptive evolution. As such, species that moved with climate have conserved niches, species that didn't move fast enough had to adapt. Ackerly (2009) points out that survival may be heavily dependent on biotic contexts and for those species not migrating with the climate it may be the presence or absence of competition from new species arriving (or not) that dictates whether a species survives the new regime (rather than it being wholly necessary to 'adapt' to the new climate). In light of this, successful 'adaptive' response may simply be factors that are barriers to dispersal of other species. This may be even a depleted gene pool in the potentially competing taxa. Ackerly states “By this logic, the greatest opportunity for adaptive evolution will occur on the trailing edge of species ranges during episodes of climate change, as changing conditions kill off the existing vegetation”. Assuming there will always be a ‘trailing edge’ near the 30th parallel due to the position of the jet stream and its physical limits, one can tentatively hypothesize that the ecotone will always be a hotspot of potential for adaptive evolution under any climate change regime.

7.1.6 Conclusions

Since the southern extent of the jet stream does not pass further south than the 30th parallel, it is likely that there has long been a transition in the vegetation near the 30th parallel in northwestern Baja California, corresponding to the southern limit of winter precipitation originating from the west. It follows that plant taxa ranging through this region would be unable to follow synclimatic migration routes, and thus migration in the ecotone is likely to have been anticlimatic (favoring adaptive radiations). Assuming the climate change theories of Jansson (2003), the southern end of the CFP may hold more relict diversity and more neo-endemic lineages than other regions of the CFP. However, it is likely that the increased temperatures during the Pleistocene shifted some species farther north during the Pleistocene.

There are many putatively ancient ‘paleoendemic’ taxa in the ecotone region (Raven and Axelrod 1978); however, the absence of fossil packrat middens and a dearth of detailed fossil and molecular information on the region makes identification of paleoendemics challenging. There are also several genera in the ecotone that have many closely related species occupying small allopatric ranges (e.g., *Astragalus*, *Dudleya*, *Hazardia*), which might be considered neoendemics. I hypothesize that the 30th parallel ecotone has been a refugium through times of global climate change, fostering both ancient lineages and neoendemics. Predicting the severity of climate change as part of future Milankovitch cycles may be particularly valuable in assessing whether the ecotone will remain a refugium, or be likely to experience a high rate of extinction. Future research should look at range sizes of endemics in Baja California to allow mapping and phylogenetic distance analyses. The effects of species interactions remain unstudied, and nurse plant effects are only reported from the arid regions to the south. It seems probable that similar processes may be active in the ecotone, and perhaps other undiscovered interspecific processes are contributing to the distributions of the narrow endemics.

Water plays a vital role in the distribution of plants in the ecotone of northwest Baja California, and other dryland systems. Life-strategies, distributions, trophic interactions, phenological timings and evolutionary histories are strongly linked to patterns in water availability, and systems for drought-tolerance. Future research should address the resource-pulses caused by sporadic rainfall events and their effects on the entire ecosystem.

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7.2 Ecuador

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7.2.1 Physical Geography of Continental Ecuador

Continental Ecuador, situated in northwestern South America (latitudes 2°N to 5°S) and bordering the Pacific Ocean at the Equator, is divided into three broad biogeographical zones, the western coastal zone, the central Andes mountains (Sierra or highlands), and parts of the Amazon Basin (Oriente) to the east. Almost all rivers rise in the Andes region and flow eastwards to the Amazon River or westwards to the Pacific Ocean. The highest mountains are Chimborazo (6,310 m) and several others over 4,000 and 5,000 m.

The main temperatures range from 23 to 26 °C at the coast and 28 °C in the Amazon Basin to c. 0–3 °C at the highest summits where some parts are constantly covered with ice and snow. Pleistocene moraines occur in paramo zones. These indicate that many parts of the high mountain regions were glaciated during cold periods.

Extremely small differences between the average of the warmest and coldest months can be measured e.g. in Izobamba, Province Pichincha (3,058 m), and in Otavalo, Province Imbabura (2,555 m), where the difference is only 0.5 °C. In Quito (2,818 m) an amplitude of 0.6 °C and e.g. in Esmeraldas (6 m) an amplitude of 0.8 °C represent extremely low amplitudes in a global context (Deutscher Wetterdienst 2002, 2008, 2010). However, dependent on altitude, humidity and geomorphology diurnal temperatures can vary considerably, from cold mornings to hot afternoons.

Precipitation per year ranges from less than 300 mm in the driest parts to more than 5,000 mm in the wettest. Arid regions are located along the southern coast and in valleys of the Andes mountains, whereas northern coastal regions and western or eastern foothills of the mountains and the Upper Amazon Basin show high precipitation values. Precipitation in general decreases with increasing altitude and decreasing temperature in regions of the Andes.

According to Groombridge and Jenkins (2002) Ecuador is one of the endemic- and species-richest countries in the world. Large parts of two Biodiversity Hotspots, the Tropical Andes Hotspot and the Tumbes-Chocó-Magdalena Hotspot, together cover two thirds of the country's area (Mittermeier et al. 2005). The main vegetation belts from the coast to the highest mountains are mangroves, rain forest, wet to dry and deciduous forest, scrub paramo, other paramo types, rock and scree habitats.

7.2.2 Red List Analysis

Fortunately a very comprehensive Red List of endemic plants in Ecuador was published in 2000 (Valencia et al. 2000). This book is the basis and reason for the following review and analysis. If no other reference is given in this chapter, Valencia et al. (2000) is the source.

We counted numbers of endemics per vegetation type and altitude, for the list as a whole and specifically for certain plant families. Because a lot of species occur in more than one habitat type many of the following numbers represent overlapping species compositions and not necessarily different taxa.

13 habitat groups were defined by Valencia et al. (2000: 2 f.). These are:

Páramo húmedo or wet paramo (1), Páramo seco or dry paramo (2), páramo arbustivo or scrub paramo (3), bosque andino alto or high Andean forest above 2,000 m (4), Bosque andino bajo or Andean forest at mid-altitudes between 1,000 and 2,000 m (5), Vegetación interandina seca o húmeda or dry or moist Andean vegetation in the central Andean valleys normally at elevations between (1,000) 1,500 and 3,000 m (6), Bosque litoral piemontano or forest of western Ecuador in the transition zone between coast and mountain range at elevations from 500 to 1,000 m (7), Bosque litoral humédo or wet coastal forest at the northern coast (8), Bosque (o vegetación) litoral seco or dry coastal vegetation at the southern coast (9), Bosque amazónico piemontano or forest between 500 and 1,000 m in the transition zone between Andes and Amazonia (10), Bosque amazónico periodicamente inundato or inundated Amazonian forest below 500 m (11), Bosque amazónico de pantano or palm forest below 500 m normally with the palm *Mauritia flexuosa* (12), and finally (13) Bosque amazónico de tierra firma or Amazonian forest below 500 m on well drained soil.

Here we classify altitudes below 1,000 m as lowland, elevations between 1,000 and 2,000 m as mid-altitudes, and forests over 2,000 m as high-mountain forests.

7.2.3 Endemic Vascular Plants of Ecuador and Their Relationship to Ecological Conditions and Habitats

Of the 4,011 endemic vascular plant species in the whole of Ecuador (including 177 taxa from the Galapagos archipelago) a third (33 %) belongs to the Orchidaceae, 9 % to the Asteraceae, 5 % to the Melastomataceae, 4 % to Araceae, 4 % to various fern families, 4 % to Bromeliaceae, 3 % to Piperaceae, 3 % to Ericaceae, 2 % to Rubiaceae, 2 % to Campanulaceae, and 31 % to other plant families.

Most endemics are epiphytes (36 %), 26 % are shrubs or dwarf shrubs, 22 % are herbs, 8 % are small or high trees, 6 % are lianas and vines, and 2 % are hemi-epiphytes or others.

In the regions of continental Ecuador most endemics (more than three quarters) occur in forest or woodland and only a minority occurs in paramo vegetation, including scrub paramo in the subalpine belt and other habitat types such as scrub or thicket in the dry parts of the Andes or of SW Ecuador. Some opportunists occur in different habitat types. The orchid *Elleanthus ecuadoriensis*, for example, tolerates disturbed areas such as roadsides.

In the continental regions of Ecuador (without Galapagos) 2,965 endemic species occur in the Andes, 743 in the coastal zone (western Ecuador), and 453 in Upper Amazonia (eastern Ecuador).

Endemism peaks between 1,300 and 2,500 m. This finding is roughly consistent with results of the analysis of van der Werff and Consiglio (2004; their Fig. 2A) for Peru. When comparing Ecuador and Peru it must be remembered that the coastal zone in Peru is much norrower and extremely dry and the average elevation in the country as a whole is higher than in Ecuador. van der Werff and Consiglio (2004) found the richest belt in Peru between 2,500 and 3,000 m. They also found different elevational patterns for different functional types. Herbs and shrubs showed maximum numbers between 2,500 and 3,000 m, the majority of epiphytes was found at altitudes between 500 and 2,000 m, and trees, lianas and vines showed highest absolute numbers in the lowlands below 500 m.

However, different plant families also prefer different altitudinal zones and habitats. The two species-richest plant families in the world – Orchidaceae and Asteraceae – are also the two richest families in Ecuador. 1,318 orchid species (of 3,013 species in total) and 318 composite species (of 863 in total) are listed as endemic to Ecuador. Unlike orchids, ferns or bromeliad taxa, asteraceous species do not normally live as epiphytes, but, in Ecuador, are mostly shrubs or perennial herbs which root in the ground.

The endemic species diversity of the family Asteraceae peaks at higher altitudes in Ecuador than the orchids do. In paramo habitats there are the same number of endemic Asteraceae as orchids (c. 115). 22 endemic Asteraceae are catalogued for the dry inner parts of the Andes, whereas only a single endemic orchid occurs there. In high mountain forests the number of endemic orchids (536) is more than twice the number of endemic Asteraceae species (207), whereas below 2,000 m the number of endemic orchids explodes in relationship to Asteraceae (c. ten times more orchids).

Endemic ferns are also concentrated at relatively high altitudes e.g. with far more species in high mountain forest of the Andes (81 species in bosque andino alto) in comparison to mid-altitude forests (49 species in bosque andino bajo).

In contrast, the Bromeliaceae, for example, are represented by 70 endemic species at mid-altitudes and 40 species in high mountain forest.

Obviously, the high number of endemics in such a small country must be discussed in the context of high spatial heterogeneity combined with relatively stable climate conditions. The neighbourhood of old stable landscapes sensu Mucina and Wardell-Johnson (2011), as in the western and eastern parts of Ecuador, to high younger landscapes, such as the Andes, might have favoured total species richness and the development and survival of endemic vascular plants. The relatively low endemism in the Amazon Basin is most likely related to reduced topographical and geological heterogeneity.

Many endemics are threatened by the same human activities as in many other (wet) tropical parts of the world, such as deforestation and destruction of habitats as a result of the expansion of arable lands, settlements, roads, extraction of oil, and so on. There is no indication of threats caused by global warming.

7.3 Central Chile Ecoregion

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7.3.1 Introduction

Chile's biota, trapped at the southern cone of South America by immense geographical barriers, has evolved in isolation, gaining a unique character. The limits of this "biogeographic island" are the Pacific Ocean to the west, the Andean cordillera to the East, the Peruvian Desert to the north and Cape Horn to the south. The condition of isolation dates at least from the Pliocene, when the Southern Andes gained their maximal altitude, setting the geographical (climatic, geomorphic, edaphic) and biological conditions for the evolution of a unique flora with high levels of endemism; nevertheless, the origin of several lineages has much deeper roots, associated with ancient Earth processes like the fragmentation of Gondwana (Moreira-Muñoz 2011). According to this interplay between ancient and newer conditions for the development of endemism, the vascular native flora of Chile shows high levels of endemism especially at high taxonomic levels: while having around 1,930 endemic species, it also has 80 endemic genera and 3–4 endemic families. The endemism at genus and family level is higher than in other territories widely recognized due to their high level of endemism, like Peru or Ecuador, that base their endemism at the species level. Only the Cape Flora of South Africa shows higher levels of endemism at genus and family level (Moreira-Muñoz 2011).

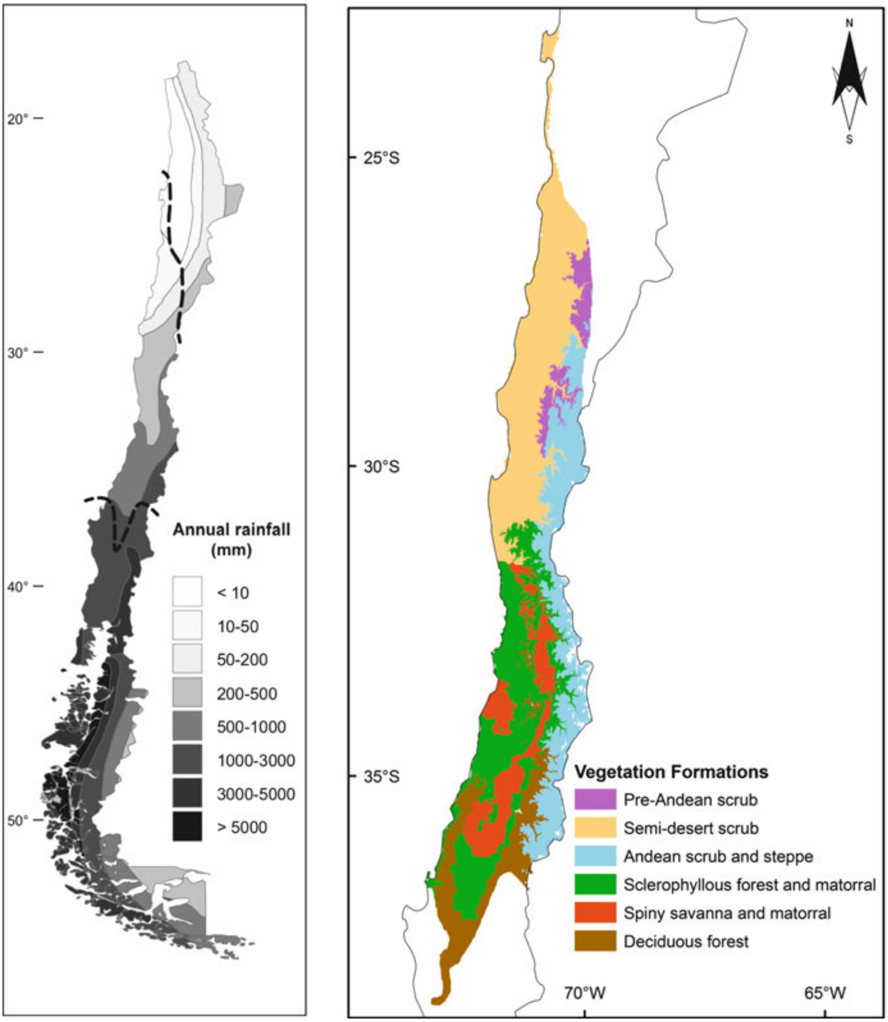

Fig. 7.2 *Left side*: Mediterranean Central Chile (*segmented line*) upon the annual precipitation gradient scheme; *right side*: Vegetation formations in Mediterranean Chile (Adapted from Schmithüsen 1956; Luebert and Pliscoff 2006)

7.3.2 *Plant Endemism in Central Chile*

The core of this notable floristic unique condition is Mediterranean Central Chile south of the Atacama Desert at latitude 23 °S (coast) and extending to the limit with temperate Chile at 38 °S (Fig. 7.2). The ecoregion shows a climatic gradient characterized by an increase in annual rainfall from less than 10 mm to more than 1,000 mm towards the South, generating many different habitats for plant growth and evolution (Fig. 7.2). This is one of five Mediterranean-type climate ecoregions of the world that have been recognized as main global centres of plant diversity (Cowling et al. 1996; Davis et al. 1997; Dallman 1998), and as biodiversity global hotspots. This last concept explicitly searches for global territories that show high species richness and endemism and are the subject of ample threats that currently affects their biota (Myers et al. 2000).

The original conception of the Chilean hotspot was restricted to the Mediterranean-type climate of Central Chile (Myers 1990); while nowadays it has been expanded towards temperate Chile including also the oceanic islands (Mittermeier et al. 2005). This broader conception of the Chilean hotspot increased its area from 180,000 km^2 to almost 400,000 km^2. The quantity of habitats also increases when expanding the hotspot towards the south. Several remarkable biotic characteristics justify this wider conception, like several faunistic groups and also floristic communities dominated by iconic native tree species such as araucaria (*Araucaria araucana*) and alerce (*Fitzroya cupressoides*). But the core of plant endemism is still to be found in Mediterranean Chile, more related to semiarid climatic conditions than to temperate ones.

Mediterranean Chile contains about 2,500 native species, i.e. 58 % of the country's native flora in 19 % of the territory. Endemics comprise around 1,200 species, related to an exceptional high habitat diversity (Myers 1990). From those Chilean endemics around 900 are strictly endemic to Central Chile (Arroyo et al. 2003).

The objective of this contribution is to address spatial patterns of plant endemism in main habitats (vegetation types) of Mediterranean Central Chile. Such studies are still lacking (see Beard et al. 2000), or have been developed partially for specific taxonomic groups, such as the genera *Adesmia* (Mihoc et al. 2006), and *Valeriana* (Kutschker and Morrone 2012), or the families Cactaceae (Guerrero et al. 2011) or Asteraceae (Moreira-Muñoz and Muñoz-Schick 2007).

7.3.3 Material and Methods

The checklist of species endemic to Chile, together with their distribution, has been compiled from different sources for the project "Plant Geography of Chile" (Moreira-Muñoz 2011). A main source has been the so far available volumes of the *Flora de Chile* (Marticorena and Rodríguez 1995 onwards) complemented and updated with available monographs and recent checklists (Zuloaga et al. 2008). When groups/families appear taxonomically inflated, a conservative approach has been preferred, e.g. for Chilean Alliaceae and Alstroemeriaceae (Muñoz-Schick and Moreira-Muñoz 2000, 2003b). Subspecies and varieties were considered as occupying part of the distribution range of the typical species. Some highly diverse groups within the Asteraceae have been recently revised by Moreira-Muñoz et al. (2012).

Table 7.1 Families rich in Chilean endemic species and occuring in Mediterranean Chile

Family	Endemic Chilean species
Asteraceae	222
Fabaceae	99
Solanaceae	61
Cactaceae	59
Calceolariaceae	43
Boraginaceae	38
Poaceae	37
Brassicaceae	34
Alstroemeriaceae	28
Apiaceae	24

The habitats at a meso-scale are the vegetation formations defined by means of bioclimatic methods by Luebert and Pliscoff (2006). These units are being considered as main ecosystems and as the appropriate units for conservation planning in Chile (Pliscoff and Luebert 2008). The distribution ranges of endemic species and vegetation formations were compared by means of ArcGis 9.3. To complement the analysis, a comparison with the different altitudinal levels was undertaken, on the base of the GTOPO30 elevation data set (www.usgs.gov). Species presence was compared with altitude ranges of 250–4,250 m asl.

7.3.4 Results: Endemism in Central Chile

Mediterranean Central Chile ranges from latitude 23 °S (coast) to 39 °S according to bioclimatic classifications (Amigo and Ramírez 1998; Luebert and Pliscoff 2006) (Fig. 7.2). The vegetation formations that compose this biodiversity hotspot show a north–south gradient of increasing vegetation cover from a semiarid sparse scrub to the sclerophyllous matorral and deciduous forests, reaching the northern limit of the austral conifer and laurifolious forests at 39 °S. The west–east gradient is a coast-Andean gradient, and ranges from the coastal scrubs through thicker matorral and forests towards the Andean scrub and the sparse treeline around 2,200 m depending on latitudinal position.

Mediterranean Chile harbours 1,164 Chilean endemic species. Most of them pertain to the Asteraceae (222), the Fabaceae (99), the Solanaceae (61, including genus *Nolana*), Cactaceae (59), and Calceolariaceae (43) (Table 7.1). These families are among the species-richest families in the Chilean flora (Moreira-Muñoz 2011, p. 59). Within these families we find also the species-richest genera (Table 7.2).

The overlap in distribution ranges with the vegetation formations shows a preliminary picture of the distribution of endemism within the Central Chilean hotspot. Table 7.3 shows the number of endemic species for each vegetation

Table 7.2 Genera rich in Chilean endemic species and occuring in Mediterranean Chile

Genus	Endemic Chilean species
Adesmia (Fabaceae)	61
Senecio (Asteraceae)	60
Calceolaria (Calceolariaceae)	41
Nolana (Solanaceae)	34
Haplopappus (Asteraceae)	27
Alstroemeria (Alstroemeriaceae)	26
Copiapoa (Cactaceae)	20
Oxalis (Oxalidaceae)	20
Viola (Violaceae)	20
Heliotropium (Boraginaceae)	15

Table 7.3 Vegetation formations from Central Chile and their number of endemic species

Vegetation formation	Area (km^2)	Chilean endemic species
Semi-desert scrub	54,738	677
Sclerophyllous forest and matorral	45,340	655
Spiny savanna and matorral	19,803	362
Andean scrub and steppe	37,000	355
Deciduous forest	22,019	301
Pre-andean scrub	8,230	63

formation. The highest number of Chilean endemic species is found in the Semi-desert scrub (677 endemics), (Photos 7.3, 7.4) followed by the Sclerophyllous forests and matorral (655 endemics), (Photos 7.5, 7.6) both reaching almost twice the numbers than the Spiny savanna (362), the Andean scrub and steppe (355), (Photos 7.7, 7.8) and the Deciduous forest (301). The Pre-Andean scrub, situated towards the north of the ecoregion, shows the lowest number of endemics, since it is also has the smallest area of the units analysed here.

In the altitudinal profile, there is a marked decrease in endemics towards higher belts, ranging from almost 750 endemic species at the coast between 0 and 250 m, decreasing to 500 at 1.000 m, 170 at 2.000 m, 140 at 3.000 m, and 50 at 4.000 m (Fig. 7.2). The profile shows little increases, e.g. around 2.250 m, associated with the increased richness in the Andean scrub around latitude 33° (Muñoz-Schick et al. 2000). The lower level of endemism at higher altitudes has to do with two facts: the overall decrease in species with altitude, and the presence of more native species that are also distributed in adjacent Argentina (Muñoz-Schick et al. 2000).

The overall tendency of decreasing numbers with increasing altitude will surely vary in each vegetation formation. Figure 7.3 shows that this tendency is emphasized by the two richer formations, the semi-desert scrub and the sclerophyllous forest and

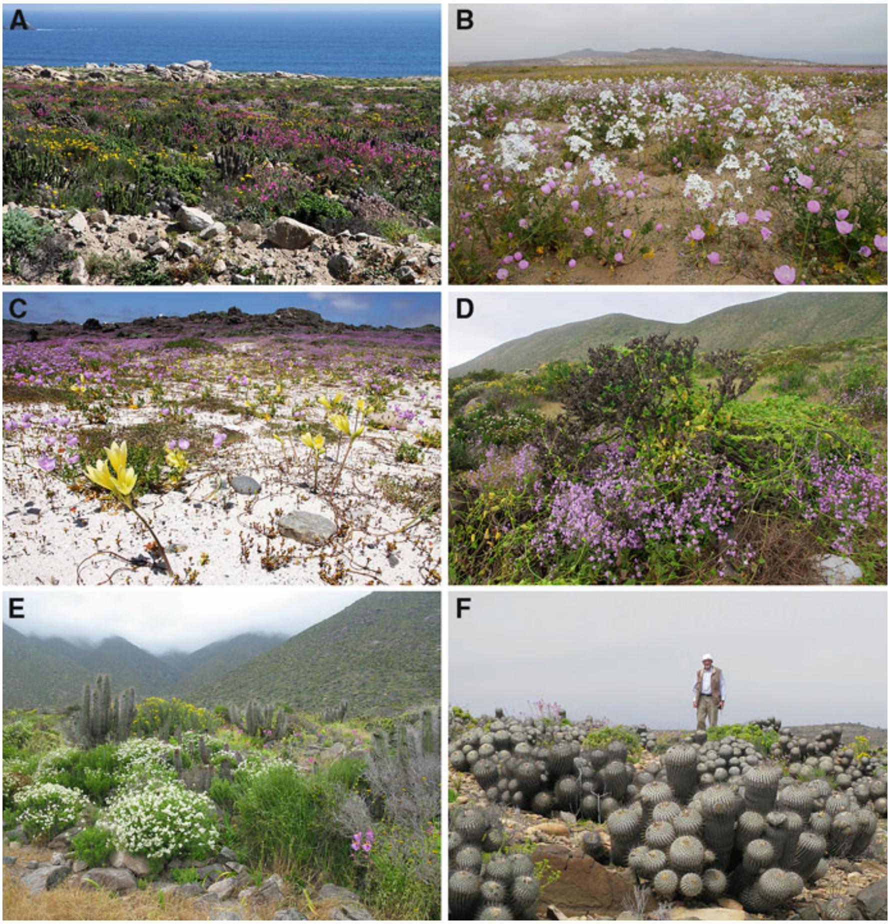

Photo 7.3 Representative photographs of the Central Chilean Semi-desert scrub. (**a**) Coastal scrub North of Huasco, (**b**) *Cristaria cyanea and Zephyra elegans* fields at Aguada Tongoy, (**c**) *Rhodophiala bagnoldii* at Isla Damas, (**d**) Scrub with *Schizanthus litoralis* North of La Serena, (**e**) Inland scrub with *Bahia ambrosioides*, (**f**) *Copiapoa dealbata* fields at Carrizal coast, with Marinus Werger (Photographed by Andrés Moreira-Muñoz)

matorral. The spiny savanna and the deciduous forest show an opposite trend around 750 m, which has to do with the macro-relief morphology: the deciduous forest is practically absent from the Central Depression, while the Spiny savanna occupies a big area in this orographic unit (see Fig. 7.4). Contrary to the overall tendency, the Pre-Andean scrub and Andean scrub show different endemism peaks, more marked in the second one. This is due to overlap in formations at 1,500 m, a peak at 2,750 m, and a slow decrease towards the highest altitudes (Fig. 7.5).

Photo 7.4 A photographic selection of plant species endemic to the Central Chilean Semi-desert scrub. (**a**) *Dinemagonum gayanum* (Malpighiaceae), (**b**) *Calceolaria picta* (Calceolariaceae), (**c**) *Schizanthus candidus* (Solanaceae), (**d**) *Adesmia argentea* (Fabaceae), (**e**) *Pleurophora polyandra* (Lythraceae), (**f**) *Cistanthe longiscapa* (Montiaceae), (**g**) *Leucocoryne vittata* (Alliaceae), (**h**) *Centaurea chilensis* (Asteraceae), (**i**) *Cyphocarpus rigescens* (Campanulaceae) (Photographed by Andrés Moreira-Muñoz)

Photo 7.5 Sclerophyllous forest and matorral, Central Chile (Photographed by Andrés Moreira-Muñoz)

7.3.5 *Discussion and Notes on Conservation*

Mediterranean Chile, considered a global biodiversity hotspot, has a long history of anthropogenic impacts, including native forest and scrub substitution for urbanization, grazing and agriculture, habitat fragmentation, and direct exploitation of natural resources. This situation is similar to the other Mediterrranean regions in the world (Underwood et al. 2009). No wonder that most Chilean threatened species are located within the ecoregion (Muñoz-Schick and Moreira-Muñoz 2003a). A high amount of endemic species is found in the Semi-desertic scrub, which is mainly composed of shrubs and herbaceous species. Indeed, the two genera that are rich in endemic species, *Adesmia* and *Senecio*, do show the herbaceous to shrubby growth form. Coincidently, many Semi-desertic endemic species tend to show restricted geographical ranges and are of concern for conservation purposes (Squeo et al. 2001, 2008). This is also the case for endemic-rich genera from the Cactaceae, such as *Pyrrhocactus* and *Copiapoa*.

But not only genera rich in endemics are of interest for conservation planning. Many endemic species pertain to monotypic genera that are supposed to have also a high interest for biogeographers due to their phylogenetic uniqueness. Relative novel approaches like phylogenetic diversity should account for this so far cryptic

Photo 7.6 A photographic selection of plant species endemic to the Central Chilean Sclerophyllous forest and matorral. (**a**) *Peumus boldus* (Monimiaceae), (**b**) *Placea ornata* (Amaryllidaceae), (**c**) *Miersia chilensis* (Alliaceae), (**d**) *Bomarea salsilla* (Alstroemeriaceae), (**e**) *Adenopeltis serrata* (Euphorbiaceae), (**f**) *Lathyrus subandinus* (Fabaceae), (**g**) *Lithrea caustica* (Anacardiaceae), (**h**) *Schinus latifolius* (Anacardiaceae), (**i**) *Escallonia illinita* (Escalloniaceae) (Photographed by Andrés Moreira-Muñoz)

Photo 7.7 Spiny savanna, Central Chile (Photographed by Andrés Moreira-Muñoz)

diversity. Some of these genera are concentrated in the Semi-desertic scrub, such as *Balsamocarpon* (Fabaceae)*, Dinemandra* (Malpighiaceae)*, Leontochir* (Alstroemeriaceae), or *Pintoa* (Zygophyllaceae). Others have their main distribution in the Sclerophyllous forests and matorral, such as *Avellanita*, *Adenopeltis* (Euphorbiacea), and *Miersia* (Alliaceae). The Spiny savannah and the Andean scrub show less endemic monotypic genera, e.g. *Calopappus* (Asteraceae), occurring in the Andean scrub (Photo 7.8).

A constant question in assessments of endemism is whether the patterns are the result of rapid diversification or the remaining of old lineages, or "plant cradles" versus "plant museums" (López-Pujol et al. 2011). This has also to do with the latitudinal diversity gradient of increasing diversity towards the tropics, a global biogeographical pattern that has been mentioned recurrently but also contested. It is in part explained by a combination of processes, including large scale climate changes, tectonic and geological events, interactions among species, and differential rates of speciation and extinction of lineages (Ackerly 2009; Lomolino et al. 2010). In this ecoregion, plant richness and endemism seems to be related to climatic conditions and soils, but also to relief and morphology, i.e. to its heterogeneous geodiversity. In fact, research on other Mediterranean biodiversity hotspots like the California Floristic Province shows that diversity is not evenly distributed, mainly due to geographic complexity (Crain and White 2011, and this chapter).

Photo 7.8 Andean scrub, Central Chile (Photographed by Andrés Moreira-Muñoz)

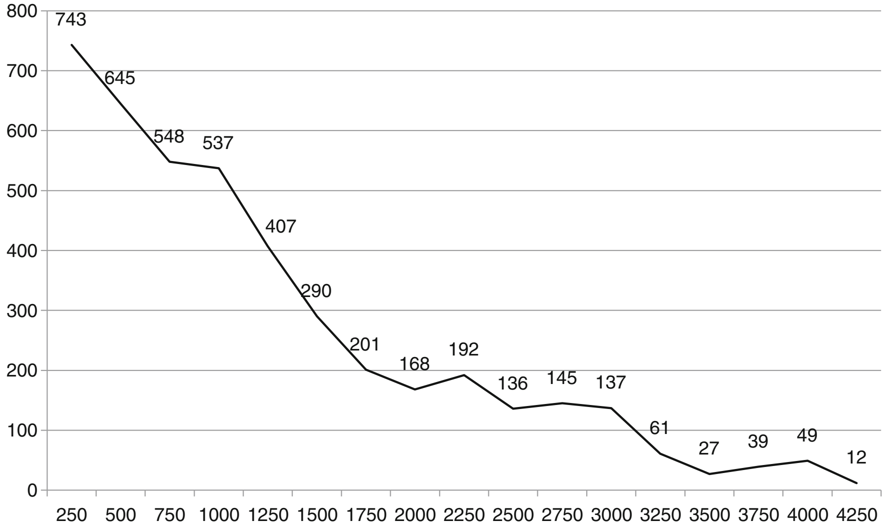

Fig. 7.3 Number of endemic species in each stretch of 250 m increase in altitude (y-axis: number of endemic taxa, x-axis: altitude in m)

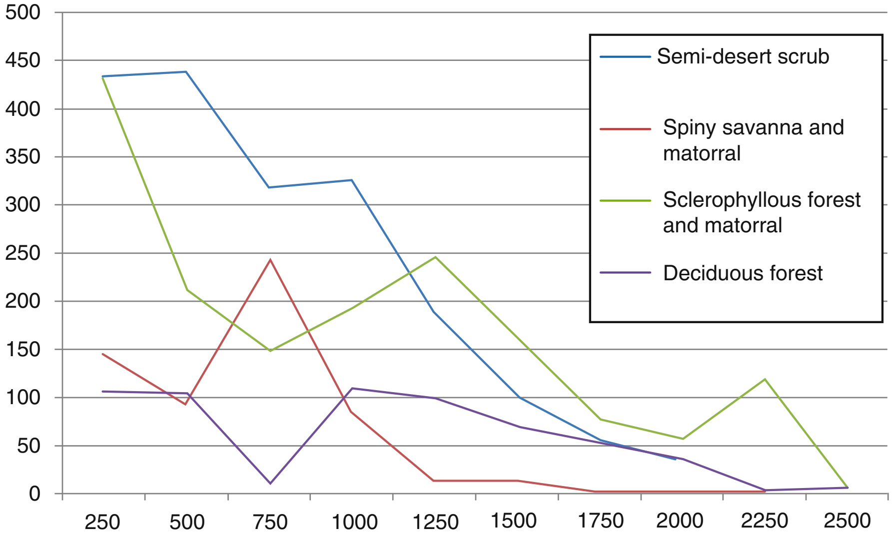

Fig. 7.4 Endemic species in different low altitude formations (y-axis: number of endemic taxa, x-axis: altitude in m asl.)

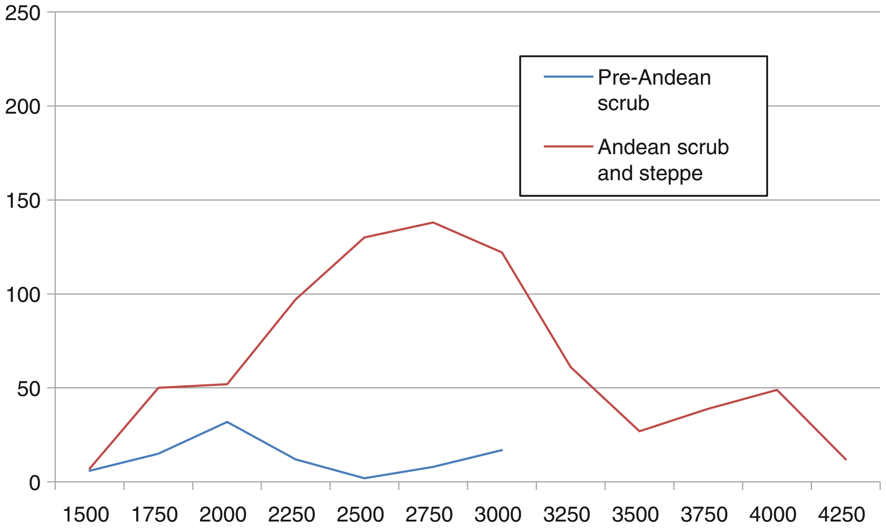

Fig. 7.5 Endemic species at different altitudes for high altitude formations (y-axis: number of endemic taxa, x-axis: altitude in m asl.)

Anyhow, endemism seems to be, at least in Mediterranean-type ecoregions, a consequence of a long interaction between relative dynamic speciation processes for several groups and species persistence for others. This last process seems to usually encompass extinctions and can be the reason for the high presence of monotypic genera. In this sense, centres of endemism can be considered as past centres of cladogenesis (Croizat et al. 1974; Jetz et al. 2004; Heads 2009). Indeed, Central Chile has been recognized as a contact zone between the Austral realm and the Neotropical floristic realms (Moreira-Muñoz 2007), composed by pre-Mediterranean lineages (Verdú et al. 2003), and with deep roots in old Gondwanic connections.

In the contact to the tropics, palaeoclimatical trends towards increasing aridity can explain the floristic and ecomorphological patterns detected in the Mediterranean ecoregions (Axelrod 1975). This seems to be the case of the Semi-arid desert scrub endemics. Regional broad geological-climatic events like the Middle-Miocene to Pliocene Andean uplift seem to be highly related to the increasing aridity of the Atacama Desert, having crucial effects on the relative rapid evolution and consequently high level of endemism of several groups. This is potentially one of the main causes for the origination of endemics via vicariant speciation, in unrelated genera such as *Heliotropium* (Luebert and Wen 2008), *Nolana* (Dillon et al. 2009), or *Copiapoa* (Guerrero et al. 2011). This might be also the case for disjunct distribution patterns in Desert-scrub endemics (Viruel et al. 2012).

It is highly necessary to improve the knowledge of the ecological, evolutionary and landscape-level processes that are responsible for the high level of endemism, integrating range size data with molecular-based estimates of taxon age (Kraft et al. 2010). In the near future a better understanding of endemism patterns and processes at different scales will be crucial for conservation planning and reserves design (Crain et al. 2011). Taxonomic knowledge is still incomplete and constantly changing, and endemic species are being revised, renamed and resurrected (e.g. Muñoz-Schick and Moreira-Muñoz 2008; Muñoz-Schick et al. 2011). Geographic distribution knowledge is usually even more elusive (e.g. Muñoz-Schick et al. 2010). These are the most important challenges for biodiversity information and decision-making within the novel approach of conservation biogeography (Whittaker et al. 2005).

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7.4 Europe's Mainland

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7.4.1 Physical Geography of Europe's Mainland

The climate in the North of Europe is arctic or subarctic, in Central Europe temperate, in South Europe Mediterranean with winter rain and summer drought. Mean temperatures range from some degrees below 0 °C in northern Scandinavia, northern Russia and high mountain zones of the Alps to c. 19 °C in some parts of the Mediterranean.

Annual precipitation totals range from <200 mm at Cabo de Gata, SE Spain, to over 2,000 mm in high mountain zones of the Alps and in oceanic regions of South Norway (e.g. Bergen: 2,250 mm/a).

Continentality increases from the West to the East. The difference between the average temperature of the coldest and the warmest month is less than 15 °C in some western parts (e.g. W France), but also in the highest mountain zones of the Alps. The difference is much larger in eastern parts of European Russia, with values >30 °C (e.g. Astrakhan: –5.5 °C in January, 25.2 °C in July, Syktyvkar –16.7 °C in January, 17.2 °C in July; cf. Deutscher Wetterdienst 2002, 2008).

Most substrates (granite, gravel, sand, organic layer) in the North are acidic, whereas the amount of calcareous and/or alkaline substrates increases to the South (Ewald 2003).

Vascular plant endemism and species richness at regional scales is higher in regions of the Pyrenees, Alps, Carpathians, mountains of the Balkan Peninsula and in countries bordering the Mediterranean Sea than in northern regions which were flattened by glaciers or affected by extremely cold arctic climate during the Pleistocene.

7.4.2 Analysis of EvaplantE

The goal of this chapter is to analyse mainland endemism of the vascular plants in Europe in relation to habitat and to compare the results with findings from islands, other mainland regions, or the whole of Europe, i.e. mainland and island regions combined (Bruchmann 2011).

Therefore, all data and information about island regions in EvaplantE (latest updated version) were eliminated. Data of taxa which occur on both mainland and islands of Europe were also eliminated.

Mainland Europe as defined here excludes the larger islands of the Mediterranean Sea and the Atlantic Ocean: Cyprus, Crete, Sicily, Corsica, Sardinia, the Balearic Islands, the Canary Islands, Madeira Islands, the Azores, Great Britain, Ireland, Faroe Islands, Iceland and Svalbard (with some smaller islands and islets in their vicinity; cf. Tutin et al. 1996a, b, c, d, e; Fontaine et al. 2007), but includes e.g. the Channel Islands and many Greek islands.

We predefined Mainland Europe into 28 regions. *Mainland endemics* are restricted to one or more regions We define an endemic which occurs in a single region out of the 28 predefined regions of mainland Europe as *1-region-endemic* (*local-endemics* sensu Bruchmann 2011). *European endemics* are all taxa which are restricted to the continent (42 predefined regions), independent of the fact as to whether these occur on islands or the mainland, in a single region or in many regions of Europe.

The percentage values in the table are standardised to a sum of 100 % (see Bruchmann 2011 or Hobohm and Bruchmann 2009). This is important because many endemics are listed in more than one habitat category. Thus, the non-standardised percentage-values would be higher and add up to more than 100 %.

7.4.3 Endemism of Mainland Europe

The flora of Europe is relatively well known. However, the number of vascular plant taxa and endemics has often been seriously underestimated. Davis et al. (1994), for example, estimate the number of endemic vascular plant species at 3,500, whereas Hobohm and Bruchmann (2009) estimate that at least 6,500 vascular plant taxa (species, subspecies and groups of microspecies) are endemic to Europe. This number would be even higher if a narrower concept of what constitutes a species would be applied. We estimate that about 20–30 % of all European vascular plant taxa are endemics.

According to EvaplantE (latest updated version), Europe is inhabited by 6,242 European endemics (of which 4,827 are characteristic for specific habitats), including 4,243 mainland endemics (3,084 characteristic). 1,805 mainland endemics are restricted to one of the 28 regions (1,761 1-region-endemics characteristic).

Table 7.4 shows numbers of European mainland endemics and 1-region-endemics of the European mainland characterised by habitats.

Rocky habitats harbour the highest number of mainland endemics (>1,800). The second largest group is grassland endemics (>1,100) followed by scrub and heath (>600), forest (>400), arable lands, horticultural and artificial habitats (>250), coastal/saline habitats (200), freshwater habitats (>150), and finally mires and swamps (>50).

Obviously, the mean altitudes of endemics occurring in rocky habitats or grassland, and most other habitats, are higher than the mean altitudes of endemics in coastal or anthropogenic habitats.

The proportion of basiphytic endemics in Mainland Europe is higher than that of acidophytes. Only the inhabitants of swamps and mires show comparable numbers of basiphytes and acidophytes.

Large regions in southern Europe, such as Spain, France or former Yugoslavia, show high total numbers of endemics.

Table 7.4 Numbers of European mainland- and 1-region-endemics in relation to habitat (EvaplantE; latest updated version, numbers of taxa are minimum values)

	Coastal/saline	Freshwater	Mires and swamps	Forest	Scrub and heath	Grassland	Rock and scree habitats	Arable, horticultural, artificial
Proportion of the whole area (Hobohm and Bruchmann 2009)	<1 %	A few %	A few %	<30 %	>10 %	<10 %	A few %	>>30 %
No. of European mainland endemics in total	200	178	58	422	639	1,134	1,813	277
In %	4.2	3.8	1.2	8.9	13.5	24.0	38.4	5.9
Min. altitude (m asl., median)	0	510	350	300	300	700	800	50
Max. altitude (m asl., median)	400	2,000	2,100	1,780	1,750	2,100	2,100	1,230
No. of basiphytes	46	30	12	83	167	243	694	50
No. of acidophytes	4	17	10	23	56	84	127	14
No. of 1-region-endemics	111	46	10	100	212	300	845	137
In %	6.3	2.6	0.6	5.7	12.0	17.0	48.0	7.8
No. of European mainland endemics by region								
Al (Albania)	3	12	5	71	93	179	266	24
Au (Austria)	6	62	19	143	164	363	310	16
Be (Belgium, Luxembourg)	2	1	1	15	16	23	9	7
Bu (Bulgaria)	10	18	7	98	116	248	252	29
Cz (Czech Republik, Slovakia)	7	34	13	112	108	220	131	17
Da (Denmark)	9	2	2	9	9	13	3	3

(continued)

Table 7.4 (continued)

	Coastal/saline	Freshwater	Mires and swamps	Forest	Scrub and heath	Grassland	Rock and scree habitats	Arable, horticultural, artificial
Fe (Finland)	11	1	5	16	7	19	5	2
Ga (mainland France)	31	71	18	127	178	379	444	48
Ge (Germany)	13	54	19	100	102	232	177	18
Gr (Greece, except Crete)	17	17	4	75	112	181	459	74
He (Switzerland)	1	50	14	91	109	270	239	19
Ho (The Netherlands)	4	2	1	7	8	10	1	6
Hs (mainland Spain)	94	72	21	121	292	302	566	129
Hu (Hungary)	10	8	8	82	73	114	53	16
It (mainland Italy)	15	55	19	149	184	436	522	44
Ju (former Yugoslavia)	25	41	20	179	204	455	519	51
Lu (mainland Portugal)	48	31	10	45	115	68	103	60
No (Norway, without Svalb.)	5	7	4	13	8	18	11	2
Po (Poland)	9	27	11	77	75	159	103	14
Rm (Romania)	13	32	16	134	131	279	216	22
RsB (f. Eur. SU, Baltic)	10	5	6	20	12	23	5	3
RsC (f. Eur. SU, Central)	7	9	4	42	40	52	27	15
RsE (f. Eur. SU, East)	2	6	0	18	16	34	22	6
RsK (f. Eur. SU, Krim)	8	1	0	20	17	32	45	10
RsN (f. Eur. SU, North)	4	1	4	11	4	16	6	2
RsW (f. Eur. SU, West)	17	34	9	99	95	181	106	13
Su (Sweden)	11	7	7	18	12	30	20	2
Tu (European part of Turkey)	3	3	1	14	12	25	21	6

7.4.3.1 Coastal and Saline Habitats

This group includes 4.2 % of the endemic vascular plants that are restricted to the mainland of Europe as defined in this chapter. Endemism of coastal and saline habitats shows a southwestern gradient. The Iberian Peninsula and western part of the Mediterranean is richer in endemic plants that occur in salt marshes, sand dunes or coastal rocks than the eastern part of the Mediterranean or northern parts of the Atlantic coasts. This might be due to climate conditions in the past, the age of water bodies, marine currents and the constancy of local ecological conditions including age of the geological surface.

7.4.3.2 Freshwater Habitats, Mires and Swamps

3.8 % of the European mainland endemics are associated with freshwater habitats, 1.2 % with mires and swamps. Plant endemism of water bodies, swamps and mires, or seasonally inundated habitats, is relatively low, as in most wetlands of the world. We explain this fact by the young age of most aquatic habitats: swamps, mires, lakes, rivers, or seasonally inundated habitats are almost all much younger than 10,000 years old. Additionally, these habitats are very often isolated. Isolation combined with young age restricts endemism.

7.4.3.3 Forest

According to numbers published by FAO (2010) forest coverage is 34 % for the whole of Europe excluding the Russian Federation and 45 % including the Russian Federation. These relatively high percentages depend on the definition of *forest*. The definition of the FAO covers much more than what biologists would normally include. Hobohm and Bruchmann (2009) estimate that the percentage of forest (defined as vegetation type which is dominated by trees, crown cover >50 %) for the whole of Europe (including the European part of the Russian Federation) is less than 30 %. However, the area is much larger than the area of e.g. rocks and screes, coastal and saline habitats, grassland or scrub and heath.

Compared to endemics of other habitat types the number of forest endemics (8.9 %) is relatively low. We assume that this is due to Pleistocene glaciation periods which destroyed most of the forests. Many forest plants which nowadays occur in temperate or boreal climate zones of Europe survived during the cold periods in refugia of southern Europe (cf. e.g. Médail and Diadema 2009; Krebs et al. 2004).

7.4.3.4 Scrub and Heath

About 13.5 % of the European mainland endemics are associated with scrub and heath. We do not know much about distribution patterns of scrub and heath habitats or about the size of these habitats in Europe. They probably cover a little more than 10 % of the surface. However, in Europe more endemics are related to scrub and heath than e.g. to forest. Additionally, the mean ranges seem to be smaller than those of forest endemics; the mean range size (median) covers a single region in the case of endemics related to scrub or heath and two regions for forest endemics.

Portugal has more endemics in scrub and heath communities than in any other habitat category (Table 7.4).

7.4.3.5 Grassland

In comparison to the whole of Europe including the islands (Bruchmann 2011) the percentage values for grassland endemics that are restricted to the mainland is higher (24 % as opposed to 18.3 % for the whole of Europe). This trend is also reflected by a higher number of 1-region-endemics (17 % grassland-endemics on the mainland and 10 % for the whole of Europe).

Grassland endemics which only occur in a single region of the mainland are the largest group in 5 regions, whereas endemics of rocky habitats are the largest group in 16 regions (cf. Bruchmann 2011).

The situation is the opposite if one compares numbers of all mainland endemics. In this case, most regions have higher numbers of endemics associated with grassland rather than rocky habitats. Grassland endemics are the largest group in 19 regions; in 8 regions, endemics of rocks and screes represent the largest group.

This is in accordance with the finding (Hobohm and Bruchmann 2009) that shows that the mean ranges of rock endemics in Europe are smaller (median 1) than the ranges of grassland endemics (median 3). Thus, many grassland endemics of mainland Europe are distributed over two, three or more regions (countries). This may result from the connectivity of grassland habitats and transhumance in the past.

Furthermore, grassland endemics are stronger concentrated in temperate regions, in Central and eastern Europe, than endemics of other habitat types. Almost all northern and eastern regions as well as regions in Central Europe (Switzerland, Austria) harbour more grassland taxa that are endemic to mainland Europe than endemics of other habitat types (see Table 7.4).

7.4.3.6 Rock and Scree Habitats

Rocky habitats including rock outcrops, screes and caves, in general, can be found all over the mainland of Europe and in all altitudinal zones. At the moment we do not know the exact coverage of this habitat category in Europe, but we assume that rocks and screes cover a few percent of the total surface (Hobohm and Bruchmann 2009).

More than a third (38.4 %) of the European mainland endemics inhabits rocky habitats. In 16 regions of continental Europe rocky habitats harbour the highest number of 1-region-endemics (Bruchmann 2011).

The large number of endemics in rocky habitats of Europe might be explained by *stability* of ecological conditions (high diversity of microclimates over short distances) and short-distance *vertical displacement* of the inhabitants during climate change (cf. Rull 2004). The large number cannot simply be explained by area because other habitat types cover larger areas and have lower endemism.

7.4.3.7 Arable, Horticultural and Artificial Habitats

Compared to other regions in the world, a relatively large proportion of endemics (5.9 %) occurs regularly in anthropogenic habitats of European mainland. A few taxa, such as *Anthemis lithuanica, Bromus secalinus ssp. multiflorus, Bromus interruptus, Carduus litigiosus, Centaurea polymorpha, Erucastrum gallicum* and *Urtica atrovirens,* are relatively strongly associated with arable lands or ruderal habitats and do not normally occur in semi-natural or natural habitats (Hobohm and Bruchmann 2009; Hobohm 2008). Gams (1938) and Pignatti (1978, 1979) discussed the possibility of the coevolution between plant and man.

7.5 Turkey

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7.5.1 Introduction: Regional Overview

The territory of the Turkish Republic covers c. 783.000 km^2, surpassing France as the largest EU-country (with c. 540.000 km^2). Only 3 % of this area belongs to Europe (Eastern Thrace), the other 97 % forms the westernmost protrusion of Asia, and is named Anatolia or Asia Minor. This region forms part of the Alpide Belt, and was covered by the Tethys during the Mesozoic. The final uplift of Anatolia did not begin until the end of the Neogene. The resulting highland resembles a ramp, emerging from the Mediterranean Sea in the west, reaching maximum elevations in the east and enclosed by impressive mountain chains in the north and south. Turkey is one of the most mountainous countries in the world, with an average elevation of 1,130 m asl. (Swiss: 1,307 m, Spain: 660 m). Due to this rugged surface and its large area Turkey has a highly diversified climate, resulting in the occurrence of three major phytogeographical regions.

The Euxine Province of the Euro Siberian Region extends along N. Anatolia, where the climate is dominated by humid westerly winds all the year round. Climax vegetation on the seaward slopes of the Pontic Mountains consists of lush deciduous forests, often dominated by *Fagus orientalis* and – at high altitudes – *Abies nordmanniana*. Annual precipitation in this region oscillates mostly between 500 and 1,300 mm, but rises sharply in the Colchic sector east of Ordu to a maximum of 2,241 mm in Rize. Leeward of the coastal ranges humidity drops rapidly to <500 mm, paralleled by a change in climax vegetation to pure stands of hardy and drought-resistant *Pinus sylvestris*, which in the west is partially substituted by *Pinus nigra*.

The Mediterranean region is confined to the seaward parts of W. and S. Anatolia. Annual precipitation is about the same as in the Euro Siberian sector (from 448 mm in Mut to 1,197 mm in Manavgat), but the seasonal distribution is completely different. Wet winters are contrasted by a pronounced summer drought, which is longest in the south and also includes the high mountains. What is left of climax vegetation is sclerophyllous forest, dominated by *Quercus coccifera* and *Pinus brutia*. Nowadays, however, the fertile alluvial plains are almost exclusively dedicated to agricultural use, whilst the remainder has mostly been replaced by Mediterranean maquis or even further degraded phrygana. The timberline in the Taurus is made up of *Pinus nigra* ssp. *pallasiana, Abies cilicica* und *Cedrus libani*, on the much drier northern side partly also of *Juniperus excelsa* and *J. foetidissima*.

The Irano-Turanian Region is by far the largest of the three zones, comprising Central and E. Anatolia. Due to its position behind the coastal ranges, precipitation is low and winters are cold. The area is subdivided by the Taurus mountains which cross it diagonally ("Anatolian Diagonal") into two ecologically distinct territories.

The western part consists of a system of sedimentary basins (ovas) und hills formed of basement rocks. Annual precipitation oscillates mostly between 320 and 420 mm, but drops to values of 270–300 mm in the central ovas of the Great Salt Lake (Tuzgölü), Konya and Yeşilhizar. It is generally agreed that recent steppe or salt-steppe vegetation there is of natural origin, whereas climax vegetation on the hillsides and mountain slopes is dry forest of a submediterranean type, with *Quercus pubescens, Q. cerris, Pinus nigra* and peripherally also *Quercus coccifera*. But after 4,500 years of forest destruction it became difficult to distinguish between natural steppe, semi natural-steppe (due to forest destruction) und subalpine thorn-cushion formations. Moreover this issue is nowadays increasingly of theoretical interest only, as huge steppe areas have been transformed into monotonous fields over the last 40 years.

East of the Anatolian Diagonal altitudes increase considerably, with Van Lake basin (1,650 m) lying more than 700 m higher than Tüzgölü basin (925 m). A lot of mountains surpass 3,000 m, some even reach 4,000 m (Mt. Ararat, Süphan Daği, Cilodağ), and huge areas are covered by young volcanic material. Climate is very

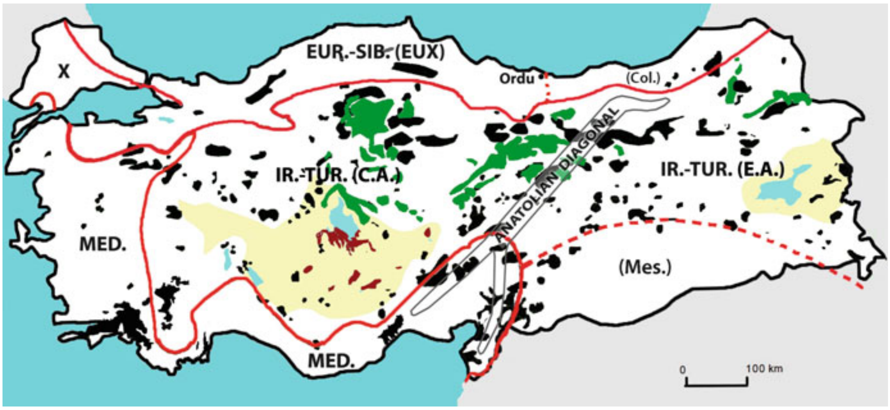

Fig. 7.6 Climatic and edaphic diversity in Turkey. *Red lines*: approximate limits of the phytogeographical regions in Turkey after Davis (1971). EUR.-SIB (EUX): Euro-Siberian Region (Euxine province); *Col.*: Colchic sector of Euxine province; *MED.*: Mediterranean Region (east Mediterranean province); *IR.-TUR.*: Irano-Turanian Region; *C.A.*: central Anatolia; *E.A.*: E. Anatolia; (*Mes.*: Mesopotamia); *X*: Probably central European/Balkan province of Euro-Siberian Region. – *Light yellow* shaded areas: endorheic basins (Elektrik İşleri 2012); *black*: ophiolites (Billor and Gibb 2002); *green*: evaporites (Doğan and Özel 2005); *red*: salt steppe (Atlas Harita Servisi 2004)

severe, with average temperatures in January corresponding to those of northern Turkestan (Erzurum: −8.9°, Kars: −18.3°). Large areas are treeless and most of the remaining forests are degraded to humble scrub, consisting mainly of deciduous oaks (*Quercus brandtii, Q. infectoria, Q. libani, Q. robur* ssp. *pedunculiflora, Q. petraea* ssp. *pinnatiloba*) .

The driest region of Turkey is the Aras valley between Kağızman and the Armenian border, with an average precipitation in Iğdır of only 252 mm (in dry years only 114 mm, Atalay and Mortan 2003). Drought is so severe there that snow-like patches of salt outlets are leaking out of the barren hills. A considerable number of more easterly distributed (semi) desert plants enter Turkish territory only in this remote corner, e.g. *Limonium meyeri* (Plumbaginaceae), *Calligonum polygonoides* (Polygonaceae), *Halanthium rarifolium, H. roseum, Salsola verrucosa, S. dendroides, Halogeton glomeratus, Suaeda microphylla, S. linifolia* (Chenopodiaceae), *Tamarix octandra* (Tamaricaceae).

The genesis of the recent Turkish flora began at the end of the Palaeogene, when the Anatolian mass had just formed but still remained partly submerged by transgressions of the Tethys. Subtropic conditions at that time can be deduced from widespread brown coal deposits in the Neogene basins, with remains of *Taxodium, Cinnamomum, Glyptostrobus, Sequioa* etc. (Gemici and Akgün 2001). East of Ankara, sediments of this period contain huge masses of evaporits, which nowadays form the impressive gypsum hills around Çankırı and Sivas (Fig. 7.6, Günay 2002). This suggests higher aridity towards the east, a supposition which is also supported by palynological evidence, showing an increase of Compositae, Chenopodiaceae and Poaceae from Middle to Late Miocene (Akgün et al. 2007). Towards the end of the Neogene, temperatures and humidity sank to recent levels and the final uplift of the Pontus and Taurus chains began. Parts of the Palaeotropic flora disappeared, others formed the basis for the evolution of the present day Mediterranean (sclerophyllous) flora, and some survived as relicts, mainly in the Colchis. Dry central Anatolia was invaded by the ancestors of the recent Irano-Turanian genera, which experienced explosive radiative evolution, some of them also penetrating into the Mediterranean zone (e.g. *Verbascum, Onosma*).

Glaciations during the subsequent Pleistocene period were of much less importance in Anatolia than in the Alps. Local mountain glaciers were mainly restricted to the northern slopes of the highest mountains. The most extensive glaciations occurred in the Kaçkar Mountains (3,932 m) in the northeast and on Çilo Dağları (4,135 m) in the southeast, where the longest of these local glaciers reached 10 km and descended to 1,600 m (Güldali 1979). Pollen profiles from the lower regions of central Anatolia (Eski Acigöl, 1,270 m, Nevşehir Province) show an Artemisia-Chenopod steppe towards the end of the last glacial period (16.000 BP., Roberts et al. 2001). There is evidence that Irano-Turanian genera like *Cousinia* not only easily survived glacial periods, but in fact were more abundant and more widespread than in interglacials (Djamali et al. 2012). In the Mediterranean zone, thermophilous plants disappeared and vegetation consisted of a dry forest steppe with *Prunus amygdalus* s.l, *Pinus* sp., deciduous oaks and again much *Artemisia* and Chenopodiaceae (Emery-Barbier and Thiébault 2005). As to the Euro-Siberian Flora of northern Anatolia, there is general agreement that temperate forests were able to survive glacial periods at least in the Colchic sector, as well as in the adjacent Caucasus and Hyrcanian regions (DellaSala 2010).

During the Holocene, temperature and humidity increased, causing the development of a mosaic of woodland with deciduous oaks, shrubs (e.g. *Corylus*) and open grassland about 8,000 BP. After 6,500 BP the more mesophilous trees such as *Ulmus* and *Corylus* disappeared, probably due to an increase in aridity. Human impact becomes noticeable in the Bronze Age (c. 4,500–4,000 BP), with a marked decline in oak pollen paralleled by a spread of anthropogenic species (Roberts et al. 2001). Since then huge areas of Central Anatolia have been cleared of any forest cover. The same is true for the Mediterranean region, where all types of degraded vegetation, from maquis and phrygana to open rock- and scree vegetation, experienced dramatic increases since prehistoric times.

Today the flora of Turkey numbers about 9,000 species of vascular plants, with an endemism ratio of 1/3 (33,3 %). Both values are astonishingly high and unique for the western Palaearctic. Even when distorting effects of different territory size on endemism ratios are reduced by comparing Bykov's index instead of mere species numbers, Turkey (2,29; using data from Güner et al. 2000) is far ahead of Greece (1,18) and continental Spain (−1,08), and comes second only after isolated islands like the Canary Islands (10,68), Madeira (10,36) or Crete (3,08; Bruchman 2011).

7.5.2 Material and Methods

If not stated otherwise, data on climate, geology or geomorphology are taken from Atalay and Mortan (2003) and Hütteroth and Höhfeld (1982), data on Turkish plants from Flora of Turkey (Davis 1965–1988) and its supplements (Güner et al. 2000; Özhatay and Kültür 2006; Özhatay et al. 2009, 2011). Important additional information about the distribution of regional endemics in Turkey was extracted from Boulos et al. (1994) and Özhatay et al. (2003).

Of very limited use are existing maps showing the frequencies of Turkish endemics within Turkey (Kutluk and Aytuğ 2001). Such maps seriously underestimate regional endemism in all borderline grids. If such a methodology was applied to Europe a whole, Switzerland lying in the centre of Europe and therefore containing 30 % European endemics would range far ahead of Greece with only 21.9 % European endemics (calculations based on data from Bruchmann 2011).

Knowledge about the ecology of Turkish plants is still rather rudimentary, leading to such unspecific descriptions as “rocky slopes”, “mountainous districts”, “pastures”. Clear ecological distinction between the different kinds of steppes, pastures or rock associations entails a profound knowledge of the Turkish flora. For any single researcher this was virtually impossible to achieve before completion of the “Flora of Turkey”. Unfortunately it is not much easier today, due to bureaucratic restrictions on research and collecting samples for non-Turkish citizens (Pils 2006).

7.5.3 The Main Components of the Turkish Endemic Flora

Table 7.5 shows important genera in the Turkish endemic flora. The first 10 genera on the list are those with the highest numbers of endemics in Turkey. Excluded is the mostly apomictic genus *Hieracium*. Turkish values compiled from Davis (1965–1988), Güner et al. (2000), Özhatay and Kultür (2006) Özhatay et al. (2009, 2011), European values from Flora Europaea.

The most important share in the Turkish endemic flora falls upon genera with global distribution centres in the Irano-Turanian region, i.e. the dry regions of Turkey and eastwards to Mongolia and Afghanistan. Such Irano-Turanian genera are by definition poor in European species, as is shown in Table 7.5 for the Flora Europaea area. In this sense *Astragalus* and *Verbascum*, the two most diversified genera in Turkey are perfectly Irano-Turanian. The same is true for *Salvia, Onosma* and 11 other examples listed in Table 7.5 Some of these are represented in the Flora Iranica region with far more species than in Turkey, e.g. *Astragalus* (965 species!), *Acantholimon* (>160) or *Cousinia* (c. 350), others such as *Verbascum* and, to a lesser extent, *Onosma* and *Salvia* are clearly “Turkish”.

As stated already by Hedge (1986), the highest numbers of species in Anatolia do not necessarily indicate highest level of morphological variation here. Hedge illustrated this with *Salvia*; Turkey has by far the most species (95) of this genus, but in Afghanistan which has only 23 species there is a greater range of morphological

Table 7.5 Endemic-rich genera of vascular plants in Turkey (for further information see text)

	No. of endemics in Turkey	No. of species in total	Level of endemics (%)	No. of species in Europe
Astragalus	277	437	63	133
Verbascum	194	242	80	87
Centaurea	122	193	63	221
Allium	66	163	40	110
Silene	66	147	45	194
Campanula	63	112	56	144
Galium	55	109	50	145
Alyssum	59	96	61	70
Salvia	50	95	53	36
Onosma	49	96	51	33
Further examples for important irano-turanic genera in Turkey				
Gypsophila	31	84	37	27
Cousinia	26	38	68	1
Alkanna	26	35	74	17
Acantholimon	25	39	64	1
Fritillaria	23	40	58	23
Phlomis	22	36	61	12
Aethionema	21	41	51	9
Muscari	20	31	65	13
Paracaryum	19	28	68	0
Delphinium	17	32	53	25
Consolida	14	28	50	13
Ebenus	14	14	100	2

variation. It seems probable, therefore, that Anatolia is not the primary centre of evolution for most of its Irano-Turanian genera, but a centre for secondary adaptive radiation, giving rise to numerous knots of closely related, often vicarious, neoendemic species. Such a point of view is also in accordance with the relatively recent genesis of the Anatolian micro-continent as outlined above.

All of these successful Irano-Turanian genera are well adapted to treeless, dry and heavily grazed habitats, in some cases also to soils with high contents of heavy metals (e.g. Brassicaceae like *Alyssum*, *Aethionema*) or gypsum soils (*Gypsophila*). *Astragalus* as the most successful genus in terms of species numbers is also the most plastic one with regard to niche exploitation in such habitats. There are annuals (9 sections), acaulous perennials with their leaves pressed to the ground (sect. *Myobroma*), high-growing but unarmed perennials relying on chemical defence (sect. *Alopecias*) and several sections of heavily armed thorn-cushions, which are very characteristic for the subalpine regions of Irano-Turanic Anatolia. Such thorn-cushions evolved convergently in different *Astragalus* sections, but also in *Onobrychis cornuta, Acantholimon* (Plumbaginaceae), some Asteraceae (e.g. *Centaurea urvillei, C. iberica, Lactuca intricata*) and Caryophyllaceae (e.g. *Minuartia juniperina*).

Very successful under Irano-Turanian conditions are thistles (e.g. *Onopordum* with 17 species, *Cousinia* with 38 species) or prickly herbs such as many *Onosma* species. The latter are covered by clusters of stiff setulae or spinules, which in some cases may be as annoying as the hair-like glochides of *Opuntia*. A rather singular Anatolian success story are the mostly pannose, tap-rooted candelabras of *Verbascum* spp., which are highly unpalatable to cattle and sheep. Turkey alone has c. three times as many species of *Verbascum* (242) as the whole Flora Europaea area (87).

An outline of the Turkish endemic flora would be incomplete without mentioning the numerous bulbous Monocotyledons, which are preferential "objects of desire" to rock gardeners all over the world. Species formation also seems to be in full progress in some of these genera. An instructive example is *Crocus*. At the moment about 37 *Crocus* species are accepted for Turkey (depending on the species concept applied); 24 of these are endemic. A closer look reveals that some of these "species" are better referred to as "superspecies". This is true especially for *Crocus biflorus* s. latiss., which is distributed all over Turkey in a broad spectrum of habitats and at altitudes from 200 to 3,000 m. Today 17 Anatolian subspecies are accepted within *C. biflorus* (Euro+Med 2006-), excluding some better feasible forms, that are accepted as good species (e.g. *C. nerimaniae* and *C. wattiorum*). However, still more local populations exist, whose allocation to one of the already described subspecies is unresolved (Kerndorf and Pasche 2006). Typically each of these shows a certain degree of morphological differentiation and occupies its own territory, often a slightly isolated mountain range. The ecological niches of some of these geographical races show broad overlap, but areas of distribution as a rule are neatly separated. Delimitation of such "microspecies in statu nascendi" probably works by competitive exclusion, and in the case of strictly allogamous species also through positively frequency-correlated fitness functions (Pils 1995).

Situations are similar in other actively evolving species clusters in Turkey, e.g. *Ranunculus dissectus* s.latiss. At present 7 subspecies are distinguished, but 3 taxa have already gained greater evolutionary distance and are therefore treated as good species (*R. fenzlii, R. crateris, R. anatolicus*). They all have mutually excluding distribution areas covering the major part of Anatolia in the form of a somewhat irregular mosaic. One of the main reasons for evolving towards such a high degree of differentiation obviously comes from the highly patchy structure of Anatolia (Fig. 7.6), possibly in combination with a temporary increase of separation between populations due to changing forest cover, as recently suggested for *Cousinia* (Djamali et al. 2012).

Crocus biflorus is a nice example for the mutual dependence of progress in systematics and a better understanding of endemism. Still more striking is the case of *Ornithogalum* s.lat., a traditionally rather sidelined genus due to its scant interest to rock gardeners. Its initial treatment in "Flora of Turkey" comprised 23 species, only 2 of which are endemic to Turkey, thus resulting in an endemism rate of 8.7 %. This changed drastically in recent decades when a wave of descriptions of local endemics increased species numbers in Turkey by nearly 100 % (up to 55, Bağci et al. 2011) and the endemism rate to >50 %.

Of special interest are monotypic endemic genera. Their isolated positions are an indication of a somewhat relictic nature. The following 17 species fall in this category: *Crenosciadium siifolium, Ekimia bornmuelleri, Microsciadium minutum, Olymposciadium caespitosum* (all Apiaceae); *Leucocyclus formosus* (Asteraceae); *Physocardamum davisii, Tchihatchewia isatidea* (Brassicaceae); *Phryna ortegioides, Thurya capitata* (Caryophyllaceae); *Cyathobasis fruticulosa, Kalidiopsis wagenitzii* (Chenopodiaceae); *Sartoria hedysaroides* (Fabaceae); *Dorystoechas hastata* (Lamiaceae); *Necranthus orobanchoides* (Orobanchaceae); *Nephelochloa orientalis, Pseudophleum gibbum, Oreopoa anatolica* (Poaceae).

The two Chenopodiaceae-species are endemics of the Central Anatolian salt steppe. *Crenosciadium* is restricted to moist open places in the upper region of Murat Dağ. Recently described *Oreopoda* is known only from a single location on Aktepe (Beydağları, southwestern Taurus Mts. 2,700 m, Parolly and Scholz 2004). The rest grows on dry, open, mostly rocky places in mid to higher altitudes (mainly 900–2,000 m). Distribution areas as a rule range between small and tiny and not a single member of this group is reaching the Euxinic region.

7.5.4 Regional Endemism in Turkey

On a global scale, local endemism shows a very strong correlation with high mountain zones. Turkey is no exception to this rule. Mill (1994) ranks the entire Taurus and the eastern Pontus among the most important centres of plant diversity in SW Asia. The most outstanding numbers in his statistics are those for SW Anatolia (mainly western Taurus, about 3,365 species, with >300 local endemics) as well as for the large area around the Anatolian Diagonal (3,200 species, with c. 390 local endemics).

The privileged position of SW Anatolia can be explained by a combination of factors which favour the development of local endemism. This begins with the discontinuous structure of the high mountains there. Between Kaz Dağ and Mendeşe Dağ there is a system of horsts and grabens, which finds its continuation in the western Taurus, where a series of isolated chains is separated by lower sedimentary basins (ovas) or abrasion zones (Atalay and Mortan 2003). A similar "patchy structure" is exhibited by the geological structure of the region. High massifs consist mainly of limestone, but there are also large areas of ultrabasic peridodites in the region, e.g. the whole Marmaris Peninsula as well as the 2,294 m high Sandras Dağ near Muğla. And finally there is a strong climatic gradient from the Mediterranean area on the coast to the Irano-Turanian sector towards central Anatolia. Annual precipitation in Antalya is 1,041 mm, but in Beyşehir north of the Taurus range only 447 mm. This endemism centre is also the most important one with respect to relict species, with 8 out of 17 monotypic genera having at least part of their distribution areas here. A "living fossil" of SW Anatolia is *Liquidambar orientalis* ("Turkish sweetgum", Hamamelidaceae), which was a constant part of the Neogene browncoal forests of the whole of western Turkey (Gemici and Akgün 2001). Closely related forms extended into much of Europe and the Caucasus. Today *Liquidambar* is confined to some flood plains or marshy valleys in a small part of SW Anatolia (mainly around Marmaris) and the nearby island of Rhodes. Its closest relative is *L. styraciflua* from eastern N America (Photos 7.9 and 7.10).

In the adjacent section of the Taurus between Antalya and Adana concentration of local endemics remains on a similar high level. Local hotspots of particular importance are Bolkar Dağları (3,524 m) and Ermenek Valley. The latter is up to 1,000 m deep and was formed by excavation of the Ermenek River into a vast plateau of remarkably soft limestone, which was deposited during a middle Miocene transgression of the Tethys. About 50 species are more or less confined to this marvelous region (Özhatay et al. 2003), e.g. the monotypic genus *Sartoria (S. hedysaroides)*, which is closest to *Hedysarum* (Fabaceae).

The Anatolian Diagonal connects Aladağları (3,756 m) in the south with Munzur Dağları (3,462 m) in the north, thus forming a mountainous borderline between W and E Anatolia. Factors favouring general diversity and local endemism are roughly the same as in SW Anatolia. Calcareous Munzur Dağları are in a relatively isolated position in otherwise mainly siliceous (often volcanic) central Anatolia, which explains their unusually high number of local endemics. Again there are numerous outcrops of ultrabasic serpentine rocks in the region, the largest of these being Avcı Dağları (3,345 m) east of the Munzur Dağları. Of special importance for local endemism are large areas of lime marls and gypsum in the lower sections of the Taurus mountains, mainly east and south of Sivas. Monotypic *Tchihatchewia isatidea* has its centre of distribution in the northern and central parts of the Anatolian Diagonal.

The Amanus Mountains (Nur Dağları, 2,240 m) form a bridge between the Anatolian Diagonal and the “Levantine Uplands”, running parallel to the eastern shore of the Mediterranean Sea into northern Israel. A total of 139 species is endemic to the Amanus, and 128 further species are subendemic (Mill 1994). One reason for these exceptionally high values might be the special position of the Amanus as an “island of humidity” between sea and desert. Precipitations exceed 1,700 mm in altitudes over 1,750 m and even summers are not completely dry here, thus enabling the survival of local *Fagus orientalis*-forests with Euxinic elements such as *Ilex colchica, Rhododentron ponticum, Tilia argentea, Prunus laurocerasus, Gentiana asclepiadea, Staphylea pinnata* etc. On the eastern slope, towards the Syrian desert, annual precipitation soon drops to <600 mm, resulting in a much more xerophilous forest vegetation. Edaphic diversity is very high, with hard limestones composing northern and central sectors, and ultra basic peridodites building up the south. The latter are covered mainly by open *Centaurea ptosimopappa-Pinus brutia* forests with a large number of local endemics (Özhatay et al. 2003).

The SE Taurus reaches its maximum heights in the Cilo Dağları (4,135 m) near the Iraqi border. Forest destruction is extremely severe in this area, but smaller remnants of dry deciduous oak forests still exist in many valleys in the southern part of this region. Floristic affinities are higher with the adjacent mountainous regions of the neighbouring countries than with the rest of the Taurus. Such a

Photo 7.9 *Liquidambar orientalis*, a living fossil of Tertiary relict swamp forests. This species is endemic to SW Anatolia, Turkey, and Rhodes, Greece (Photographed by Gerhard Pils)

Photo 7.10 *Liquidambar orientalis*, flowers and leaves (Photographed by Gerhard Pils)

"transnational" endemism region with SW Anatolia, NW Iran and N Iraq contains about 500 endemic species, which exceeds by far the other Centres of Diversity in Anatolia as delimited by Mill (1994). Examples of species confined to this extended area are *Pelargonium quercetorum* (in moist oakwoods), *Eryngium thyrsoideum, Papaver curviscapum, Scrophularia kurdica, Acantholimon petuniiflorum, Salvia atropatana* and *Colchicum kurdicum*. Recent maps showing totals of "Turkish endemics" per grid (Kutluk and Aytuğ 2001) seriously disadvantage these central regions of Turkish "Wild Kurdistan", with further negative implications if such biased diversity maps were to be used as a basis for conservation planning, as proposed e.g. by Türe and Böcük (2010). But also by using such an arbitrary delimitation c. 100 species remain as "Turkish" local endemics of the mountains of SE Anatolia. Examples are *Gypsophila hakkiarica, Eryngium bornmuelleri, Crepis hakkarica, Campanula hakkarica, Rhynchocorys kurdica, Galium zabense, Senecio davisii, Allium rhetoreanum* etc.

The NE Anatolian Center of Endemism is centred in the Colchic part of the Euxinic region, where the Pontus rises to its greatest heights in the Kaçkar Dağları (3,932 m). About 160 local species – including a lot of apomictic *Alchemilla* and *Hieracium* microspecies – are endemic to the Turkish sector (Mill 1994). Further >130 species are subendemic as they extend into Georgian territory. The edaphic diversity of this region is rather low, with predominantly igneous rocks. But there is a very steep climatic gradient between northern and southern slopes of the Kaçkar Range. Conditions on the Turkish Black Sea coast are generally very oceanic, becoming particularly moist and cloudy in the Colchic sector east of Ordu. These conditions also remained relatively stable during Pleistocene glaciations, thus enabling the survival of a considerable number of Arcto-Tertiary species (DellaSala 2010). These are typically confined to very humid forest habitats of the Colchis. A very illustrative example is *Quercus pontica*, which is morphologically distinct from the rest of the Turkish oaks. Its nearest relative is *Q. sadleriana*, a local endemic of mountain slopes on the Californian – Oregon border (Denk and Grimm 2010). Two dwarf, evergreen shrublets of the Ericaceae family have similar long-range disjunctions: *Epigaea gaultherioides* (also Georgia), with two related species in Japan und eastern N America, and *Rhodothamnus sessilifolius* (subalpine, endemic) with the only remaining species of this genus in the eastern Alps. Further fairly isolated subendemics of the region are *Picea orientalis, Osmanthus decorus* (Oleaceae), *Pachyphragma macrophylla* (a monotypic Brassicaceae), *Hypericum bupleuroides* (which reaches into Armenia), *Rhododendron smirnovii* (endemic, subalpine) and *Rh. ungernii*. Due to the mesophytic character of the Colchic vegetation, Irano-Turanian genera such as *Astragalus, Cousinia* or *Phlomis* are without local endemics there.

In the Euxinic region west of Ordu the mountains of the coastal ranges do not as a rule surpass timberline and are covered by dense, deciduous forests. Edaphic diversity remains relatively low, with schists or sediments of mainly igneous origin. Centres of local endemism are the Ilgaz Dağları south of Kastamonu (2,587 m) and Uludağ (2,543 m) south of Bursa. Both are in fairly isolated positions within their much lower surroundings. Local endemics are concentrated in treeless habitats, with some exceptions such as *Heracleum paphlagonicum*, growing by mountain streams in mixed forests of the Ilgaz Dağları. From thoroughly explored Uludağ c. 30 local endemic taxa have been described, from Ilgaz Dağları at least 8.

Uludağ is very close to Istanbul province and European Turkey. Landscape here consists of undulating hills, mostly forest covered on the Black Sea side, but transformed into agricultural steppe on the Marmara side. One would not expect any local endemic in such unspectacular scenery. But reality is not that simple in Turkey. *Colchicum micranthum*, whose delicate flowers may be found in deciduous oak forests of the Bosporus area, is endemic here, as is *Cirsium byzantinum*. The latter has a preference for moderately disturbed places, especially dry road margins, thus excluding any major ecological change as a reason for its narrow distribution area.

This holds still more true for *Onosma propontica*, the rarest endemic of the region, whose few known localities are confined to the open hillsides E and NE of Istanbul (with one locality in neighbouring Kirklareli, Baytop 2009). The plant grows here largely disjunct from its supposed closest allies in Ucraina and Dobrutscha, making it quite probable that this is a relict species (Teppner and Tuzlaci 1994).

7.5.5 Edaphic Diversity and Regional Endemism

Ultrabasic bedrocks underlying serpentine soils are distributed over large areas of Anatolia (Fig. 7.6). Their occurrence is always strongly correlated with high levels of local endemism. For instance, in the Balkans about 6 % of the total endemic flora consists of obligate serpentinophytes (Stevanović et al. 2003). Nevertheless, these special habitats have only recently received particular attention in Turkey. One of the best explored serpentine areas is Sandras Dağ (2,294 m) near Köyceğiz on the SW Anatolian coast. Vegetation there consists of open *Pinus brutia* forest on the lower slopes, which is replaced by fine stands of *P. nigra* up to the timberline at c. 2,100 m. Systematic collecting over the last 25 years has revealed a surprisingly high degree of local endemism on this mountain. In this period 15 new taxa have been described from Sandras Dağ, raising the number of local endemics from 9 to 23 (Özhatay and Kültür 2006, Pils ined.). The same applies to the serpentine outcrop of Kızıldağ near the town of Çamlık (Konya province), from where in the last decade 9 new serpentinophytes were described, 7 of which were local endemics (Aytaç and Türkmen 2011; Duran et al. 2011). Unfortunately, no precise data exist on the relative share of serpentinophytes in the endemic flora of the Amanus region, despite some recently published plant lists from the area.

Some genera of Brassicaceae, such as *Alyssum, Aethionema* (both Table 7.5), *Thlaspi, Bornmuellera* and *Cochlearia,* are well known for their resistance to high concentrations of heavy metals. The first three of these developed considerably more species in Turkey than in the whole area of Flora Europaea and are disproportionally rich in local endemics. In *Bornmuellera* (3 sp.) and *Cochlearia* (4 sp.) all Turkish species are endemics. Nickel-hyperaccumulation abilities have recently also been detected in some Turkish *Centaurea* species. This is not really a big surprise, as 15 out of 122 endemic *Centaurea* species are supposed to be restricted to serpentine (Reeves and Adigüzel 2004). Some obligate serpentinophytes are of quite isolated systematic position (e.g. *Eryngium thorifolium, Scorzonera coriacea*), thus indicating rather a long evolution time for the Anatolian serpentine flora.

Continental salt vegetation adds considerably to the floristic diversity of the endorheic basins west of the Anatolian Diagonal. The bottom of the larger of these flat basins is covered by the Big Salt Lake (Tuzgölü), which dries up to a large extent during summer. There are a number of such salty areas in the plains of Konya, Niğde and Kayseri; some of these are occupied by temporary lakes, others are covered with salt steppe. Quite a number of genera from the surrounding steppe flora have evolved local halophytic species. Examples are *Verbascum helianthemoides, V. pyroliforme, Salvia halophila, Ferula halophila, Centaurea halophila, C. tuzgoluensis, Onosma halophila, Saponaria halophila, Scorzonera hieraciifolia, S. tuzgoluensis, Cousinia birandiana, Acantholimon halophilum, Dianthus aydogduii, Taraxacum tuzgoluensis, Senecio salsugineus* and *Astragalus demirizii*. However, typical halophytic genera are also represented here by local endemics, e.g. *Limonium* (*L. anatolicum, L. iconicum, L. lilacinum, L. adilguneri*), *Petrosimonia* (*P. nigdeensis*), *Suaeda* (*S. cucullata*), and *Salsola* (*S. grandis*). Some of these local halophyts are systematically isolated to such an extent that one has to assume an old (Tertiary) origin of these habitats. The best examples are the monotypic genera *Cyathobasis* and *Kalidiopsis* (Chenopodiaceae). Other endemics show interesting long-range disjunctions, e.g. the monotypic genus *Microcnemum* (Chenopodiaceae), with *M. coralloides* ssp. *anatolicum* on very salty soils in central Anatolia and ssp. *coralloides* in Spain, or the ditypic genus *Sphaerophysa* (Fabaceae), with *S. kotschyana* in damp salty places in Central Anatolia and *S. salsula* in Central Asia (Photos 7.11, 7.12, and 7.13).

With inland salt vegetation so rich in local species, one would expect similar conditions on the Turkish coasts, the length of which is comparable to those of Italy. Salt-swamps exist in the deltas of the large rivers discharging into the Mediterranean (Çukurova near Adana, Göksu delta near Silifke and Great Menderes delta south of Izmir). But with the exception of *Tamarix duezenlii*, a very rare shrub of the Çukurova delta with close affinities to *T. arborea* in the southeast Mediterranean, endemism is virtually non-existent there. This is possibly due to the instability of these habitats, with the Mediterranean Sea drying out in the Messinian (c. 5,5 Mill BP.) and repetitive eustatic sea level depressions for at least 100 m during periods of maximum glaciations.

A still more puzzling problem is the uniformity of the halophytic coastal rock flora. To date only one endemic *Limonium* has been described from the Turkish coasts, namely *L. gueneri*, known from a single location near Kaş (SW Anatolia, Doğan et al. 2008). However, there are 102 endemic *Limonium* (micro)species in Italy, nearly exclusively growing in coastal habitats, mainly on rocks (Conti et al. 2005).

The flora of coastal sands is clearly more strongly differentiated. Local endemics of the Çukurova delta are *Medicago* (= *Trigonella*) *halophila, Bromus psam-*

Photo 7.11 *Sphaerophysa kotschyana*, endemic to damp saline habitats in Central Anatolia, Turkey (Photographed by Gerhard Pils)

mophilus and *Silene pompeipolitana. Medicago* (= *Trigonella*) *arenicola* is confined to the Antalya region and *Anthemis ammophila* is more widely distributed on the south coast. On the Black Sea coast huge dune areas existed between Kilyos and Terkos Lake (N. of Istanbul), with an estimated total surface of c. 17.5 km^2 and dunes penetrating up to 5 km into the interior, forming forest-covered hills of up to 30 m altitude (Önal 1981; Özhatay et al. 2003). Most of this area was devastated during the 1970s due to lignite extraction, but on the remaining >4 km^2 the sand flora is still exceptionally diverse, with *Centaurea kilaea*, *Isatis arenaria, Linum tauricum* ssp. *bosphori*, *Erysimum sorgerae* and *Silene sangaria* as local (sub)endemics. An interesting large range disjunction is shown by *Asperula littoralis*, growing on this part of the Black Sea Coast and with slightly different populations also on the Mediterranean coast near Antalya.

Gypsum outcrops are frequent and widespread in the Irano-Turanian part of Anatolia, covering very large areas between Çankırı and Çorum and around Sivas. They are testimonials for a hot and dry climate at the beginning of the Neogene. Remarkable gypsophytes of the Sivas gypsum hills are e.g. *Achillea sintenisii, Allium sivasicum**, *Campanula sivasica*, Centaurea yildizii**, *Chrysocamela noeana*, Isatis sivasica, Gypsophila heteropoda* ssp. *minutiflora**, *Onosma sintenisii, Paronychia galatica*, *Reaumurea sivasica*, Scrophularia gypsicola*, S. lepidota, Scorzonera aucherana, Thesium stellerioides* and *Thymus spathulifolius** (* = only on gypsum,

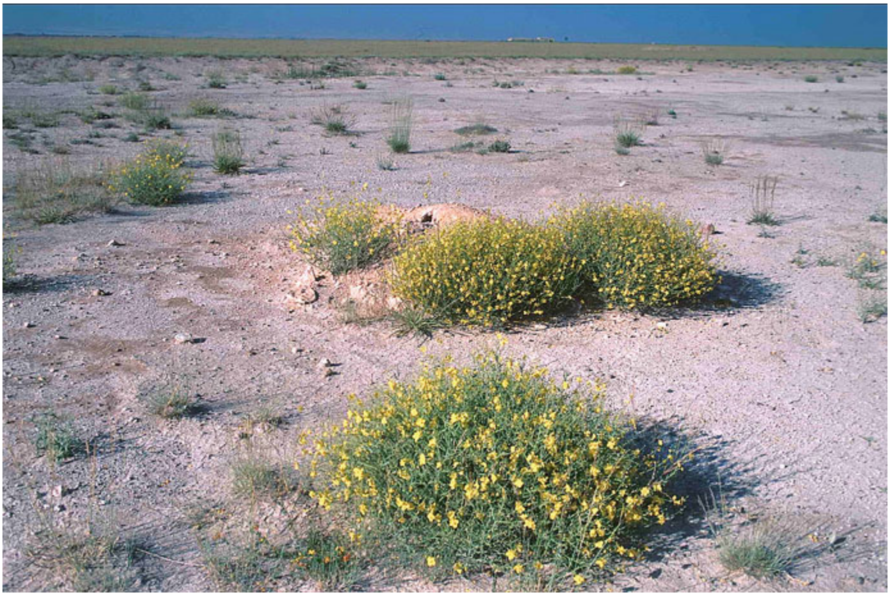

Photo 7.12 Saline inland steppe with *Verbascum helianthemoides* (Photographed by Gerhard Pils)

Photo 7.13 *Verbascum helianthemoides* (Photographed by Gerhard Pils)

Akpulat and Celik 2005). Some of these species are without closer relatives, indicating the high (pre Pleistocene) age of these gypsum habitats.

Neogene marls containing gypsum form large badland areas around Beypazarı (c. 120 km west of Ankara). From these barren hillsides two very local endemics have recently been described: *Verbascum gypsicola*, with a total population of less than 2,000 individuals (Vural 2009), and *Salsola grandis*. The latter grows very locally in some bedland ravines together with *Anabasis aphylla*, which is next found at the Armenian border, and *Petrosimonia nigdeensis*, a central Anatolian endemic (Freitag et al. 1999).

7.6 High Mountain Regions in Iran

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7.6.1 Physical Geography of Mountain Ranges in Iran

Iran with a total surface area of c. 1.6 million km^2 is a typical high mountain country. Almost half the country consists of high elevations, and Alborz and Zagros are the major high mountain chains (Fig. 7.7). The highest mountains are Damavand (5,671 m asl.), Alamkuh (4,850 m), Sabalan (4,810 m), and Hezar (4,465 m). More than 100 mountain peaks exceed 4,000 m.

There are glaciers in the higher elevations, i.e. Damavand, Alamkuh, Sabalan and Zardkuh (Ferrigno 1991). According to Schweizer (1972) the present snowline in Alborz, north and central Zagros, and the NW Iranian mountains lies between 4,000 and 4,200 m. In the mountains of central and southern Iran, e.g. Shirkuh, Dena, and Hezar-Lalehzar Mts. it is between 4,500 and 5,000 m. The higher elevations of Iran have a continental climate with Mediterranean precipitation regime. The annual precipitation in the higher altitudes of Alborz reaches almost 1,000 mm (Khalili 1973).

The alpine habitats are almost above 3,000 m, and are found scattered across different parts of the country (see Fig. 7.7). The Iranian alpine flora is of Irano-Turanian origin (Zohary 1973; Klein 1982, 1991; Frey et al. 1999). A conspicuous feature of this flora is the high rates of endemism. A total of 682 vascular plant species are known from alpine habitats of Iranian mountains, and of this total 394 species are endemic or subendemic to Iran (Noroozi et al. 2008). These habitats are less known, and plant species are still being discovered and described as new to

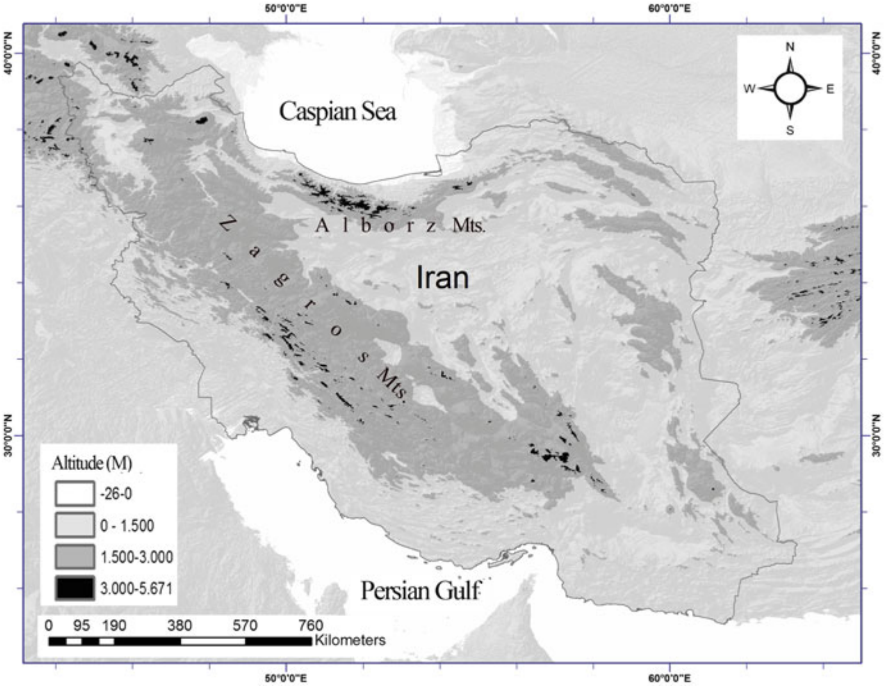

Fig. 7.7 Alborz and Zagros are the major mountain chains of Iran. The alpine habitats (*black spots*) are scattered around different parts of the country

science (e.g. Jamzad 2006; Khassanov et al. 2006; Noroozi et al. 2010a; Noroozi and Ajani 2013; Razyfard et al. 2011).

Several different vegetation types are found in the high regions of Iran. The dry slopes of the subalpine zone are usually covered with tall herbs and umbelliferous vegetation types (Klein 1987, 1988). Small patches of subalpine wetlands are found scattered on dry slopes (Naqinezhad et al. 2010). Thorn-cushion grasslands occur in alpine meadow and windswept areas, and snowbed vegetation types in snow patches or snow melting runnels (Klein 1982; Noroozi et al. 2010b). Scree vegetation types with sparse vegetation cover occupy high alpine and subnival steep slopes with a high percentage of screes and stones on the ground (Klein and Lacoste 2001; Noroozi et al. 2013).

7.6.2 Analysis of Floras and Phytosociological Investigation

To select the local endemic species, the Flora Iranica (Rechinger 1963–2012) and Flora of Iran (Assadi et al. 1988–2012) were used as the main sources.

The main data on endemism in alpine habitats of Iran and the percentage of endemism in alpine and subnival-nival zones were extracted from Klein (1991), Hedge and Wendelbo (1978) and Noroozi et al. (2008, 2011).

The rate of endemism in different habitats is based on phytosociological vegetation studies of the author in Central Alborz. This rate is measured from all character species which were recorded for each habitat. Some species which were characteristic for two different habitats were separately calculated for both habitats. For example *Astragalus macrosemius* is a character species for alpine thorn-cushion grasslands and alpine-subnival scree grounds and was thus counted separately for both habitats as a character species.

7.6.3 Endemism in Different High Mountain Areas and Habitats

Three monotypic genera are found exclusively within Iranian alpine habitats, *Elburzia* in Central Alborz (Hedge 1969), *Sclerochorton* in northern Zagros (Rechinger 1987), and *Zerdana* in central, south and southeastern Zagros (Rechinger 1968). There are also some interesting ditypic genera in these habitats, such as *Clastopus* with two species endemic to Iran (Hedge and Wendelbo 1978), *Didymophysa* with one species occurring in Iran and Transcaucasus, and another one in central Asia and Hindukush (Hedge 1968), and *Dielsiocharis* with one endemic species in Iran (Hedge 1968) and one local endemic in central Asia (Al-Shehbaz and Junussov 2003). All the above-mentioned genera belong to the Brassicaceae except *Sclerochorton*, which belongs to Apiaceae. The author has only seen *Zerdana, Clastopus* and *Didymophysa* in the wild, and all of these are restricted to scree habitats.

A total of 110 vascular plant species were considered to be rare and narrow endemic to Iranian alpine habitats and have only been recorded from one or very few locations. These species are found in Zagros, Alborz, and in the northwestern part of the country (Sahand and Sabalan Mts.). They are classified into four mountainous regions as below:

Rare species in Alborz:
Alchemilla amardica, A. rechingeri, Allium tuchalense, Astragalus aestivorum, A. herbertii, A. montis-varvashti, A. nezva-montis, Cousinia decumbens, C. harazensis, *Diplotaenia damavandica, Elburzia fenestrata, Erodium dimorphum, Festuca rechingeri, Galium delicatulum, Iranecio oligolepis, Myopordon damavandica, M. hyrcanum, Nepeta allotria, N. pogonosperma, Oxytropis aellenii, O. cinerea, O. takhti-soleimanii, Paraquilegia caespitosa, Phlomis ghilanensis, Saxifraga koelzii, S. ramsarica, S. iranica, Scorzonera xylobasia, Scutellaria glechomoides, Senecio iranicus, Silene demawendica, Thlaspi maassoumi, Trachydium eriocarpum, Veronica euphrasiifolia, V. paederotae, Vicia aucheri.*

Rare species in the mountains of northwestern Iran:
Astragalus azizii, A. pauperiflorus, A. savellanicus, Dianthus seidlitzii, Euphorbia sahendi, Festuca sabalanica, Nepeta sahandica, Ranunculus renzii, R. sabalanicus, Thlaspi tenue.

Rare species in north, central and southern Zagros (from Kordestan to Fars provinces):
Acantholimon eschkerense, Allium mahneshanense, Arenaria minutissima, Astragalus mahneshanensis, A. montis-parrowii, Bufonia micrantha, Chaerophyllum nivale, Cicer stapfianum, Cousinia concinna, C. eburnea, Crepis connexa, Cyclotrichium straussii, Dianthus elymaiticus, Dionysia aubrietioides, D. iranshahrii, Dracocephalum surmandinum, Erysimum frigidum, Euphorbia plebeia, Festuca iranica, Galium schoenbeck-temesyae, Jurinea viciosoi, Myopordon aucheri, Nepeta archibaldii, N. chionophila, N. iranshahrii, N. monocephala, N. natanzensis, Potentilla flaccida, Psychrogeton chionophilus, Ranunculus dalechanensis, Salvia lachnocalyx, Satureja kallarica, Sclerochorton haussknechtii, Scorzonera nivalis, Scrophularia flava, Senecio kotschyanus, Seratula melanocheila, Silene hirticalyx, Tragopogon erostris, Veronica daranica.

Rare species in southeastern Zagros (mountains of Yazd, Kerman and Baluchestan provinces):
Acantholimon haesarense, A. kermanense, A. nigricans, A. sirchense, Allium lalesaricum, Astragalus hezarensis, A. melanocalyx, A. pseudojohannis, Chaenorhinum grossecostatum, Cousinia fragilis, Dionysia curviflora, Helichrysum davisianum, Hymenocrater yazdianus, Hyoscyamus malekianus, Nepeta asterotricha, N. bornmulleri, N. rivularis, Polygonum spinosum, Rubia caramanica, Senecio eligulatus, S. subnivalis, Silene dschuparensis, Verbascum carmanicumm.

Since alpine habitats have been less well investigated than lower elevations, our knowledge about the distribution range of species living in high mountain regions is low. This means that it is more likely that new explorations at these elevations will produce new records and localities for local endemics. Nonetheless, the above mentioned species are rare, with narrow geographical and altitudinal distribution. Most of the above-mentioned species can be categorised as Endangered (EN) and Critically Endangered (CR) according to IUCN Red List criteria. However, more field studies are needed to clarify this. Some of these species are only known from type specimens. For instance, *Sclerochorton haussknechtii* has not been found for 140 years, since it was first collected. This could be because the species has become extinct in the wild or, more likely, because of a lack of information due to a scarcity of field investigations.

Based on the vegetation data of the author from Central Alborz, the highest rate of endemism occurs in alpine-subnival scree grounds (60 % taxa), followed by alpine thorn-cushion grasslands (49 % taxa), subalpine dry slopes covered with umbelliferous vegetation types (41 % taxa), alpine snowbeds (36 % taxa) and subalpine wetlands (6 % taxa).

Photo 7.14 *Astragalus macrosemius* (3,700 m) in Central Alborz with Mt. Damavand (5,671 m) in the background (Photographed by Noroozi)

Examples for endemics adapted to alpine-subnival scree grounds are: *Asperula glomerata* subsp. *bracteata, Astragalus capito, Cicer tragacanthoides, Clastopus vestitus, Crepis heterotricha, Dracocephalum aucheri, Galium aucheri, Jurinella frigida, Leonurus cardiaca* ssp. *persicus*, *Nepeta racemosa, Scutellaria glechomoides, Senecio vulcanicus, Veronica paederotae, Veronica aucheri* and *Ziziphora clinopodioides* subsp. *elbursensis.*

Examples for endemics which occur in alpine thorn-cushion grasslands are: *Acantholimon demawendicum, Allium tuchalense, Astragalus chrysanthus, A. iodotropis, A. macrosemius* (Photo 7.14), *Bufonia kotschyana, Cousinia crispa, Draba pulchella, Minuartia lineata, Oxytropis persicus, Scorzonera meyeri, Silene marschallii, Tragopogon kotschyi* and *Veronica kurdica.*

Examples of endemics which inhabit subalpine dry slopes covered with umbelliferous vegetation are: *Aethionema stenopterum, Allium derderianum, A. elburzense, Astragalus aegobromus, Cousinia adenosticta, C. hypoleuca, Echinops elbursensis, Galium megalanthum, Iris barnumae, Parlatoria rostrata, Ranunculus elbursensis* and *Rumex elbursensis.*

Examples of endemic taxa of alpine snowbeds are: *Cerastium persicum, Erigeron uniflorus* ssp. *elbursensis, Potentilla aucheriana* and *Ranunculus crymophylus.*

An example of endemics of subalpine wetlands is *Ligularia persica.*

According to Naqinezhad et al. (2010), of 323 vascular plant species recorded for the wetland flora on the southern slopes of Alborz, only 7 % are endemic and subendemic to Iran, which is consistent with our local findings. This rate of endemism is very low in comparison to other high-elevation habitats in Iranian mountains.

The percentage of endemic species for the true subnival-nival flora is 68 % (Noroozi et al. 2011), and for alpine habitats (including the subnival-nival zone) 58 % (Noroozi et al. 2008). This rate is much higher than that for the entire Iranian flora (24 %, Akhani 2006). It means that c. 23 % of Iranian endemics are concentrated in alpine habitats, suggesting that the alpine zone can be considered one of the centres of endemism. Most studies on plant biodiversity of Iranian mountains demonstrate that the proportion of narrowly distributed plant species increases consistently from low to high elevations (Klein 1991; Noroozi et al. 2008, 2011; Naqinezhad et al. 2009, 2010; Kamrani et al. 2011).

The major factors increasing the extinction risk for geographically restricted alpine species of Iran could be climate change and overgrazing. The evidence of global warming impacts on the upward shift of plant species has been demonstrated for European mountains (e.g., Grabherr et al. 1994; Walther et al. 2005; Gottfried et al. 2012; Pauli et al. 2012). The persistence of the unique cryophilic flora of Iran would be seriously threatened under the impact of ongoing global warming where the potential to migrate to appropriate habitats is very limited (Noroozi et al. 2011).

High elevations in Iran have been used as summer pastures, and overgrazing is very severe in these habitats. Thus, the high mountain flora and vegetation are seriously disturbed (personal observation).

Since alpine habitats are floristically less well researched, we have insufficient knowledge about the habitats of rare species in the various mountain ranges. We thus strongly recommend more field exploration of high mountain areas to determine the ecology, biology and conservation status of local endemics according to IUCN criteria, and to improve the protection status of the country's high mountain flora and vegetation.

7.7 The Role of Edaphic Substrate Versus Moisture Availability in Montane Endemic Plant Distribution Patterns – Evidence from the Cape Midlands Escarpment, South Africa

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7.7.1 *Introduction: Physical Geography and Biodiversity of the Great Escarpment*

7.7.1.1 The Great Escarpment of Southern Africa

Southern Africa's macro-topography – in the simplest terms – consists of a raised, centrally dipped interior (part of the extensive African Erosion Surface, Burke and Gunnell 2008) separated from a skirting coastal plain by a steep drop-off (Partridge and Maud 1987; McCarthy and Rubidge 2005). The interior forms a saucer in cross-section, with the rim – running parallel to the coastline – forming the highest regions. This rim is generally known as the 'Great Escarpment' (Partridge and Maud 1987; Gilchrist et al. 1994; Kooi and Beaumont 1994; McCarthy and Rubidge 2005; Moore et al. 2009) and can be taken as occurring from Angola southwards through Namibia to South Africa and east and north up through Lesotho and Swaziland into eastern Zimbabwe and adjacent Mozambique (Clark et al. 2011d, Fig. 7.8). While debates on definitions, delimitations, origins and age are numerous (Birkenhauer 1991; Gilchrist et al. 1994; Matmon et al. 2002; McCarthy and Rubidge 2005; Moore and Blenkinsop 2006; Burke and Gunnell 2008), the Escarpment's effect on biodiversity has been consistent: a series of uplands and mountains with significant endemism in both plants and animals (Stuckenberg 1962; Huntley and Matos 1994; Van Wyk and Smith 2001; Steenkamp et al. 2005; Clark et al. 2011d).

7.7.1.2 The Cape Midlands Escarpment

A portion of the Great Escarpment is the Cape Midlands Escarpment, located in the Eastern Cape Province of South Africa, between 31°–32°30′S and 24°–27°E (Figs. 7.8 and 7.9). Because of deep inland incursion by the Great Fish and Great Kei River systems, through headward erosion, the Cape Midlands Escarpment is comprised of three mountain blocks: the Sneeuberg ('Snow Mountains' – 'berg' refers to 'mountain' in South Africa; Clark et al. 2009 provide a detailed overview of the Sneeuberg), the Great Winterberg–Amatolas (GWA, detailed overview in prep.), and the Stormberg (Photo 7.15a–e). The Cape Midlands Escarpment is unique in the context of the total Escarpment in that it forms a roughly circular band of mountains (rather than simply linear) bounding a large inselberg-studded plain formed from the inland advance of the Great Fish River. This Cape Midlands Basin (Photo 7.15f) is some 100 km wide and as long, while the mountains cover a total area of approximately 31,500 km^2. Although not high by world standards, the Cape Midlands Escarpment reaches reasonable heights by southern African standards: the highest peak is the Compassberg (2,504 m), followed by the Nardousberg (2,429 m – see Fig. 7.11 and Photo 7.20f), both in the Sneeuberg, and then by the Great Winterberg peak (2,369 m), in the GWA. Several other peaks in the Sneeuberg and GWA rise above 2,200 m, while the highest peak in the Stormberg is the Aasvoëlberg ('Vulture Mountain', 2,207 m). Large upland plateaux occur between

Fig. 7.8 The Great Escarpment of southern Africa (indicated by the *grey line*)

1,700 and 2,100 m. The base of the mountains varies between ca. 900 m on the coastward side to ca. 1,200 m on the inland side.

7.7.1.3 Geology and Geomorphology

The geology of the Cape Midlands Escarpment is fairly simple, mostly consisting of the arenaceous and argillaceous sediments of the Beaufort Group (Karoo Supergroup, Photo 7.16a, b, f) massively intruded by Jurassic-era Dolerites (Hill 1993; Johnson et al. 2006; Van Zijl 2006, Photo 7.16c–e). The central and eastern parts of the Stormberg are dominated by Molteno sandstones and capped sporadically by Drakensberg basalts (Johnson et al. 2006); these are excluded from the study area in favour of the western Stormberg, which has the same geology as the Sneeuberg and GWA.

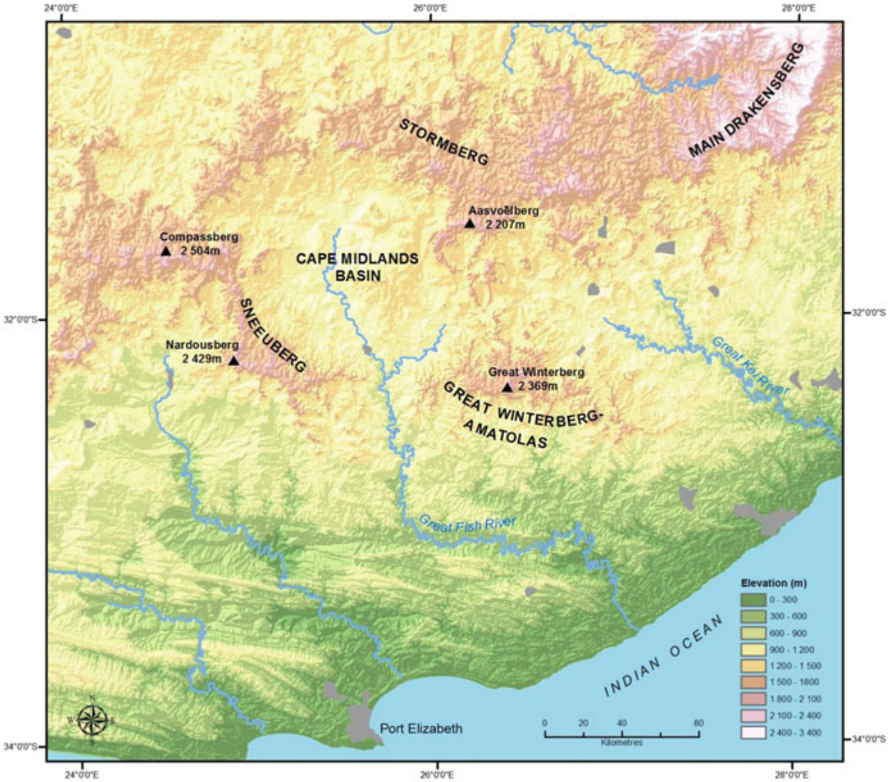

Fig. 7.9 The Cape Midlands Escarpment, South Africa

While finer details in the Karoo stratigraphy vary between the mountain blocks (Johnson et al. 2006), the general landscape features are similar: layered horizontal sediments (Photo 7.16j) intruded by dolerite either as near-vertical sill cappings (e.g. the Great Winterberg peak and the Hogsbacks) or steeply inclined sheets (e.g. the Compassberg and Nardousberg, Photo 7.16i). Throughout these mountains dolerite is the most important rock geomorphologically: while dolerite denudes rapidly in the moister eastern parts of South Africa (Brink 1983), in the drier Cape Midlands Escarpment it is much less susceptible to denudation than the Karoo sediments and has almost invariably formed the highest peaks and plateaux (Du Toit 1920; Agnew 1958; Partridge and Maud 1987, Photo 7.16k, l). Consequently almost all of the highest peaks are doleritic (Agnew 1958; Phillipson 1987; Clark et al. 2009).

7.7.1.4 Soils

Soils arising in mountainous areas differ according to *inter alia* parent material, altitude, moisture availability, mechanical processes, aspect, vegetation cover and

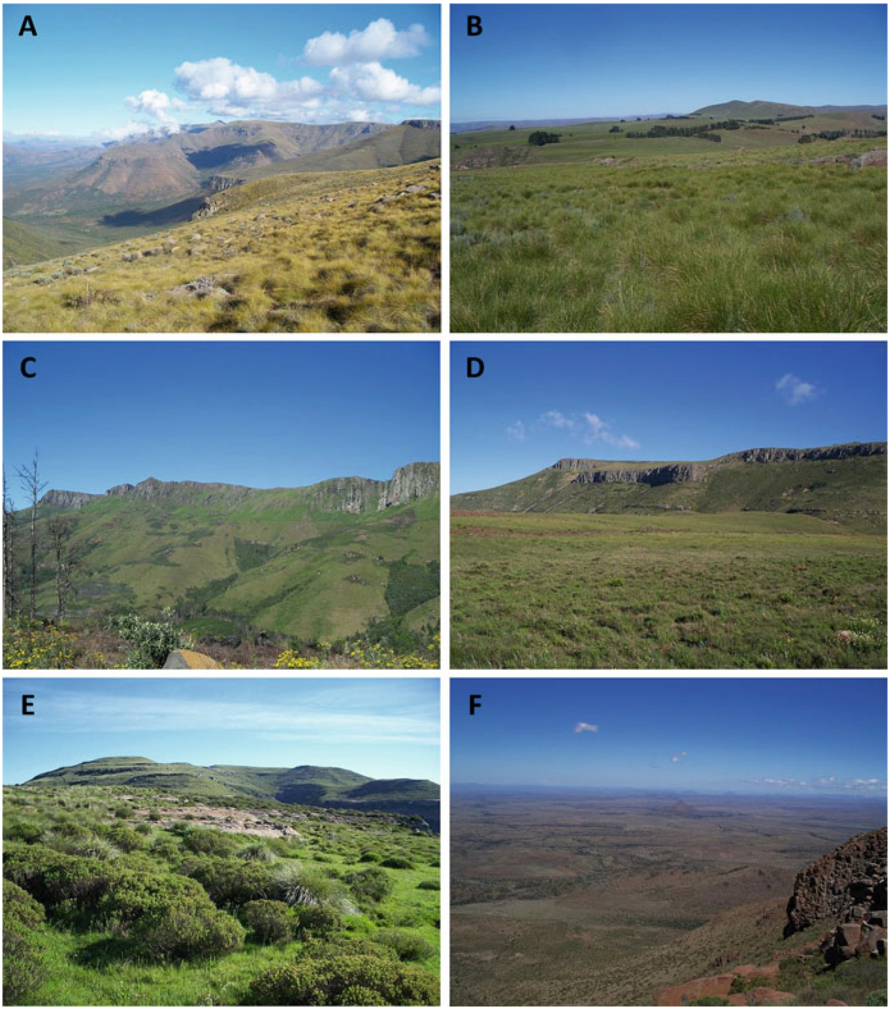

Photo 7.15 Representative photographs of the Cape Midlands Escarpment, Eastern Cape, South Africa. (**a**) The Nardousberg area, Sneeuberg, taken from an altitude of ca. 2,100 m, looking west, (**b**) The Great Winterberg plateau, ca. 1,700 m, west of the main Great Winterberg peak, Great Winterberg–Amatolas (GWA), (**c**) The Didima Range, with the Katberg on the far right, taken from Katberg Pass, GWA, (**d**) A view towards Aasvoëlberg, Stormberg, taken from the first plateau at 1,900 m, (**e**) The Bamboesberge on the farm 'Bamboeshoek', Stormberg, taken from the plateau at 1,900 m, (**f**) The Cape Midlands Basin as viewed looking east from the Wapadsberg, Sneeuberg (Photographed by V.R. Clark)

slope steepness (Macvicar et al. 1977; Laffan et al. 1998; Turner 2000; Burke 2002; Osok and Doyle 2004, etc.). It should be noted that while sandstone is less resistant to denudation on a landscape level – and therefore forms softer landforms – dolerite, although harder, produces better soil. Thus in the Cape Midlands Escarpment,

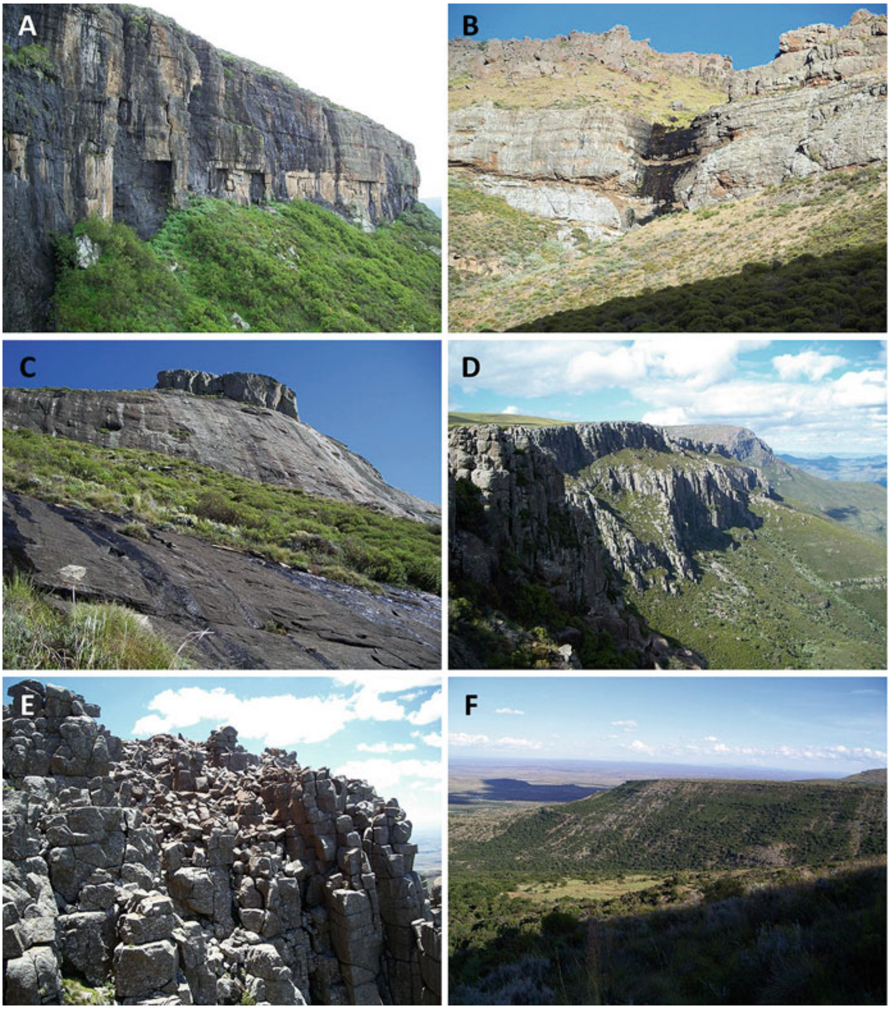

Photo 7.16 Typical sedimentary and igneous landforms in the Cape Midlands Escarpment. (**a**) Sandstone cliffs in the Toorberg, Sneeuberg, (**b**) Metamorphic sedimentary cliffs capped with dolerite, western slopes of the Koudeveldberge, Sneeuberg, (**c**) A dolerite batholith forming part of the Blinkberg, Sneeuberg, (**d**) A massive dolerite sill outcropping on the eastern edge of the Toorberg plateau, Sneeuberg, (**e**) Jointed, columnar dolerite forming the eastern ramparts of the main Wapadsberg, Sneeuberg, (**f**) A sedimentary spur off the Kamdebooberge, Sneeuberg, consisting largely of shale (note the poor vegetation cover), (**g**) The northern summit area of the Blinkberg, Sneeuberg, consisting of flat, shattered sandstone, (**h**) The summit plateau of the Schurfteberg, Sneeuberg, consisting of small dolerite boulders, (**i**) Dolerite sills forming typical cuesta-shaped hills in the Kikvorsberge, Sneeuberg, (**j**) Deep fluvial incision of harder sandstones forming Fenella Gorge, GWA, (**k**) A rounded sandstone hill resulting from the absence of a protective dolerite capping, taken from the nearby dolerite-capped Oppermanskop, Kikvorsberge, Sneeuberg, (**l**) A rounded sandstone and shale hill resulting from the absence of a protective dolerite capping, compared to the angular, flat-topped dolerite sill-capped plateau behind, Kamdebooberge, Sneeuberg (Photographed by V.R. Clark)

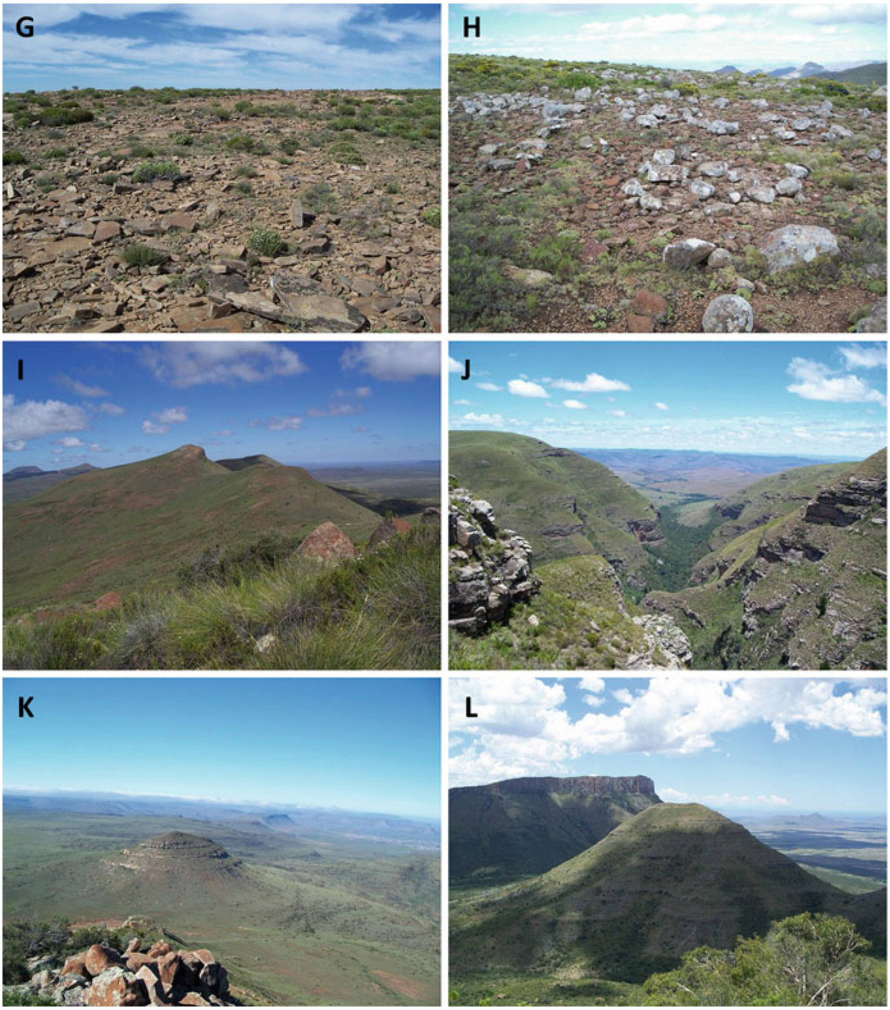

Photo 7.16 (continued)

dolerite tends to form better soils than any other substrate, forming shallow reddish loamy-clays to deeper black turf clays (Turner 2000; Clark 2010, Photo 7.17a–c). Sandstone soils on summit plateaux are generally either almost non-existent (Photo 7.16g), to poorly developed in the drier (<700 mm per annum, e.g. Sneeuberg) mountains (Photo 7.17d, e), to fairly well developed and often indistinguishable from dolerite soils in moister mountains (>700 mm per annum, e.g. on the GWA and Stormberg scarp and summit). Soils on steep slopes are typically a mixture of regolith and occasional large boulders from various parent substrates (Turner 2000). A humus-rich colluvium develops on wetter slopes where the vegetation has stabilised the loose material, and deep colluvial soils are formed on gentler slopes

(Osok and Doyle 2004, Photo 7.17g). Shale generally provides no soil, and simply weathers to a purple-grey gravel locally called ‘gruis’ (Photo 7.16f). Metamorphic sandstone (‘baked’ from contact with intruded dolerites) behaves much like shale and very little or no soil is formed. Extensive wetlands in upland areas generally host deep, humus-rich clay soils regardless of parent substrate (Photo 7.17h, i), and deep alluvial deposits occur along more permanent streams (Photo 7.17f).

7.7.1.5 Climate

A steep moisture gradient exists from south to north across each of these mountain blocks: the southern slopes and adjacent plateaux are the wettest, receiving between ca. 700 mm to in excess of 1,000 mm rainfall per annum (Phillipson 1987; Hoare and Bredenkamp 1999; Clark et al. 2009, 2011e). The northern slopes in contrast are much drier (down to ca. 400 mm), and rainfall quickly diminishes away from the south-facing scarps (Clark et al. 2011e, unpublished data). The combination of high altitude and exposure to frequent mid-latitude cyclones renders the mountains vulnerable to regular snowfalls, especially in winter (Phillipson 1987; Clark et al. 2009, 2011e).

7.7.1.6 Vegetation and Endemism

The vegetation of the Cape Midlands Escarpment is primarily montane vegetation consisting of upland grassland, azonal fynbos (the African version of heathland, consisting of temperate ‘Cape elements’, Levyns 1964; Oliver et al. 1983; Linder 1990; Carbutt and Edwards 2001; Galley et al. 2007; Devos et al. 2010, etc.), wetlands, scarp forest, mesic woodlands and sub-tropical thicket in a matrix of lower-altitude, arid Nama-Karoo (a shrubby semi-desert vegetation type common in the arid central-west of South Africa) and *Acacia karroo* Hayne (=*Vachellia karroo* (Hayne) Banfi & Galasso) savannoid grassland (Cook sine anno; Phillipson 1987; Palmer 1988, 1990, 1991; Mucina and Rutherford 2006; Clark et al. 2009, 2011a). Four biomes are represented on these mountains: Grassland (here including azonal fynbos as opposed to the Fynbos Biome of the Cape Floristic Region), Forest, Sub-tropical Thicket, and Nama-Karoo (Mucina and Rutherford 2006; Clark et al. 2011e).

Local plant endemism in the Cape Midlands Escarpment is high, with a current total of 88 endemic taxa (Fig. 7.10, Photos 7.18 and 7.19). Currently, the GWA has the highest number of local endemics, followed by the Sneeuberg, while a similar number is shared by all three mountain blocks. The Sneeuberg was recently described as a centre of floristic endemism (Clark et al. 2009), and based on the same standards the GWA deserves the same recognition (in prep.). The comparable number of shared endemics however suggests a case for resurrecting the old concept of a combined centre comprising all three mountain blocks, as originally described by Nordenstam (1969). Future work on the Stormberg – the

Photo 7.17 Representative soil profiles in the Cape Midlands Escarpment. (**a**–**c**) Dolerite-derived soils, Bankberg, Sneeuberg – note the well-developed A horizons on saprolite, and the presence of near-surface rocks from either gravitational slope processes (in **b**), or as core stones (in **c**), (**d**–**e**) Shallow, rocky soils on sandstone/sandstone-dolerite colluvium, Nardousberg area, Sneeuberg, (**f**) Stratified alluvial deposits along a stream-line at the base of the Blinkberg, Sneeuberg, (**g**) Deep colluvial deposits along an eroded stream-line at the base of the Blinkberg, Sneeuberg, (**h**–**i**) Black turf clays in two upland valley wetland systems: Blinkberg, Sneeuberg (**h**), and near the base of the Great Winterberg peak, GWA (**i**) (Photographed by V.R. Clark)

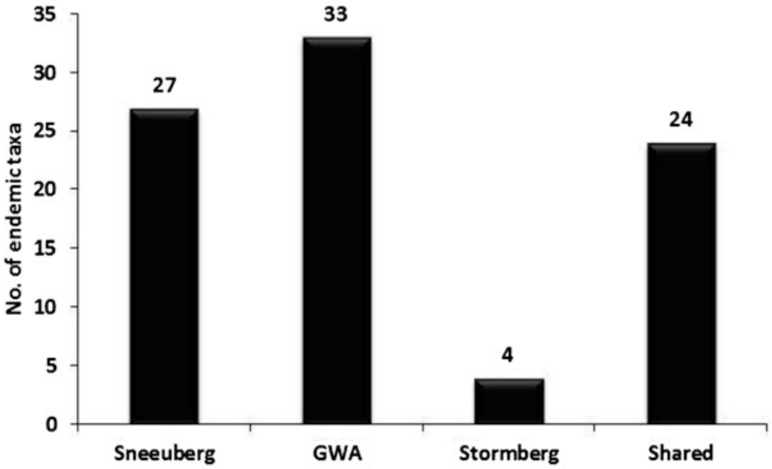

Fig. 7.10 Plant endemism in the Cape Midlands Escarpment

least well-researched mountain block, with only four known local endemics – will allow a more quantitative assessment in this regard. With approximately nine species new to science having been discovered since 2005 (Goldblatt and Manning 2007; Clark et al. 2009; Nordenstam et al. 2009; Stirton et al. 2011), the total number of Cape Midlands Escarpment endemics is likely to increase as research in these poorly explored mountains continues.

Extra-Cape Midlands phytogeographical links are mostly with the eastern Escarpment (particularly the high Drakensberg-Maluti system), west along the southern Escarpment (particularly with the Nuweveldberge), with the Albany Centre of Endemism, and loosely with the Cape Floristic Region (Cook *sine anno*, Phillipson 1987; Van Wyk and Smith 2001; Carbutt and Edwards 2006; Clark et al. 2009, 2011a, c, e).

7.7.2 Aims and Hypothesis

While the role of edaphic substrate is known to be a key player in plant speciation and ecology the world over, and no less so in South Africa (Matthews et al. 1991; Balkwill and Balkwill 1999; Carbutt and Edwards 2001; Siebert et al. 2001; Van Wyk and Smith 2001; Mucina and Rutherford 2006, etc.), this has not been explored in detail as a factor in local endemism in the Cape Midlands Escarpment, with its mosaic of sedimentary and igneous substrates. Although both dolerite and sandstone substrates are known to be rich in local endemics in other parts of southern Africa (e.g. the Hantam region, Western Cape, for dolerite endemics, and the Pondoland region, Eastern Cape, for sandstone endemics, Van Wyk and Smith 2001), this doesn't necessarily take into account the role of moisture availability in these areas (Bergh et al. 2007). The aim of this study is thus to determine

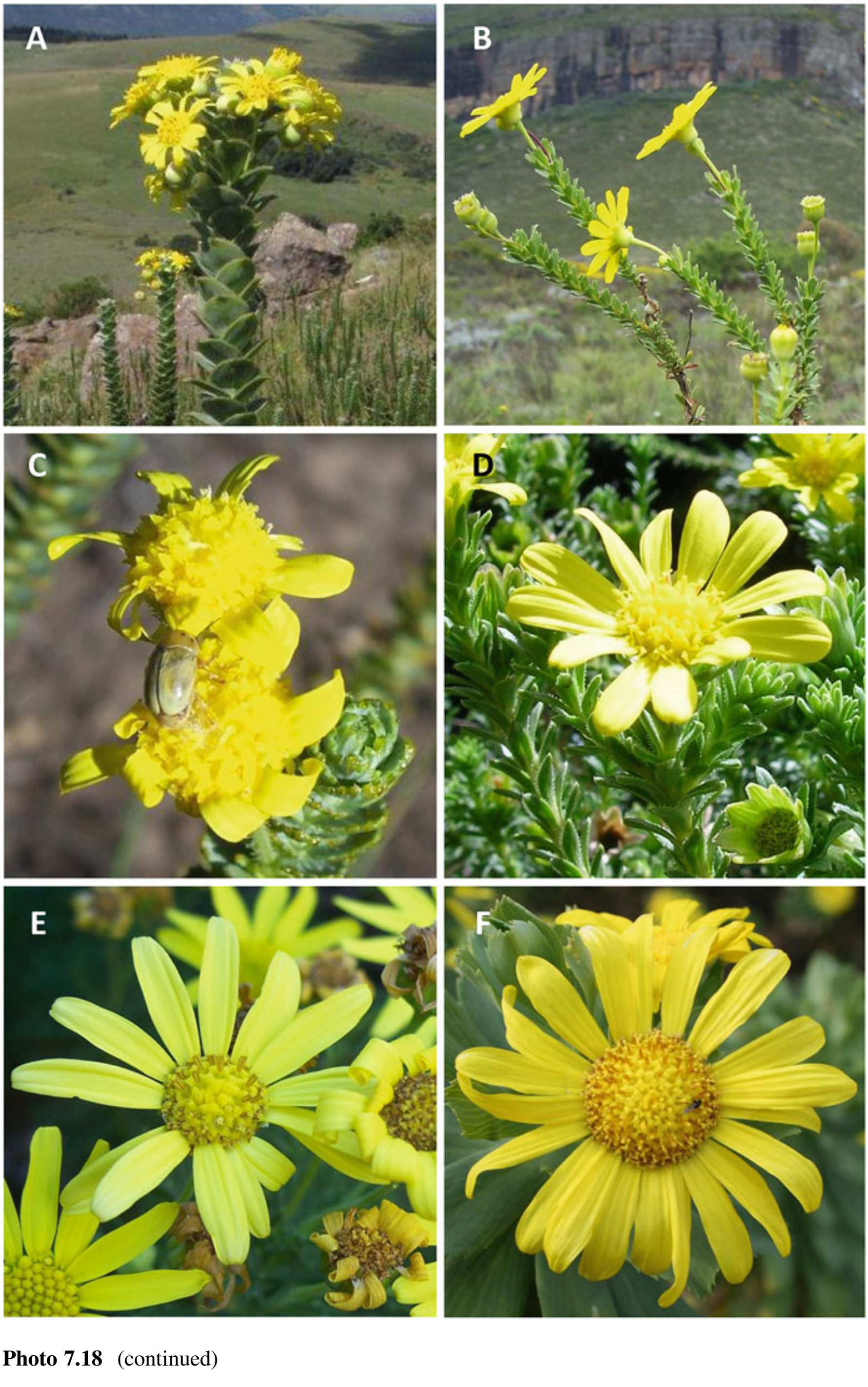

Photo 7.18 (continued)

if edaphic substrate plays a primary role in the distribution of endemics in the Cape Midlands Escarpment, or if moisture availability (represented by altitude and primary vegetation habitat as proxies, given an absence of fine-scale climate data) is a more important determining factor in their distributions (Clark et al. 2011b, c, e). We also include primary geomorphological niche as a characteristic, to determine if there are patterns in niche specialisation by endemic taxa.

We hypothesise that edaphic factors do not play a major role in the distribution of endemics, and that moisture availability plays the dominant role. The Cape Midlands Escarpment is a good region in which to examine this issue, as there are large areas dominated by both sedimentary and dolerite substrates at all altitudes and in all local moisture regimes, and the basic geology is consistent throughout the study area. Furthermore, the soils present are predominantly lithosols arising from *in situ* weathering: they are thus less likely to be contaminated by movement of soils from slope processes, except on steeper slopes where soil movement from gravitational processes is prevalent.

7.7.3 Methods

7.7.3.1 Selection of Endemic Taxa

The Cape Midlands Escarpment has been part of the focus of a detailed and intensive floristic study on the southern Great Escarpment since 2005 (Clark 2010; Clark et al. 2009, 2011a, b, c, e), resulting in ca. 13,000 herbarium specimens and field notes with detailed ecological data. Edaphic, lower altitude limit, primary vegetation habitat and primary geomorphological niche data were collated for 50 of the endemic taxa from this data and supplemented where necessary from available published sources. The necessary data for the other 38 endemic taxa is currently incomplete or unavailable. Four typical Cape Midlands Escarpment 'endemics' (*Ficinia compasbergensis* Drège, *Helichrysum tysonii* Hilliard, *Lessertia sneeuwbergensis* Germish. and *Ruschia complanata* L. Bolus) are now also known from the Nuweveldberge (Clark et al. 2011c) and have been excluded from this study. We have however kept *Indigofera elandsbergensis* Phillipson in the study even though there is one outlier recorded in the Main Drakensberg (Phillipson 1992).

◄

Photo 7.18 (continued) A photographic selection of plant taxa endemic to the Cape Midlands Escarpment – Part 1: A world of *Euryops* (Asteraceae). (**a**) *E. ciliatus* B. Nord. – endemic to the Great Winterberg–Amatolas (GWA), (**b**) *E. dentatus* B. Nord. – endemic to the Sneeuberg, (**c**) *E. exsudans* B. Nord. & V.R. Clark – endemic to the Sneeuberg (discovered in 2005), (**d**) *E. galpinii* Bolus – endemic to the Sneeuberg, GWA and Stormberg, (**e**) *E. trilobus* Harv. – endemic to the Sneeuberg and Stormberg, (**f**) *E. proteoides* B. Nord. & V.R. Clark – endemic to the Sneeuberg (discovered in 2005) (Photographed by V.R. Clark, except for (**a**), Nick Helme)

Photo 7.19 A photographic selection of plant taxa endemic to the Cape Midlands Escarpment – Part 2: Other colours of endemism. (**a**) *Crassula exilis* ssp. *cooperi* (Regal) Tölken – endemic to the Sneeuberg, Great Winterberg–Amatolas (GWA) and Stormberg, (**b**) *Delosperma dyeri* L. Bolus – endemic to the Sneeuberg and GWA, (**c**) *Erica* sp. aff. *reenensis* Zahlbr. – endemic to the Sneeuberg and GWA (yet to be photographed at maturity), (**d**) *Gazania caespitosa* Bolus – endemic to the Sneeuberg, (**e**) *Garuleum tanacetifolium* (MacOwan) Norl. – endemic to the Sneeuberg and GWA, (**f**) *Geranium grandistipulatum* Hilliard & B.L. Burtt – endemic to the GWA, (**g**) *Psoralea margaretiflora* C.H. Stirt. & V.R. Clark – endemic to the Sneeuberg (discovered in 2005) (Photographed by V.R. Clark)

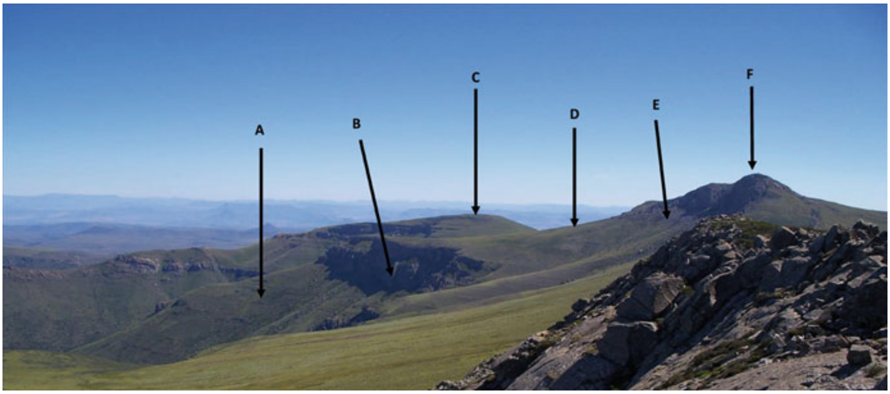

Fig. 7.11 Principal geomorphological habitat niches in the Cape Midlands Escarpment. (*A*) Moist scarp, (*B*) Cliffs, (*C*) Plateau, (*D*) Upland slope, (*E*) High scree, (*F*) High peak (Photo: V.R. Clark (Nardousberg, Sneeuberg))

7.7.3.2 Edaphic Substrate

Edaphic substrate options were reduced to two main categories, namely dolerite and sandstone. Sandstone is used here to include metamorphic rocks found along contact zones with dolerites. Shale was excluded from this study as it generally supports little vegetation in the study area. An attempt to classify soil types binomially (as per Macvicar et al. 1977) was not made given the complicated and often inaccurate results without specialist assistance.

7.7.3.3 Altitude

Lower limit altitude refers to the lowest altitude from which a taxon has been recorded.

7.7.3.4 Primary Vegetation Habitat

Because of the complexity of vegetation types in these mountains, primary vegetation habitats were simplified into Open and Closed Habitats:

Open Habitats: namely Montane Grassland (including azonal montane fynbos, wetlands and shrublands) and Nama-Karoo.

Closed Habitats: a lumping of the intergrading and inter-digitating varieties of woodland, thicket and forest that grade into each other with aspect and altitude.

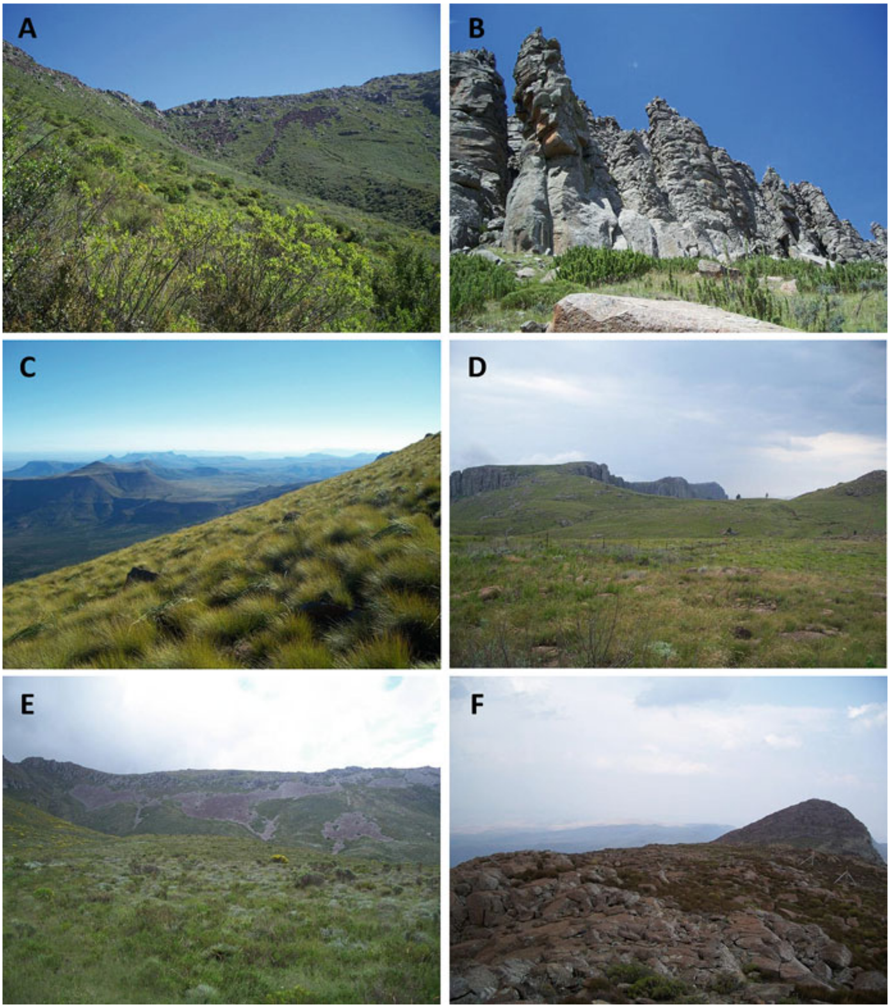

Photo 7.20 Geomorphological habitat niches. (**a**) Moist scarp (Koudeveldberge, Sneeuberg), (**b**) Cliffs (Great Winterberg peak, Great Winterberg–Amatolas (GWA)), (**c**) Upland slope (Nardousberg area, Sneeuberg), (**d**) Plateau (Didima Range, GWA), (**e**) High scree (Koudeveldberge, Sneeuberg), (**f**) High Peak (Nardousberg) (Photographed by V.R. Clark)

7.7.3.5 Primary Geomorphological Niche

Primary geomorphological niche refers to the typical physical location of a taxon on the characteristic topography of the Cape Midlands Escarpment (Fig. 7.11, Photo 7.20). Although the three mountain blocks have distinct features unique to themselves (and various local differences within them), there is a common basic geomorphological theme. A conservative approach was adopted, with taxa placed in their least specialised niche if they occur in more than one (e.g. a taxon occurring in both Plateaux and High Peaks was placed under Plateaux).

Moist Scarps are those south- and south-east-facing slopes from the base of the Escarpment to generally the first line of cliffs. 'Moist' here differentiates these slopes from the much drier north- and west-facing scarps.

Cliffs refers to major cliff-lines at all altitudes – usually at ca. 1,400/1,500 m, then again at 1,800/2,000 m, and sometimes again at 2,300 + m on the highest peaks.

Upland Slopes refer to the higher altitude slopes (ca. >1,600 m) which are too steep to constitute plateau.

Plateaux refer to extensive flat or gently sloping regions. These are typically tiered on the Escarpment, occurring primarily at 1,200/1,300 m, again at 1,400/1,500 m, and extensively between 1,700–2,100 m.

High Screes refer to extensive steep or near-horizontal dolerite screes and boulder fields occurring above 1,800 m (often >2,000 m) – these often consist of massive stable boulder beds.

High Peaks refer to the prominent highest peaks that sit above the main summit plateaux, reaching altitudes of 2,200–2,500 m. These peaks are typically isolated from each other, are flanked with extensive High Screes, and cover a much smaller surface area than the rest of the mountain blocks.

7.7.3.6 Data Manipulation and Presentation

The data was tabulated (Table 7.6), and analysed through simple statistical means and graphical presentation using Microsoft Excel and PowerPoint. Although more complex means of statistical analysis could have been employed, a simpler approach has been deemed suitable in this study.

7.7.4 Results and Discussion

The results are shown in Figs. 7.12 and 7.13. Each point is considered separately.

7.7.4.1 Edaphic Substrate

Almost half of the taxa are edaphic ubiquitists, with approximately a third restricted to dolerite, and a smaller proportion restricted to sandstone (Fig. 7.12). There is thus no strong bias towards substrate. Edaphic indifference is easily explainable in the moister mountains as there is often a less discernible difference in the soils arising on dolerite and sandstone because of more equitable weathering and humus production. The humus content of the soil is possibly the critical factor, being as important to soil fertility in these mountains as is mineral content. In moister

Table 7.6 Selected taxa endemic to the Cape Midlands Escarpment, indicating distribution and key characteristics used in this study

Endemic taxon	Distribution	Substrate	Lower altitude limit (m)	Primary vegetation habitat	Primary geomorphological niche
Acmadenia sp. nov. aff. *sheilae* I. Williams	S	Dolerite	1,600	Montane grassland	Plateau
Alepidea macowani Dummer	S, GWA	Dolerite & sandstone	1,400	Montane grassland	Plateau
Arrowsmithia styphelioides DC.	GWA	Dolerite & sandstone	1,100	Montane grassland	Upland slope
Bergeranthus nanus A.P. Dold & S.A. Hammer	S, GWA	Dolerite & sandstone	1,300	Montane grassland	Upland slope
Brachystelma cathcartense R.A. Dyer	GWA	Sandstone	1,200	Montane grassland	Upland slope
Ceropegia macmasteri A.P. Dold	GWA	Sandstone	1,200	Montane grassland	Upland slope
Conium sp. no. 4 (Hilliard and Burtt 1985)	S, GWA	Dolerite & sandstone	1,800	Montane grassland	Cliffs
Crassula exilis subsp. *cooperi* (Regal) Tölken	S, GWA, ST	Dolerite & sandstone	1,500	Montane grassland	Cliffs
Delosperma alpinum (N.E.Br.) S.A. Hammer & A.P. Dold	GWA	Dolerite	1,800	Montane grassland	High scree
Delosperma katbergense L. Bolus	GWA	Sandstone	1,200	Montane grassland	Cliffs
Delosperma dyeri L. Bolus	S, GWA	Dolerite & sandstone	1,600	Montane grassland	Plateau
Diascia ramosa Scott-Elliot	S	Sandstone	1,200	Montane grassland	Moist scarp
Dierama grandiflorum G.J. Lewis	S	Dolerite	1,500	Montane grassland	Plateau
Drimia montana A.P. Dold & E. Brink	GWA, ST	Sandstone	2,000	Montane grassland	Upland slope
Encephalartos cycadifolius (Jacq.) Lehm.	S, GWA	Dolerite	1,400	Montane grassland	Upland slope
Erica sp. aff. *reenensis* Zahlbr.	S, GWA	Dolerite & sandstone	1,800	Montane grassland	High peak
Erica passerinoides (Bolus) E.G.H. Oliv.	S	Dolerite	1,800	Montane grassland	Plateau
Euryops ciliatus B. Nord.	GWA	Dolerite	1,600	Montane grassland	Upland slope
Euryops dentatus B. Nord.	S	Dolerite	1,400	Montane grassland	Upland slope
Euryops dyeri Hutch.	GWA	Dolerite & sandstone	1,700	Montane grassland	Upland slope
Euryops exsudans B. Nord. & V.R. Clark	S	Dolerite & sandstone	1,600	Montane grassland	Upland slope
Euryops galpinii Bolus	S, GWA, ST	Sandstone	1,800	Montane grassland	Upland slope
Euryops trilobus Harv.	S, ST	Dolerite & sandstone	1,800	Montane grassland	Upland slope
Euryops proteoides B. Nord. & V.R. Clark	S	Dolerite & sandstone	1,300	Montane grassland	Upland slope
Faurea recondita MS J. Rourke	S	Dolerite & sandstone	1,300	Montane grassland	Moist scarp
Ficinia sp. nov. aff. *gracilis* Schrad.	S, GWA	Dolerite & sandstone	1,500	Montane grassland	Upland slope

Garuleum tanacetifolium (MacOwan) Norl.	S, GWA	Dolerite & sandstone	1,600	Montane grassland	Upland slope
Gazania caespitosa Bolus	S	Dolerite	1,600	Montane grassland	Plateau
Geranium amatolicum Hilliard & B.L. Burtt	GWA	Dolerite & sandstone	1,400	Montane grassland, Closed	Upland slope
Geranium contortum Eckl. & Zeyh.	GWA	Dolerite	1,900	Montane grassland	Upland slope
Geranium grandistipulatum Hilliard & B.L. Burtt	GWA	Sandstone	1,800	Montane grassland	Upland slope
Haworthia marumiana var. *batesiana* (Uitewaal) M.B. Bayer	S	Dolerite & sandstone	1,200	Closed	Cliffs
Hermannia sneeuwbergensis MS D. Gwynne-Evans	S, GWA	Dolerite & sandstone	1,300	Montane grassland	Upland slope
Hermannia crassifolia MS D. Gwynne-Evans	S	Dolerite	1,200	Closed	Upland slope
Hermannia violacea (Burch. ex DC.) K. Schum.	S, GWA	Sandstone	1,000	Closed	Moist scarp
Hesperantha helmei Goldblatt & J.C. Manning	S	Dolerite & sandstone	2,000	Montane grassland	High peak
Hesperantha stenosiphon Goldblatt	GWA	Dolerite & sandstone	1,500	Montane grassland, Closed	Cliffs
Indigofera elandsbergensis Phillipson	GWA	Sandstone	1,600	Montane grassland	Upland slope
Indigofera magnifica MS B. Schrire	S	Dolerite	1,800	Montane grassland	Plateau
Indigofera asantasanae MS B. Schrire	S	Dolerite & sandstone	1,800	Montane grassland	Upland slope
Jamesbrittenia crassicaulis (Benth.) Hilliard	S, GWA, ST	Dolerite & sandstone	1,800	Montane grassland	Plateau
Kniphofia acraea Codd	S	Dolerite	1,600	Montane grassland	Upland slope
Lotononis alpina subsp. *multiflora* (Eckl. & Zeyh.) B.E.van Wyk	GWA	Dolerite	1,700	Montane grassland	Upland slope
Moraea reticulata Goldblatt	GWA	Dolerite	1,200	Montane grassland	Plateau
Polemannia grossulariifolia Eckl. & Zeyh.	S, GWA	Dolerite	1,500	Montane grassland	High scree
Psoralea margaretiflora C.H. Stirt. & V.R. Clark	S	Dolerite & sandstone	1,200	Montane grassland	Moist scarp
Selago bolusii Rolfe	S	Dolerite & sandstone	1,600	Montane grassland	Cliffs
Selago retropilosa Hilliard	S	Dolerite & sandstone	1,800	Montane grassland	Plateau
Sutera glandulifera Hilliard	GWA, ST	Dolerite	1,400	Montane grassland	Cliffs
Wahlenbergia laxiflora (Sond.) Lammers	S, GWA	Dolerite	1,400	Montane grassland	Upland slope

For distribution: *S* Sneeuberg, *GWA* Great Winterberg–Amatolas, *ST* Stormberg

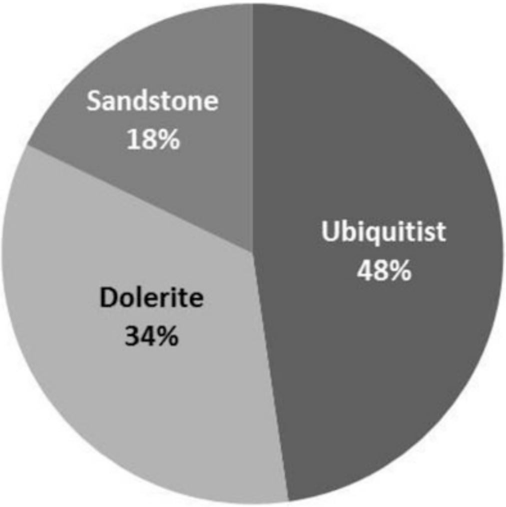

Fig. 7.12 The proportion of endemic taxa per substrate entity in the Cape Midlands Escarpment

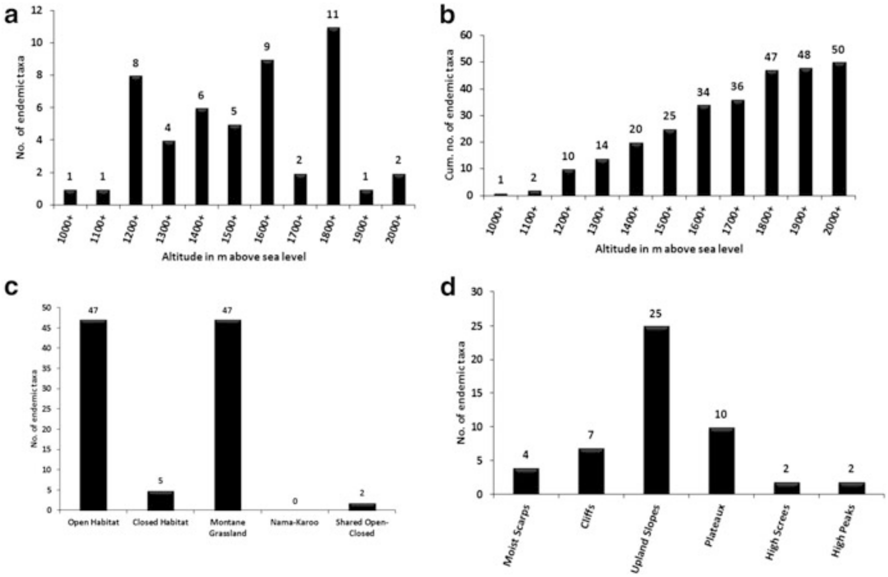

Fig. 7.13 Results for three moisture availability proxies, and primary geomorphological niche, for endemic plant taxa in the Cape Midlands Escarpment. (**a**) Minimum altitude thresholds, (**b**) accumulation of endemics with altitude, (**c**) primary vegetation habitats, (**d**) primary geomorphological niches

areas the production of plant material – and therefore humus content – is likely to be similar on both substrates, thus enriching the soil on both substrates equally well (forming a more ubiquitous A horizon). In drier areas, the deeper weathering and minerally richer dolerite (Burke 2002) encourages better vegetative cover and therefore higher humus content in the soil, thus favouring more fertile dolerite soils while sandstone soils remain comparatively stony and infertile. Thus endemics are more widespread on the richer dolerite soils. Otherwise there appears to be no significant distinction between the substrates ecologically, compared to very obvious plant specialisation on substrates with high levels of toxic heavy metals, such as the Sekhukhuneland ultramafics, the Barberton serpentines, and the Great Dyke of Zimbabwe (Balkwill and Balkwill 1999; Siebert et al. 2001; Van Wyk and Smith 2001).

7.7.4.2 Altitude

Most endemic taxa have a lower altitude limit of 1,800 m, followed closely by 1,600 m and 1,200 m respectively (Fig. 7.13a). Only two taxa have limits below 1,200 m and three above 1,800 m. Figure 7.13b indicates that there is a steady cumulative addition of endemic taxa with altitude, mostly between 1,200 and 1,800 m. Most endemics therefore occur above 1,200 m, and only three taxa are added above 1,900 m.

Lower altitude limits are easily explained as the result of increased aridity towards the base of the Escarpment in drier areas, or a change in habitat from Open to Closed (in both drier and wetter areas, discussed in *Primary vegetation habitat* below). What is surprising is the low number of endemics restricted above 2,000 + m, suggesting that the highest altitudes are not critical for endemism, or that conditions on the isolated High Peaks are not conducive to many endemic taxa (Cook *sine anno*). This is discussed further in *Primary geomorphological niche*.

7.7.4.3 Primary Vegetation Habitat

The vast majority of endemic taxa occur in Open Habitats, with only five occurring exclusively in Closed Habitats (Fig. 7.13c). Of the Open Habitat taxa, all occur in Montane Grassland and none in Nama-Karoo. Two taxa are both Open and Closed Habitat taxa, although they lean towards more open areas (forest margin, exposed cliffs in forest, etc.).

That no endemics occur in Nama-Karoo is very significant, as much of the drier leeward slopes of the mountains are dominated by Nama-Karoo and similar karroid mountain vegetation. This supports the idea that the endemics are concentrated where moisture is available, as reflected in Montane Grassland. Note however that forest, which reflects the highest rainfall in the study area, does not support many endemics. Grassland as a biome is therefore more important for endemics in these mountains than any other biome, a result that strongly supports trends in the grassland regions of South Africa (Van Wyk and Smith 2001; Mucina and Rutherford 2006). These results also overwhelmingly support Meadows and Linder's (1993) findings that montane grassland in the region is a primary, endemic-rich habitat and not a species-poor, secondary vegetation type arising from the palaeo-anthropogenic destruction of forests. The results also suggest that, being grassland taxa, most of the endemics are capable of withstanding, or even require, the periodic fires that characterise the Grassland Biome in southern Africa (Mucina and Rutherford 2006).

7.7.4.4 Primary Geomorphological Niche

Upland Slopes host by far the majority of endemic taxa, while High Screes and High Peaks host the lowest (Fig. 7.13d). Plateaux, Cliffs and Moist Scarp each host an intermediate to low number.

The dominance of Upland Slopes, followed by Plateaux, could be attributed to their majority surface area, while the other niches cover much smaller areas. It also suggests that there has been no need for these taxa to specialise into more rugged niches away from topographically gentler ones. The results also correlate well with *Altitude*: most Upland Slopes and Plateaux occur between 1,200 and 2,100 m. Similarly, Moist Scarp typically occurs below 1,200 m, and often comprises Closed Habitat with its corresponding low endemism (three of the four Moist Scarp taxa occur exclusively in Closed Habitat). Low endemism on the High Screes and High Peaks also correlates with the low addition of endemic taxa above 1,900 m. There is a definite avoidance of these highest altitudes by most taxa, a propensity also noted by Cook (*sine anno*) in the GWA, where most taxa sampled occurred between 1,500 and 2,000 m. The extreme climatic conditions prevalent on these isolated High Peaks and associated High Screes are probably the main reason for their low endemism, as could be the poor soil conditions of these habitats. The low specialisation in Cliffs, High Screes and High Cliffs in the Cape Midlands Escarpment is interesting given the impression of higher specialisation in these niches in other regions both elsewhere in South Africa and abroad (Larson et al. 2000; Pooley 2003; Van Jaarsveld 2011).

While High Peaks do not feature prominently in the results, and Cliffs only moderately, it can be noted that their role becomes more important westwards, where they compensate for increased aridity by providing moisture refugia for taxa that are more widespread in wetter areas (Larson et al. 2000; Bergh et al. 2007; Clark et al. 2009, 2011d; Clark 2010). For example, numerous endemic and more typical Afromontane taxa widespread on Upland Slopes and Plateaux in the GWA are almost completely restricted to the base of moist, south-facing Cliffs or the Highest Peaks in the drier Sneeuberg (Clark 2010). This is further augmented in the even drier Nuweveldberge (Clark et al. 2011d). It would appear then that most montane taxa will accumulate into specialised refugia only when necessary, and only require these specialist habitats in response to moisture deficits.

7.7.5 Conclusion and Conservation Implications

The majority of Cape Midlands Escarpment endemic taxa are edaphic ubiquitists, with dolerite preference as second, and are found in Montane Grassland on Upland Slopes above 1,200 m. Much fewer are sandstone ‘specialists’, and few are restricted to Closed Habitats (forest, woodland, thicket), Cliffs, High Screes or High Peaks (i.e. above 1,900 m), or occur below 1,200 m (i.e. to the base of the Escarpment). We conclude therefore that the distribution of Cape Midlands Escarpment endemics is driven primarily by moisture availability rather than edaphic substrate, and that good soil conditions in grassland on moderate topography at medium altitudes are favoured over specialised habitats such as Cliffs, High Scree and High Peaks unless moisture deficits are experienced.

Conservation implications are that the upland grasslands (and associated fynbos, wetland and montane shrublands) in the Cape Midlands Escarpment are of high conservation value and need to be well managed in order to conserve the bulk of endemic taxa, particularly against overgrazing, soil erosion and afforestation (both formal and feral). Should the effects of climate change in this region include a decrease in moisture availability, a possible concentrating of endemic taxa along the base of south-facing Cliffs and on the High Peaks can be expected. These two habitats can thus be considered the most promising refugial niches for the future and should be afforded primary conservation priority.

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7.8 Taxonomic Composition and Spatial Pattern of Endemic Seed Plant Species in Southwest China

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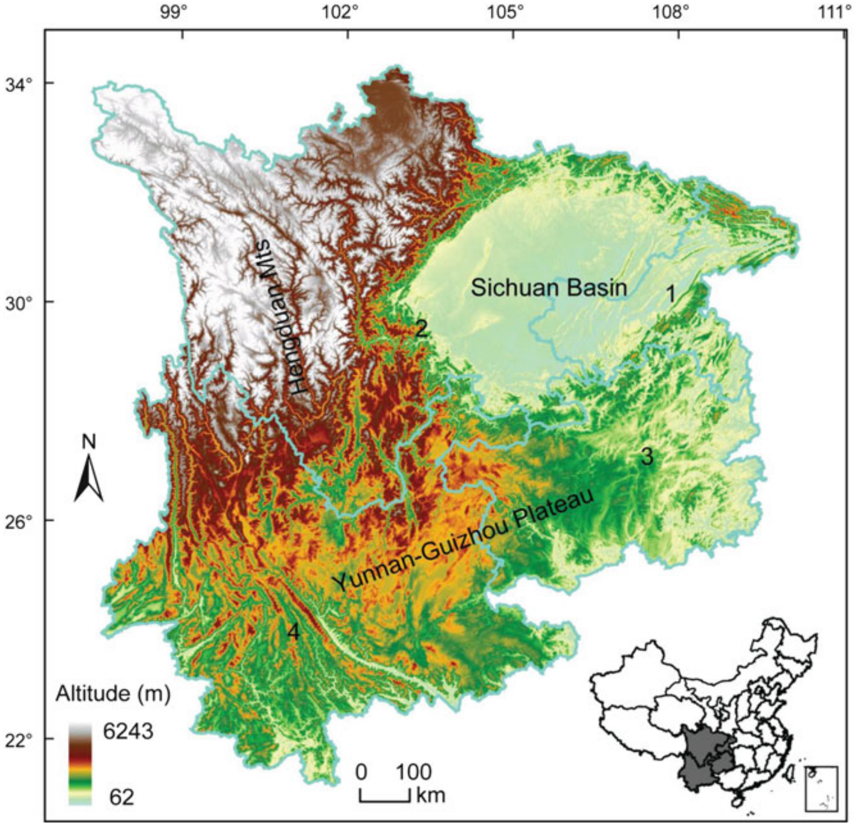

Fig. 7.14 Topographical map of southwest China. *Light blue lines* are provincial boundaries. *1* Chongqing; *2* Sichuan; *3* Guizhou; *4* Yunnan. The map in the *right bottom* shows the location of the study area. The *inset* in the *right bottom* shows islands in the South China Sea (Albers projection)

7.8.1 Physical Geography and Endemism in Southwest China

Southwest China is defined to include three provinces (Sichuan, Guizhou and Yunnan) and one municipality (Chongqing) in this study (Fig. 7.14). It lies between the easternmost edge of the Tibetan Plateau and the Central Chinese Plain and stretches over an area of 1.14 million km^2. The geology and topography of this region is complex, characterized by large mountain ranges in the west (e.g. Hengduan Moutains) with a north–south direction, and lower mountains and flat areas (e.g. Sichuan Basin) in the east. Its location in a climate transition zone and highly complex topography result in a wide range of climatic conditions, generally with subtropical climate in the Sichuan Basin and Yunnan-Guizhou Plateau, tropical climate in southernmost part of Yunnan (e.g. Xishuangbanna), and alpine climate in higher altitude areas (Pang 1996).

Southwest China is one of the botanically most diverse terrestrial regions in China (Wang 1992) as well as in the world (Myers et al. 2000). Some parts of the region fall within the Himalaya and South-Central China biodiversity hotspots (Mittermeier et al. 2005). It possesses a wide variety of vegetation types, including broad-leaved and coniferous forests, meadow, freshwater wetlands, and alpine scrub and scree communities (Wu 1980). This region has a disproportionate amount of China's overall seed plant species (c. 60 %), with 18,309 native species (Editorial Committee of Flora Reipublicae Popularis Sinicae 1959–2004), which is featured by a high level of endemism. The Hengduan Mountain region has been identified as one of the endemism centers in China (Ying et al. 1993; López-Pujol et al. 2011; Huang et al. 2012).

Because the level of endemism of an area reflects the history of diversification (speciation and extinction), studies on the geographical distribution and diversity patterns of endemic species would benefit the interpretation on phytogeographic and biodiversity patterns of the area (Qian 2001; Huang et al. 2011). Moreover, endemic species are regarded with outstanding conservation importance owing to the rarity and uniqueness of the species (Myers et al. 2000). Here, we focus on southwest China, one of the most floristic diverse regions in the world, to investigate the taxonomic composition and spatial pattern of endemic seed plant species in the region, for the purposes of improving our understanding of the phylogenetic history of the flora and providing guidance for biodiversity conservation in southwest China.

7.8.2 Analysis of Checklists and Distribution Data

We first compiled a checklist of native seed plant species in southwest China from a wide range of literature including Flora Reipublicae Popularis Sinicae (1959–2004) and Flora of China (Wu et al. 1994–2011). We defined that endemic species refer to the species that occur naturally in and are restricted to southwest China and this concept of endemism is based on administrative boundaries. A checklist of endemic seed plant species was then formulated based on literature review and experts' scrutiny. Information on their distribution was collated by consulting a wide range of literature and checking herbarium specimens through the Chinese Virtual Herbarium (http://www.cvh.org.cn/cms/en) and Chinese Educational Specimen Resource Center (http://mnh.scu.edu.cn/). Totally, 33,959 distribution records were obtained for this study. This region is politically divided into 391 counties, with an average size of 2,636 km^2 per county. We geo-referenced the distribution information to county level and used the county as the unit of our analysis.

We calculated the number of endemic seed plant species of six main phylogenetic groups (gymnosperms, basal angiosperms, monocots, basal eudicots, rosids, and asterids). Species were assigned to genera and families following the Catalogue of Life: Higher Plants in China (http://www.cnpc.ac.cn, Wang et al. 2011). The designation of angiosperm families to the main phylogenetic groups followed the

Table 7.7 Taxonomic richness of endemic seed plant species in southwest China

Group	No. of endemic species	No. of species	Proportion of endemics (%)
Gymnosperms	10	140	7.0
Angiosperms	4,563	18,169	25.1
Basal angiosperms	163	584	27.9
Monocots	677	3,292	20.5
Basal eudicots	577	1,912	30.2
Rosids	1,012	5,272	19.2
Asterids	2,134	7,107	30.0
Total	4,573	18,309	25.0

APG III system (APG 2009). ANOVA and Tukey's multiple comparisons (Bretz et al. 2010) were conducted to assess endemism differences in the six phylogenetic groups.

We counted the number of endemic seed plant species per county. The range size of each endemic species was calculated as the sum of areas of the counties in which they occurred. We compared the range sizes with thresholds of IUCN red list criteria to assess the conservation status of the species. The IUCN criteria suggest that species with range sizes smaller than 20,000 km^2 are vulnerable species; smaller than 5,000 km^2 are endangered species; and smaller than 100 km^2 are critically endangered species (IUCN Standards and Petitions Working Group 2008).

7.8.3 *Taxonomic Composition*

According to our data, southwest China has 4,573 endemic seed plant species, accounting for 25 % of the total seed plant species in the region (Table 7.7). Angiosperms have a significantly higher number of endemic species than gymnosperms. Among angiosperms, asteroids have the largest number of endemic species (n = 2,134; 47 % of all endemic species), followed by rosids, monocots, basal eudicots and basal angiosperms. Angiosperms also have a markedly higher proportion of endemic species than gymnosperms. The proportion of endemic species is highest in basal eudicots (30.2 %), while it is lowest in rosids (19.2 %).

On average, the proportion of endemic species is 14.5 % in each family and 14.0 % in each genus (Fig. 7.15). Families of asteroids have the highest proportion of endemic species (mean = 19.8 %), whereas those of gymnosperms have the lowest proportion (mean = 4.6 %) (Fig. 7.15). At genus level, the proportion of endemics in the main phylogenetic groups shows a similar pattern as that at family level (Fig. 7.15).

The endemic species identified in this study belong to 139 families. Among them, 17 families contain more than 100 endemic species. The top ten families in terms

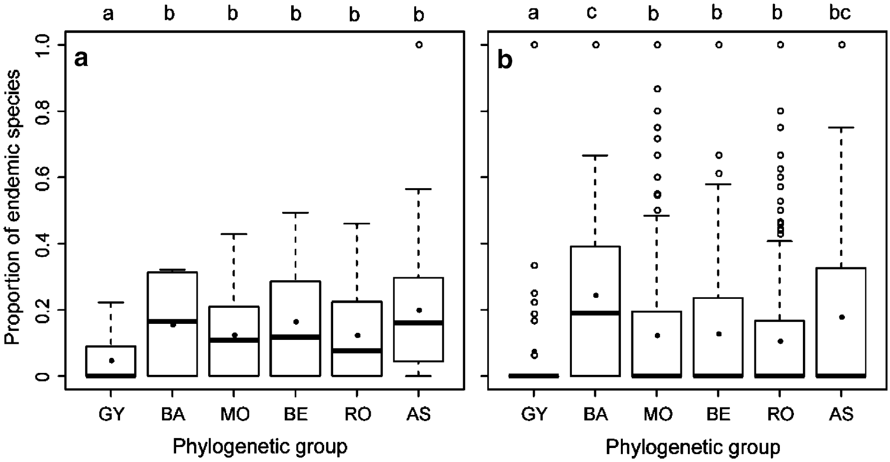

Fig. 7.15 Proportion of endemic species in each family (**a**) and genus (**b**) of the six analysed phylogenetic groups in southwest China. *GY* gymnosperms, *BA* basal angiosperms, *MO* monocots, *BE* basal eudicots, *RO* rosids, *AS* asterids. *Solid points* indicate mean values. *Letters above boxes* show the result of Tukey's multiple comparison tests

Table 7.8 Top ten families, in terms of the number of endemic seed plant species in southwest China

No.	Family	No. of endemic species	No. of species	Proportion of endemics (%)
1	Asteraceae	403	1,172	34
2	Poaceae	223	985	23
3	Lamiaceae	198	541	37
4	Scrophulariaceae	180	490	37
5	Ericaceae	179	668	27
6	Primulaceae	173	372	47
7	Ranunculaceae	156	626	25
8	Orchidaceae	148	856	17
9	Gesneriaceae	142	305	47
10	Rosaceae	142	840	17

of the number of endemic species are all large families with high species diversity (e.g. Asteraceae, Poaceae and Ericaceae). All these families have a proportion of endemics that is higher than the average value (Table 7.8). The endemic species belong to 810 genera. All top ten genera in terms of the number of endemic species are highly diversified genera (e.g. *Rhododendron*, *Pedicularis* and *Primula*) in the region, and have high proportions of endemics (Table 7.9).

Table 7.9 Top ten genera, in terms of the number of endemic seed plant species in southwest China

No.	Genus	No. of endemic species	No. of species	Proportion of endemics (%)
1	*Rhododendron*	149	479	31
2	*Pedicularis*	144	302	48
3	*Primula*	110	218	50
4	*Corydalis*	96	198	48
5	*Impatiens*	96	170	56
6	*Berberis*	77	143	54
7	*Gentiana*	67	186	36
8	*Carex*	65	230	28
9	*Begonia*	57	124	46
10	*Aconitum*	55	90	61

7.8.4 Spatial Distribution Patterns

The number of endemic species ranges from 0 to 947, with an average of 81 species per county (Fig. 7.16). Endemic seed plant species are unevenly distributed across the region. They are largely concentrated in the western part of the region especially along Hengduan Moutain ranges, whereas endemic species richness is relatively low in the east (including Sichuan Basin and Guizhou Province). Southern and southeastern Yunnan also has a high endemic richness.

Range sizes of endemic species show a Poisson distribution, varying from 719 to 523,232 km^2 (Fig. 7.17). The mean range is 30,921 km^2, while the median is 16,613 km^2. None of the species has a range of less than 100 km^2. 838 species (19.5 % of all endemics) occupy less than 5,000 km^2 and 2,439 species (56.6 % of all endemics) less than 20,000 km^2.

7.8.5 Discussion

The most derived group asterids has the largest number of endemic species, accounting for nearly half (47 %) of the total number of endemic species (Table 7.7). This is consistent with the floristic composition of endemism in East Asia and North America at genus level (Qian 2001). Endemics have generally been classified into two relative groups: palaeoendemics and neoendemics (Qian 2001; López-Pujol et al. 2011). The former refers to formerly more widespread taxa that now have restricted distributions, whereas neoendemics have arisen generally by differential evolution and have not yet spread out from their original territory (Stott 1981). The dominance of neoendemics in southwest China may be explained by the geographical and climatic histories of the region. The India-Eurasia plate collision

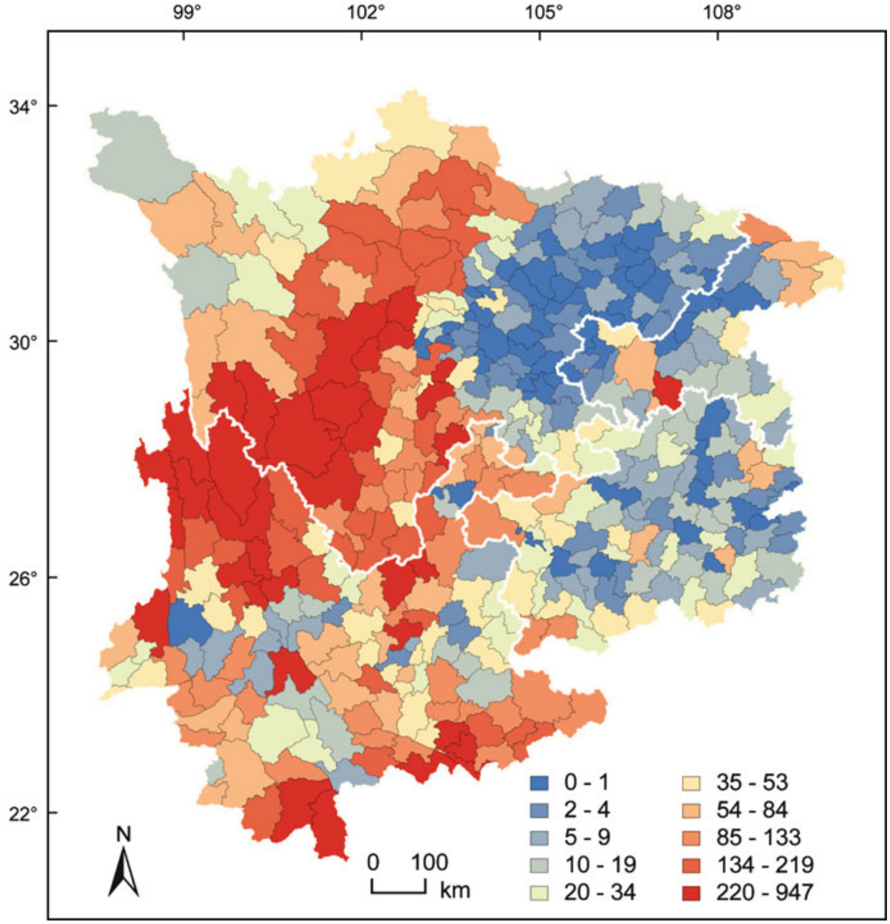

Fig. 7.16 Spatial pattern of endemic seed plant species richness in southwest China. *White lines* show provincial boundaries (Quantile classification and Albers projection)

50 million years ago has caused a major topographical transformation in southwest China (Li and Fang 1999; Zhang et al. 2000; Feng et al. 2011). The uplift of the Hengduan Mountains created a vast array of new habitats and stimulated allopatric and habitat differentiation, and ultimately gave rise to adaptive radiation (Liu and Tian 2007). Additionally, the climate became significantly colder and drier during glacial maxima. To adapt to the harsher environment, fast species differentiation occurred in many plant groups (Davis and Shaw 2001). For example, genera such as *Rhododendron*, *Pedicularis*, *Primula*, and *Corydalis*, have lineages showing adaptation to an alpine climate in southwest China (Li et al. 2007). The Hengduan Moutain region has been considered as the center of the diversification and evolutionary radiation of angiosperms (Wu 1980).

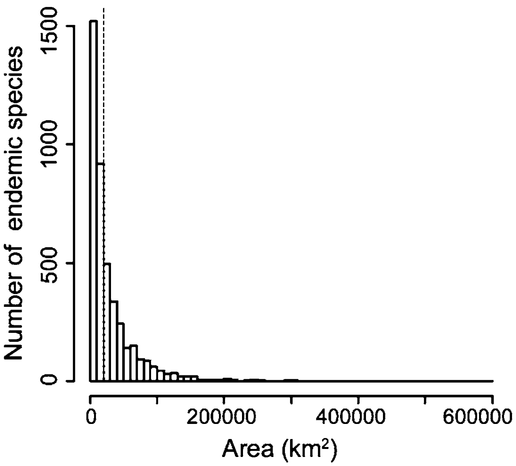

Fig. 7.17 Frequency distribution of range sizes of endemic seed plant species in southwest China. The *dashed line* is x = 20,000 km^2

The spatial pattern of endemic seed plant species richness noticeably coincides with large mountain ranges in southwest China (Figs. 7.14 and 7.16). Endemic plant species largely concentrate in the major mountain areas of the west, whereas lower mountains and flat areas in the east have low densities of endemic species. High levels of endemism in mountainous regions is probably due to the high speciation rates and low extinction rates, and especially the presence of refugia during the Pleistocene glacial episodes (Taberlet 1998; Hewitt 2000). Mountainous regions had relatively stable environmental conditions during the Quaternary, allowing plants to sustain large assemblages of a variety of living forms during glacial and interglacial periods (Hewitt 1999). Mountains also provide abundant and separated habitats where plant populations would be isolated following dispersion and colonization. Strong geographical isolation prevents genetic exchange between populations, which is a critical step for allopatric speciation and accelerates the rate of lineage diversification (Rice 1987). Moreover, geographical isolation increases the level of endemism by limiting newly evolved species to spread out from their original areas. In contrast, eco-climate conditions in lower mountains and flat areas are less stable, and are more vulnerable to various disturbances (Tribsch and Schönswetter 2003; Médail and Diadema 2009). These conditions are unfavorable for preserving endemic species.

We found that 19.5 % of all endemic species is restricted to ranges of less than 5,000 km^2 and 56.6 % to ranges of less than 20,000 km^2 (Fig. 7.17). According to the IUCN criteria (IUCN Standards and Petitions Working Group 2008; IUCN Standards and Petitions Subcomittee 2010), these species should be included in the red list either as endangered or vulnerable species. In fact, only a small proportion of the species is already in the China species red list (Wang and Xie 2004), because the selection of protected species is limited by available resources (money and effort)

(Margules and Pressey 2000). We do not find any species with range sizes smaller than 100 km^2. This is determined by the way in which we calculated range size by using 'county' as the unit area and the minimum size of the counties (115 km^2) is larger than 100 km^2. The quantification of range size would be more precise if we only include the parts that met the species' requirements of elevation and types of preferred habitats (Harris and Pimm 2007), instead of simply summing up the areas of the counties of occurrence. Nevertheless, our approach can still give a rough estimation of the range sizes of the endemic species, and would be helpful for assessing the conservation status of these species.

There are two potential sources of bias in the study. First, we use administrative boundaries to identify a species as endemic in southwest China. Ideally, endemic species are those whose distributions are delimited along natural, geographic boundaries. However, on that basis it would be difficult to identify a species as endemic species in southwest China because of the absence of data at the correct level of detail (Huang et al. 2011). Our delimitation may underestimate the levels of endemism in counties near the boundary and the levels of endemism of taxonomic groups that are narrowly distributed but not restricted in southwest China (Chen et al. 2011). Second, species distributions are often not fully documented due to the incompleteness of sampling, which would lead to an underestimation of species range sizes. We have compiled as many data as possible from herbaria and a wide range of literature to minimize this bias.

In summary, we find that the most derived group asteroids have the highest number of endemic seed plants; spatial patterns of richness of endemic seed plant species show a significant mountain character, largely coinciding with main mountain ranges in the west of the region. The overall bias in favour of asteroids and large mountain ranges results from different rates of speciation, extinction, and dispersion which primarily have been influenced by the topography, and the geological and climatic histories of the region. We also find that 19.5 % of the endemic species are restricted to ranges of less than 5,000 km^2 and 56.6 % to ranges of less than 20,000 km^2, suggesting the high conservation significance of the endemic species.

7.9 Habitats of Tertiary Relict Trees in China

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Among the many endemic plant taxa in China there are a considerable number of Tertiary relict tree species. They comprise both coniferous and broad-leaved species and evergreen as well as deciduous species (Table 7.10). Of the 40 relict tree species listed in Table 7.10 about 52.5 % are conifers as against 47.5 % broad-leaved. About 86 % of the conifer relict tree species, and about 21 % of broad-leaved relict tree species, are evergreen. Thus, among the endemic Tertiary relict tree species, evergreen coniferous species and broad-leaved deciduous species form by far the largest groups, whereas deciduous coniferous and evergreen broad-leaved species are rather few.

All of these tree species now occur exclusively in a few restricted areas in China. Tertiary relict endemic (paleoendemic) species are found mainly in southern China, including Chongqing municipality, Sichuan, Hubei, Hunan, Guizhou, Guangxi, Yunnan, Zhejiang, Jiangxi, Fujian, Guangdong, and Hainan provinces, and Taiwan, but some relict coniferous tree species of *Picea*, *Pinus* and *Tsuga* are found in the cold temperate forests of China. The regions in which the relict tree species occur mostly have a rugged topography, and have provided long-term suitable habitats, enabling the survival of the relict-endemics (López-Pujol et al. 2011).

Most of this region was never covered by ice-sheets during the Last Glacial Maximum (LGM), and it is now one of the most important global Pleistocene refugia for lineages that evolved prior to the late Tertiary and Quaternary glaciations (Axelrod et al. 1998). The paleoendemic species provide a unique opportunity to understand past and recent biogeographical and evolutionary processes because of their taxonomical isolation, rarity and phylogenetic traits. Today they are highly vulnerable and even in danger of extinction because their populations in the wild have been greatly threatened by overexploitation of the land. Their conservation is of great concern for China and for the world.

A number of Tertiary relict trees occur in particular, unstable habitats within the warm, humid transitional zone between the evergreen and the deciduous broad-leaved forests of China, with some admixture of coniferous species. The well-known living fossil and relict-endemic species *Metasequoia glyptostroboides* currently survives in the wild only on unstable wet lower slopes and in stream valleys, in the border region of Hubei and Hunan provinces and Chongqing municipality in south-central China (Tang et al. 2011), and *Cathaya argyrophylla* grows on unstable slopes on Mt. Jinfo (Guan and Chen 1986), southwestern China. *Davidia involucrata* (Photo 7.21) thrives on unstable scree slopes on Mt. Emei and other mountains in Sichuan province, and cannot successfully compete with evergreen broad-leaved trees in a more favorable environment (Tang and Ohsawa 2002). We have found

Table 7.10 Examples of paleoendemic tree species with indication of leaf morphology and natural habitats in China (including the species distributed in the boundary between China and Vietnam or between China and Myanmar)

Species	Life form	Habitat
Gymnosperm		
Abies beshanzuensis M.H. Wu	Coniferous evergreen	Mountains or hills; 1,400–1,800 m
Abies fanjingshanensis W.L. Huang et al.	Coniferous evergreen	Mountain slopes; 2,100–2,350 m
Abies yuanbaoshanensis Y.J. Lu & L.K. Fu in L.K. Fu et al.	Coniferous evergreen	Mountain slopes; 1,700–2,100 m
Amentotaxus formosana H.L. Li	Coniferous evergreen	Damp, shady places, ravines, cliffs; 500–1,300 m
Cathaya argyrophylla Chun & Kuang	Coniferous evergreen	Steep exposed mountain slopes, ridges and vertical cliffs; 900–1,900 m
Calocedrus macrolepis var. *formosana* (Florin) W.C. Cheng & L.K. Fu	Coniferous evergreen	Mountain slopes, ravines, cliffs; 500–1,300 m
Cephalotaxus oliveri Masters	Coniferous evergreen	Mountain slopes; 300–1,800 m
Cryptomeria japonica var. *sinensis* Miquel	Coniferous evergreen	Deep, well-drained soils subject to warm, moist conditions; below 1,100 m
Cunninghamia lanceolata (Lambert) Hooker	Coniferous evergreen	Mountains, rocky hillsides, roadsides; 200–2,800 m
Keteleeria davidiana (Bertrand) Beissner	Coniferous evergreen	Hills, mountains, hot and dry valleys; 200–1,500 m
Picea asperata Masters	Coniferous evergreen	Mountains, river basins; 2,400–3,600 m
Pinus taiwanensis Hayata	Coniferous evergreen	Mountains, open sites and sunny ridges on sandy areas; 600–3,400 m
Pseudotaxus chienii (Cheng) Cheng	Coniferous evergreen	Gullies, cliffs at 900–1,400 m
Taiwania cryptomerioides Hayata	Coniferous evergreen	Steep slopes, 1,800–2,800 m
Thuja sutchuenensis Franchet	Coniferous evergreen	Cliffs and ridges of the deeply cleft mountain; 1,800–2,200 m
Torreya jackii Chun	Coniferous evergreen	Shady steep slopes or by streamsides; 400–1,000 m
Tsuga chinensis (Franchet) E. Pritzel	Coniferous evergreen	Mountains, valleys, river basins; 1,000–3,500 m
Glyptostrobus pensilis (Staunton ex D. Don) K. Koch	Coniferous semi evergreen	River deltas, etc., on flooded or waterlogged soil in full sun; near sea level
Metasequoia glyptostroboides Hu & W.C. Cheng	Coniferous deciduous	River valleys, rocky soil; 800–1,510 m
Pseudolarix amabilis (J. Nelson) Rehder	Coniferous deciduous	Mountain slopes; 100–1,500 m
Ginkgo biloba Linnaeus	Deciduous	Limestone areas, rocky soil, steep slopes; 800–1,200 m

(continued)

Table 7.10 (continued)

Species	Life form	Habitat
Angiosperm		
Castanopsis carlesii (Hemsley) Hayata	Broad-leaved evergreen	Mountain slopes, valleys, limestone areas; 1,000–2,300 m
Machilus leptophylla Handel-Mazzetti	Broad-leaved evergreen	Mountain slopes, valleys, limestone areas; 400–1,200 m
Hopea shingkeng (Dunn) Bor	Broad-leaved evergreen	Moist sites; 300–600 m
Lithocarpus konishii (Hayata) Hayata	Broad-leaved evergreen	Mountains, hills; 300–1,600 m
Annamocarya sinensis (Dode) Leroy	Broad-leaved deciduous	Forests along riverbanks; 200–700 m
Camptotheca acuminata Decaisne	Broad-leaved deciduous	Forest margins,streamsides; below 1,000 m
Cyclocarya paliurus (Batalin) Iljinskaya	Broad-leaved deciduous	Moist forests on mountains, 400–2,500 m
Davidia involucrata Baillon	Broad-leaved deciduous	Mountain slopes, valleys, scree slopes; 1,100–2,600 m
Emmenopterys henryi Oliver	Broad-leaved deciduous	Valleys, limestone areas; 400–1,600 m
Eucommia ulmoides Oliver	Broad-leaved deciduous	Valleys, dry ravines; 300–2,500 m
Eurycorymbus cavaleriei (H. Léveillé) Rehder & Handel-Mazzetti	Broad-leaved deciduous	Stream sides; 150–1,600 m
Fagus hayatae Palibin	Broad-leaved deciduous	Mountain ridges; 1,300–2,300 m
Fortunearia sinensis Rehder & E.H. Wilso	Broad-leaved deciduous	Mountain slopes; 800–1,000 m
Liriodendron chinense (Hemsl.) Sarg.	Broad-leaved deciduous	Mountain slopes, valleys, limestone areas; 900–1,800 m
Nyssa sinensis Oliver	Broad-leaved deciduous	Streamsides, valleys; 300–1,700 m
Ostryopsis davidiana Decaisne	Broad-leaved deciduous	Mountain slopes; 800–2,800 m
Pteroceltis tatarinowii Maxim.	Broad-leaved deciduous	Limestone areas, river and stream banks; 100–1,500 m
Rhoiptelea chiliantha Diels & Handel-Mazzetti	Broad-leaved deciduous	Hill slopes, valleys, streamside woods; 700–2,500 m
Tapiscia sinensis Oliver	Broad-leaved deciduous	Mountain slopes, valleys, streamsides; 500–2,200 m

Data sources: Fu and Jin (1992), Ying et al. (1993), and Wu and Raven (2012)

other paleoendemic trees, such as *Ginkgo biloba* (Tang et al. 2012), *Emmenopterys henryi*, and *Liriodendron chinense,* in unstable limestone habitats near creeks in the valleys of the Dalou Mountains located between Guizhou and Sichuan provinces, as well as *Taiwania cryptomerioides* on steep slopes in the Gaoligong Mountains of Yunnan and in the Central Ridge of Taiwan.

Photo 7.21 *Davidia involucrata* trees with sprouts thrive on an unstable scree slope on Mt. Emei, Sichuan (Photographed by Cindy Q. Tang)

Many of the Tertiary relict tree species, particularly the coniferous species, persist in these unstable habitats (Table 7.10), probably because the forest stands are not so dense on such sites, and thus light conditions are less limiting. Open, well illuminated stands are particularly important for the coniferous species since their photosynthetic capacity is considerably lower than that of broad-leaved species (Larcher 1976), and as a consequence the coniferous species are likely to be outcompeted in dense mixed forest stands. Furthermore, screes and other unstable substrates more frequently experience short episodes of drought in the top soil which can cause embolism in the xylem vessels. Coniferous species possess a particular type of xylem vessels that makes them less susceptible to develop xylem embolism during such drought conditions (Choat et al. 2012).

Several of the broad-leaved deciduous species are also confined to screes and unstable slopes, or to stream banks. Apart from more favourable light conditions, such sites generally have a rapid turn-over and replenishment of nutrient resources, which is beneficial for deciduous species, as they have a faster nutrient turn-over than broad-leaved evergreen species.

Effective conservation of the paleoendemic trees requires a thorough understanding of the ecological ranges and habitats of these species, as illustrated in Photo 7.21 taken from Mt. Emei, Sichuan, and Fig. 7.18.

The ecological performance and linkage to unstable habitats of the paleoendemic tree species are well exemplified by a Tertiary relict deciduous broad-leaved forest

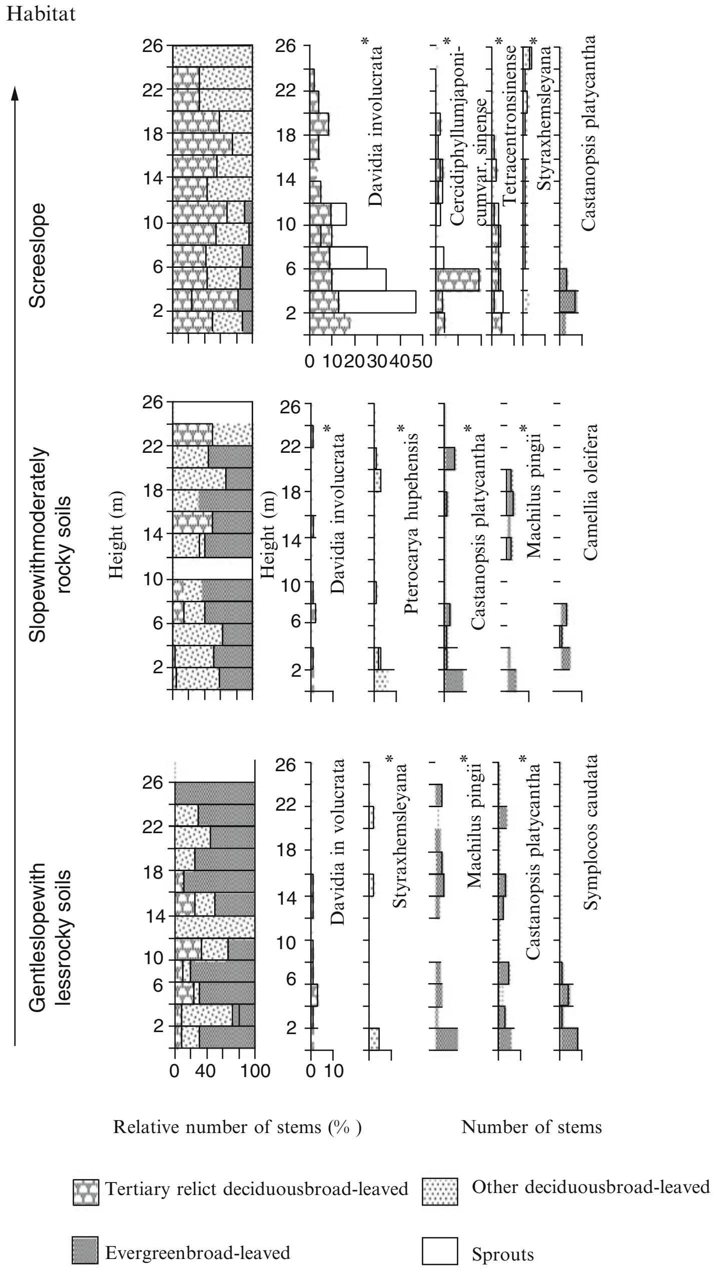

Fig. 7.18 Changes of height frequency distribution with habitat instability at altitudes around 1,600 m on the eastern slope of Mt. Emei. Dominant species are indicated by an *asterisk* (Modified from Tang and Ohsawa 2002)

growing around 1,600 m on Mt. Emei, Sichuan, on an unstable scree slope together with two other communities; one is found on moderately rocky soils and the other on a gentle slope with less rocky soils.

A comparison brings out the contrast between the unstable scree slope and the stable slope (Fig. 7.18). A site with many outcrops is characterized by an abundance of Tertiary relict broad-leaved deciduous trees, in contrast to the broad-leaved evergreen species commonly found on non-scree sites at similar altitudes. Being broad-leaved deciduous, the relict species *Davidia involucrata*, *Cercidiphyllum japonicum*, and *Tetracentron sinense* (the first one is endemic to China, the latter two are endemic to East Asia) grow well on the frequently disturbed unstable scree where new soil resources are regularly available, but where they also benefit from their high sprouting ability as an adaption to the frequent damage they are subjected to at the ground surface because of the mobility of the substrate (Photo 7.21). In contrast, evergreen broad-leaved trees, such as *Castanopsis platyacantha* and *Machilus pingii,* increase their height and canopy density on the stable habitats and outcompete the deciduous species.

The broad-leaved deciduous relict species can survive on the scree slope, probably because of frequent erosion or landslides there which keep the stands rather open. As the habitat becomes more stable, even on the scree slope, the broad-leaved deciduous relict species give way to non-relict, endemic evergreen broad-leaved species. On the gentle slopes, where relict trees are scarce, the non-paleoendemic broad-leaved evergreen *Castanopsis platyacantha* and *Machilus pingii*, with broad-leaved deciduous *Styrax hemsleyana*, dominate the forest and the canopy layer (Fig. 7.18).

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