

Ecological analysis of large floristic and plant-sociological datasets – opportunities and limitations

Dissertation for the award of the degree "Doctor rerum naturalium" (Dr.rer.nat.)
of the Georg-August-Universität Göttingen

within the doctoral program Biology
of the Georg-August University School of Science (GAUSS)

submitted by
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Göttingen, 2018

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Date of the oral examination: 4th May 2018



*Ecological niches of species are not simple
and some niches are simply not predictable.*

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Abbreviations

<i>a.s.l.</i>	above sea level
<i>AUC</i>	Area under the Curve of ROC
<i>EEA</i>	European Environmental Agency
<i>CBD</i>	international Convention on Biological Diversity
<i>DCA</i>	Detrended Correspondence Analysis
<i>DEM</i>	Digital Elevation Model
<i>ENM</i>	Environmental Niche Model
<i>GIS</i>	Geographical Information System
<i>LUCAS</i>	Land Use and Cover Area frame Statistical survey
<i>PCA</i>	Principal Component Analysis
<i>ROC</i>	Receiver Operating Characteristic
<i>SDM</i>	Species Distribution Model
<i>SD</i>	Standard Deviation
<i>spp.</i>	(multiple) species
<i>subsp.</i>	subspecies
<i>syn.</i>	synonym

Summary

This thesis comprises opportunities and limitations for the analysis of floristic and plant-sociological datasets and presents four related exemplary case studies. Woody plant species, their isolated (meta)populations and vegetation units are considered as study objects in a Mediterranean island context. Studies address the islands of Crete and Sicily. The first chapter introduces to general methodologies and positions the conducted studies within this frame.

The second chapter addresses the ecology and co-occurrence of woody species in Cretan landscape context. For precise coordinates of almost 9700 records of 37 species site-information on geology, geomorphology and climate were compiled. The resulting ecological spectra for each species were clustered by similarity, which revealed ecological species groups. These groups reflect distinct ecological units in the Cretan landscape and match partly with published vegetation and habitat schemes (EUNIS, Natura 2000, European vegetation classification). Results thus enable to compare plant ecological spectra of the woody flora of a region and their relation to vegetation patterns.

The third chapter deals with the numerical classification of plant sociological relevées of alluvial *Platanus orientalis* forests; thereby two new plant associations were described. They differ markedly from a third vegetation unit published earlier; for all three associations, species composition, ecology and distribution were discussed. Within 74 *Platanus* stands in Crete nature conservation monitoring was performed, addressing adverse effects and conservation status. About one third was in good conservation status, 42% had an inadequate status and 24% had a bad status; thereby water abstraction, pollution and garbage were the main adverse effects. The study revealed ecologically and floristically founded vegetation units within a regionally common but neglected vegetation type, which is severely threatened in habitat quality.

The study in the fourth chapter is an ecological comparison of (meta)populations of *Zelkova abelicea*, an endemic Tertiary relict in the mountains of Crete. The tree species occurs in isolation in high altitudes of the main mountain ranges, whereas a previous genetic study found intraspecific differences. The mesic woody species occurs in the drier eastern mountains merely on shady slopes, while in the west it may occupy a wider site spectrum. These differences influence the prediction of species distribution models in MaxEnt. Models trained on the larger Western (meta)populations fail to predict the smaller eastern ones. Isolation effects could apply even for these nearby mountains, which could explain (epi)genetic differentiation.

The fifth chapter comprises a study comparing 12 maquis species occurring in Crete and Sicily. Species records and environmental variables (geomorphology, climate, geology) were included into species distribution models, trained on one of the two islands and tested on the other.

Methodological issues in conjunction with extrapolation are discussed. We provide hints for variable selection and adjustments, allowing for better models. Differences in ecological affinities hamper the extrapolation of species distribution in the test region, whereas species with broader ecological amplitude performed worse in models. Lowered isolation barriers with their according genetic uniformity and habitat filtering processes could be involved in the formation of such patterns.

The studies comprise examples for opportunities and limitations in the analysis of large floristic and plant-sociological datasets. A conclusion in the context of several (ecological) disciplines is given in the sixth and last chapter, where also future analysis options for the region or similar datasets are presented.

Zusammenfassung

Diese Dissertation zeigt anhand von vier Studien Möglichkeiten und Grenzen für die Analyse von floristischen und pflanzensoziologischen Datensätzen auf. Gehölzarten, ihre isolierten Metapopulationen und ihre Vegetation werden im Mittelmeerraum bearbeitet, dabei beschränken sich die Arbeiten auf die Inseln Kreta und Sizilien. Im ersten Kapitel werden allgemeine Auswertungsmöglichkeiten, das Untersuchungsgebiet und die Ziele der Arbeit vorgestellt.

Die Studie im zweiten Kapitel bedient Aspekte der Pflanzenökologie und das gemeinsame Vorkommen von Gehölzarten auf Kreta. Für genaue Koordinaten von fast 9700 Funden von 37 Arten wurden Standortsangaben zu Geologie, Geomorphologie und Klima zusammengestellt. Die ökologischen Spektren der Standortsbedingungen wurden nach Ähnlichkeit klassifiziert, wodurch ökologische Artengruppen entstanden. Die Gruppen spiegeln abgrenzbare ökologische Einheiten in der kretischen Landschaft wider und stimmen teils mit Vegetationseinheiten aus der Literatur und Einheiten in Habitat-Handbüchern überein (EUNIS, Nature 2000, Europäische Vegetationsklassifikation). Damit erlauben die Ergebnisse einen Vergleich von pflanzenökologischen Spektren der regionalen Gehölzflora und deren Bezug zu Vegetationsmustern.

Das dritte Kapitel beschäftigt sich mit der Klassifikation von pflanzensoziologischen Aufnahmen von *Platanus orientalis*-Auwäldern; dadurch wurden zwei neue Pflanzengesellschaften beschrieben. Diese unterscheiden sich deutlich von einer früher beschriebenen Gesellschaft; für alle drei Assoziationen wurden die jeweilige Artenzusammensetzung, die Ökologie und die Verbreitung besprochen. Für 72 Platanenauwald-Bestände auf Kreta wurde zudem eine naturschutzfachliche Bewertung durchgeführt, nachdem negative Einflüsse und der Erhaltungszustand erfaßt wurden. Etwa ein Drittel der Bestände war in gutem Erhaltungszustand, 42 % hatten einen unzureichenden Zustand und die restlichen 24 % hatten einen schlechten Zustand; dabei waren Entwässerung, Wasserverschmutzung und Müll die entscheidendsten negativen Einflüsse. Die Studie zeigt ökologisch wie floristisch begründete Vegetationseinheiten in einem regional häufigen Vegetationstyp auf, welcher ernsthaft in seiner Ausdehnung und Habitatqualität bedroht ist.

Die Studie im vierten Kapitel stellt einen ökologischen Vergleich von Metapopulationen von *Zelkova abelicea* dar, einem endemischem Tertiärrelikt in den kretischen Bergen. Die Baumart tritt in isolierten Vorkommen in den Höhenlagen der wichtigsten Bergketten auf, wobei eine frühere genetische Untersuchung intraspezifische Unterschiede fand. Die mesophile Art ist im trockenen Osten hauptsächlich auf schattige Hänge beschränkt, während sie im Westen eine breitere Standortsamplitude einnimmt. Diese Unterschiede beeinflussen die Vorhersage von MaxEnt-Modellen zur Verbreitung der Art; sodaß die kleineren östlichen Vorkommen schlecht über Modelle

vorhergesagt werden können, welche die Westpopulationen als Grundlage haben. Es wirken vielleicht Isolationseffekte, die eine (epi)genetische Differenzierung erklären könnten.

Das fünfte Kapitel umfaßt eine Studie bei der 12 Macchia-Arten untersucht wurden, die auf Kreta und Sizilien vorkommen. Fundpunkte von Arten und Umweltvariablen (Geomorphologie, Klima, Geologie) wurden in Modellen zur Vorhersage von Artverbreitungen verwendet, um letztere auf einer Insel zu trainieren und auf der jeweils anderen zu testen. Unterschiede in den standörtlichen Spektren der Arten hemmen die Extrapolation von Artenverbreitungsmodellen im Testgebiet. Arten mit sehr speziellen Standortspräferenzen ließen sich gut auf der jeweils anderen Insel vorhersagen, während Arten mit breiter Standortsamplitude schlechter zu modellieren waren. Methodische Probleme im Zusammenhang mit Extrapolationen werden besprochen. Wir geben zudem Hinweise zur Auswahl von Variablen und Einstellungen die bessere Modelle erlauben. Geringe Isolationsbarrieren und entsprechende genetische Uniformität für Küstenarten und Habitatfilterprozesse könnten an der Entstehung solcher Muster beteiligt sein.

Die Studien enthalten Beispiele für die Möglichkeiten und Grenzen bei der Auswertung von großen floristisch-pflanzensoziologischen Datensätzen, die im sechsten und letzten Kapitel zusammengefaßt und im Kontext verschiedener (ökologischer) Disziplinen erörtert werden; außerdem werden dort Analyseoptionen aufgezeigt die sich in der Region oder mit ähnlichen Datensätzen in Zukunft ergeben könnten.

Chapter 1: General Introduction

The Framework

This thesis focusses on analysing several datasets collected in the Mediterranean region, to investigate regional species ecology and vegetation ecology and to solve questions of wide interest. Therefore big datasets are analysed; big data are more and more publicly recognized in the last years, as personal data are collected and analysed e.g. in social media. In the last decades datasets of growing size arose in various scientific fields and the availability of biological data from vast public and private collections opened perspectives also for ecologists, not least as gathering, storing and analyses of data improved. Organism-related datasets are stored in museums, herbaria and other collections, globally holding an estimated sum of 2.5 billion specimens (Lavoie 2013). For plant-related studies further plot-based plant and vegetation records exist from literature or unpublished sources (Chytrý et al. 2016; Dengler et al. 2011; Dengler and sPlot Core Team 2014; GBIF 2017; Purschke et al. 2015). The higher the numbers of records and their density in a study, the higher is the statistical power of the results; and dependent on quantity and quality of data, various methodologies may apply.

The following section gives a brief overview of general approaches and methodologies used for analyses of floristic and plant-sociological datasets across disciplines, most of which are related to ecology. The two types of data used in such analyses comprise species records with their locations; the second type includes compositional data usually taken from vegetation relevées. At least for most of those plot based samples also information on site conditions are gathered and stored (see Dierschke 1994 for methods of plot based sampling). Such datasets are versatile and thus feature research in multiple disciplines, some of which overlap in used methodologies. Depending on the evaluated scale level and the research questions asked, different aspects of information are addressed (i.e. location in space, time, genetic identity, site conditions, etc.). Fields of interest may regard ecological questions connected to species and site conditions, focussing on causalities; common patterns of taxa may be analysed, when chorology is considered. When small scales apply, plant ecology, population ecology or vegetation ecology can be featured, while wider scale studies may relate to macroecology, phylogeography or biogeography; thereby overlaps may exist (for scale issues read Huston 2002). Approaches on different scale levels benefit from each other or are depending: wider scale analyses need local ecological studies for base data, and ecological results for interpretation and reasoning. Reversely local plant studies are often supported by studies in wider context. The scale-dependence of ecological studies has been frequently discussed (Austin and van Niel 2011; Cohen et al. 2015; Ellison 2002; Franklin et al. 2013; Giakoumi et al. 2013; Gotelli et al. 2009; Kang et al. 2014). The chapters of this thesis address various scales and diverse data sources and thus allow for a discussion across disciplines. The following section lists concepts and analytical

approaches, which are mostly in relation to the performed case studies; the selection though is not comprehensive.

Distributions and diversity of organisms can be displayed in manifold ways. Floristic literature for regions, countries and larger units comprise descriptions and thematic maps. The latter display distribution patterns as points, grid cells, ranges or combinations thereof, some include further information such as data density and variation within taxa. The quality of such maps depends on the density of records, the map purpose, its generalisation, etc.; floristic atlases mainly comprise such distribution maps with layout and features being scale-dependent (e.g. Garve 1994; Haeupler and Schönfelder 2004; Jalas et al. 1996, 1999; Jalas and Suominen 1972–1994; Kurtto and et al. 2004–2018; Meusel et al. 1978; Perring and Walters 1990; Poppendieck 2011; San-Miguel-Ayanz et al. 2016; Strid 2016). For the interpretation of such maps ecological, geographical, geological, climatological and other background knowledge is helpful. Distribution patterns of plant species based on large datasets were analysed on regional (e.g. Law et al. 2009; Schmiedel 2014), national (e.g. Korsch 1999; Wasowicz et al. 2014) or global scale (e.g. Kier et al. 2005; König et al. 2017). Such patterns can be influenced by sampling intensity and may reflect the state of knowledge concerning taxonomy (Meyer et al. 2016; Yang et al. 2013, 2014). Distribution data of species were used to describe diversity patterns (Barthlott et al. 2007; Kier et al. 2005; Mutke et al. 2010) as well as centres of endemism (Kier et al. 2009; Médail and Quézel 1997; Myers et al. 2000). Species distribution and therewith diversity patterns depend on e.g. an interplay of abiotic conditions and various other environmental aspects like spatial constraints, connectedness and interactions with other organisms. Distributions of species also have relevance regarding time dimensions; i.e. distribution patterns can be compared for different points in time, including short term movements (e.g. migratory bird species; Bradsworth et al. 2017; Coxen et al. 2017), changes over years and decades (e.g. invasive organisms; Broennimann et al. 2007; Hanski and Gilpin 2008; Merow et al. 2017), but also range changes over historical and deep time periods (e.g. Graham et al. 2010; Jackson and Overpeck 2000; Svenning et al. 2011). Some of the mentioned studies comprised modeling approaches, which integrate environmental data and usually species data to predict potential species distribution or to assess (complex) species niches (Elith et al. 2006; Merow et al. 2014; Peterson et al. 2007; Peterson and Soberón 2012).

The complexity of environmental conditions along studied gradients deserves high attention in ecological studies. Environmental variables are (to varying extent) responsible for plant reactions and plant cover on various scales (biomes, vegetation zones, vegetation formations, vegetation patches, but also plant growth, etc.); whereas ecologists try to understand these plant-environment or vegetation-environment relations (e.g. Frey and Lösch 2010). A palette of quantitative

measurements and qualitative parameters is used to assess the causal relations in ecological context; thereby each set of assessed environmental conditions represents a selection within the ecological space of the study object. Measurable conditions are limited proxies to circumscribe ecological spaces and the complexity of the latter is often underestimated (Peterson 2007). Based on the concept of Hutchinson (1957) the sum of site conditions for a species form the ecological niche. Depending on the working scale, different scientific methods of measurement are available. While for plant ecological approaches, ecophysiological measures can apply, on larger scales data from geoscientific fields are used, e.g. from remote sensing. High-resolution datasets were produced describing environmental aspects of major importance, such as geomorphology (Gorokhovich and Voustianiouk 2006; Nikolakopoulos et al. 2006; Siart et al. 2009), climate (Hijmans et al. 2005; Karger et al. 2016; Kottek et al. 2006), or soils (Ballabio et al. 2016; Bockheim and Gennadiyev 2010; Brogniez et al. 2015; Panagos et al. 2015). Coarse scale studies analysed and classified environmental conditions (König et al. 2017; Stein et al. 2015; Weigelt 2014). Accuracy and resolution of global environmental datasets can be limited; and thus fundamental issues may apply when such data is downscaled. While for some applications raw data and algorithms allow for downscaling (Fridley 2009; Salzmann 2006), in other cases downscaled results can be misleading (Scherrer et al. 2011; Scherrer and Körner 2009; Schmidli et al. 2007). Along gradients and various spatial scales the environmental variability has an impact on distribution and diversity of organisms and vegetation. In conjunction to the understanding of plant affinities to site conditions, plants and vegetation units may be indicative for environmental conditions. This way ecological indicator values can be assigned to species (Ellenberg 1974, see Chapter 2). In analogy to plant taxa, also plant communities may be indicators for a certain combination of site conditions.

Variation and hidden diversity are further important aspects of ecological studies. Intraspecific variation may consider phenotypes (Violle et al. 2012) or genetic differences (e.g. haplotype variation; Christe et al. 2014; Hampe et al. 2003; Petit et al. 2003; 2004). The importance of intraspecific genetic variation is widely accepted as component of diversity (CBD 2012), but specific sampling and elaborated genetic laboratory analysis are needed for its assessment and so many aspects thereof wait to be discovered. Gaps in sampling and in taxonomic knowledge affect diversity patterns (Giam et al. 2010; Stork 1993). For various species ecological and genetic variation were jointly analysed, while for the vast majority such relations are still unknown (Lowe et al. 2004). In certain cases differences are so pronounced, that new species are found even among else well-studied organism groups (e.g. Pearson et al. 2007; Sattler et al. 2007; Shneyer and Kotseruba 2015). The growing field of landscape genetics, combines population genetics and landscape features (Holderegger et al. 2010; Manel et al. 2003; Manel and Holderegger 2013).

Co-occurrences of plant species are usually assessed by sampling of vegetation plots. Such relevées comprise compositional data, with cover or frequencies of species and site attributes, and often additional information on management and structure. Datasets with plot data were for instance used to perform vegetation classification. For Europe, being the most densely sampled continent, vegetation plots were systematically conducted since the first half of the 20th century (Braun-Blanquet 1928; Guarino et al. 2018). The compilation of Mucina et al. (2016) gave an overview on vegetation classes, orders and alliances on European scale. Most recently also European beech-forest communities were analysed (Jiménez-Alfaro et al. 2018). The authors thereby evaluated the complex interactions of land use history, biogeographical region and species pool on vascular plant diversity. Classified vegetation units are descriptors for environmentally distinct vegetation and therewith apply for nature conservation and planning. The pressure of global change makes protection of resources and biological structures a necessity, which is regarded in international treaties, conventions and laws. Environmental protection laws integrate species and also vegetation units as central elements; e.g. the member states of the European Union agreed on the common Natura 2000 framework, which includes 233 habitat types (European Commission - DG Environment 2013).

Mediterranean islands as study region

All presented studies of this thesis focus on the islands Crete and Sicily (Figure 1.1), both located in the Mediterranean basin. The “Mediterranean” is defined differently depending on specific context and authors, related to either biological, climatic, cultural or other factors (Blondel and Aronson 2010). Most importantly climatic features are used to define the regions extent. The climate of the

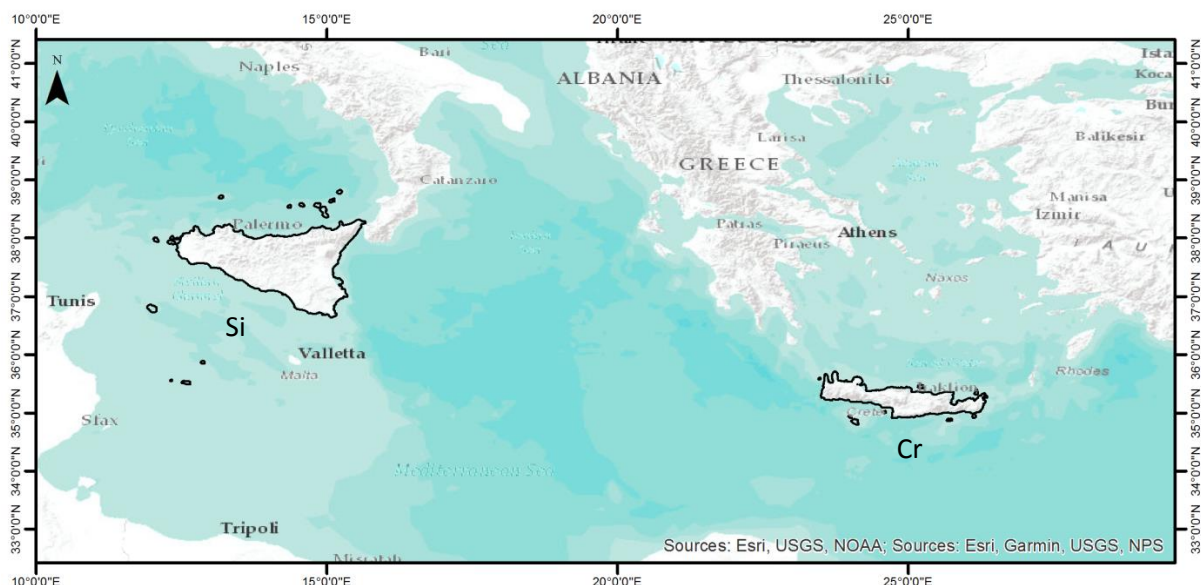


Figure 1.1 Regional topography and location of the studied islands Sicily (Si) and Crete (Cr), altitudinal variation based on ArcGis Online basemap (Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community).

Mediterranean region features high temperatures in summer and mild temperatures in winter; summers are dry as principal precipitation arrives in winter (Lionello 2012). Different climate diagrams for the region (Figure 1.1) show general similarities in the magnitude of temperatures and the annual distribution of precipitation but also differences in absolute values. Inter-annual climatic variability is a common feature (Lionello 2012).

The Mediterranean region underwent tremendous changes in climate and topography in millions of years, which influenced distribution of species. It is located at the borders of the Eurasian and the African tectonic plates. Highly dynamic tectonic processes result in, e.g. volcanism, seismic activities, and surface deformations, i.e. oceanic deeps and mountains up-folding. The study region is affected differently by suchlike phenomena. In Crete active volcanoes probably had little direct impact (Bottema and Sarpaki 2003), while on Sicily Mount Etna dominates the eastern Island, being the highest volcano in Europe (3323 m a.s.l.). A period of massive mountain uplifts started approximately during Oligocene-Miocene boundary and is partly lasting until today. Through tectonic activities and sea level fluctuations, many Mediterranean islands were repeatedly isolated and reconnected to other islands and the mainland, e.g. during the Messinian salinity crisis the Mediterranean dried out almost completely for 1.5 million years until 5 Million years ago. Thereafter the fusion of Pliocene islands led to the formation of a Crete, similar to its present form (Greuter 1979b). Sicily was repeatedly connected to North Africa during the Messinian and possibly again during Pliocene to

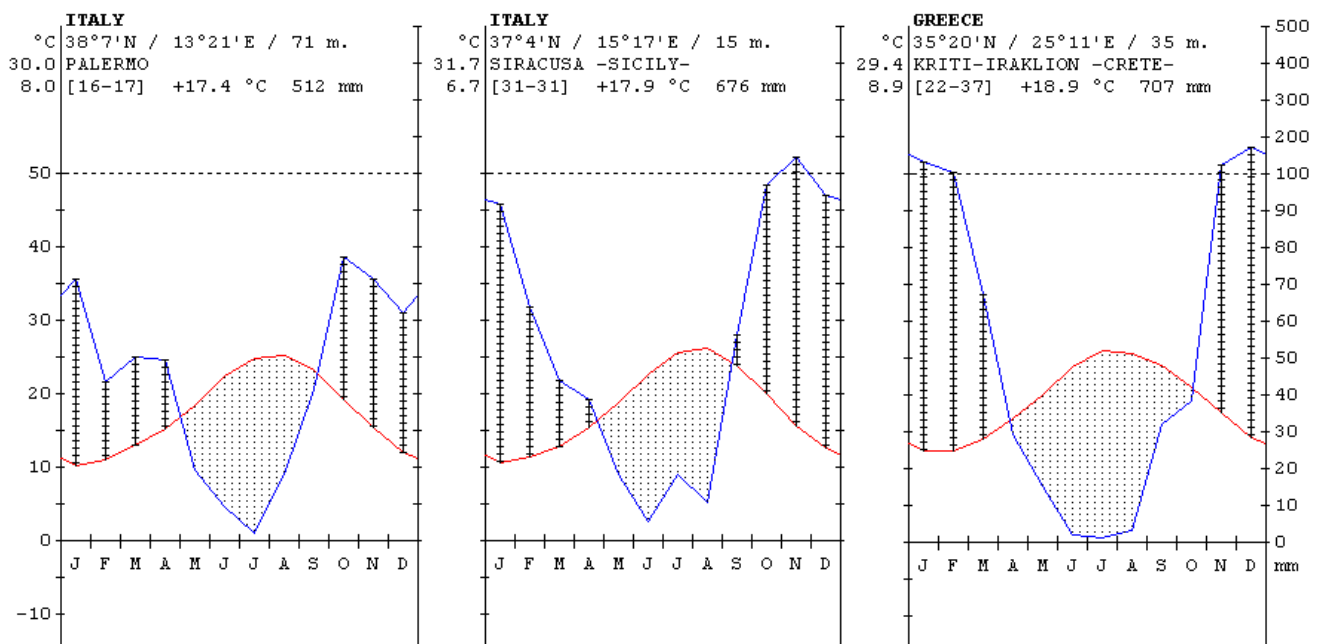


Figure 1.2 Climate diagrams for three weather stations within the study area (Palermo & Siracusa, Sicily, Italy; Iraklion, Crete, Greece; modified from Rivas-Martínez 1996-2009), all stations are located in the lowlands and share a typical Mediterranean climate with a pronounced water deficit in summer, indicated by a drop of the precipitation (blue line), temperatures (red line) are mild in winter and hot in summer.

Pleistocene (Azzaroli and Guazzone 1979; Stöck et al. 2008; Troia et al. 2012). Such ancient isolation and release processes, along with ecological gradients, were major drivers of the observed biogeographical patterns (Bonnano and Veneziano 2016; Greuter 1971; Rechinger and Rechinger-Moser 1951; Troia et al. 2011). For the South Aegean island arc, stretching from Peloponnese Peninsula over Kythera, Antikythera, Crete, Karpathos and Rhodes to South Anatolia, a biogeographical differentiation with gradual species turnover and specific endemics applies; within this row of islands Crete can be separated to a series of four distinct biogeographic units, each characterised by one of the main mountain massifs (Greuter 1971; Rechinger and Rechinger-Moser 1951).

Bedrock types are not equally distributed among the two islands (Figure 1.2); introductions to chapters 2 and 5 give in-depth information concerning geology. For Crete the geological overview maps of Creutzburg et al. (1977) and Seidel et al. (1982) are important references; in a map resolution of 1:50,000 further geological maps are available (HGME 1959–2002). A good geological reference in German is the field guide of Kull (2011). Fierotti (1988) produced a geological overview for Sicily in a map resolution 1:2,500,000. Bedrock types together with erosion, volcanic and tectonic processes shape the geomorphology of the two islands. Sedimentous rocks are characteristic and wide spread on both islands, they dominate valley bottoms, debris fans and coasts; and they feature hilly and plain land surfaces. On Sicily only, the exposed massifs of Mt. Etna, Mt. Lauro and few other places are dominated by volcanic rocks. In many parts of this island evaporites occur, which include massive minable layers of salts, but predominantly consist of gypsum. The latter bedrock occurs on small scales also on Crete. Metamorphic rocks cause usually acidic soil reactions and are merely restricted to Peloritani in Sicily, while they cover significant proportions of mountains and mid altitudes in Central and Western Crete. Limestones dominate large parts of the Cretan mountains and occur scattered in Sicilian Mountains like Madonie, Iblei and Sicani. This bedrock frequently results in a rough topography with diverse surface structures typical for karst landscapes, including dolines, sink holes and caves (Di Maggio et al. 2012; Egli 1991).

Soil layers are usually shallow in karstic landscapes, while merely in hollows and rock crevices a substantial accumulation applies. Such heterogeneous topographic structures feature different ecological conditions in close vicinity, e.g. poor and rich soils, or mesic and xeric conditions, with corresponding vegetation occurring site by site. In mid-altitudes of mountains, where mesic conditions apply, humus-rich soils are scattered allowing for small-scaled agriculture. Most of the agricultural lands though are bound to sediment areas, including softer flysch, in hilly landscapes,

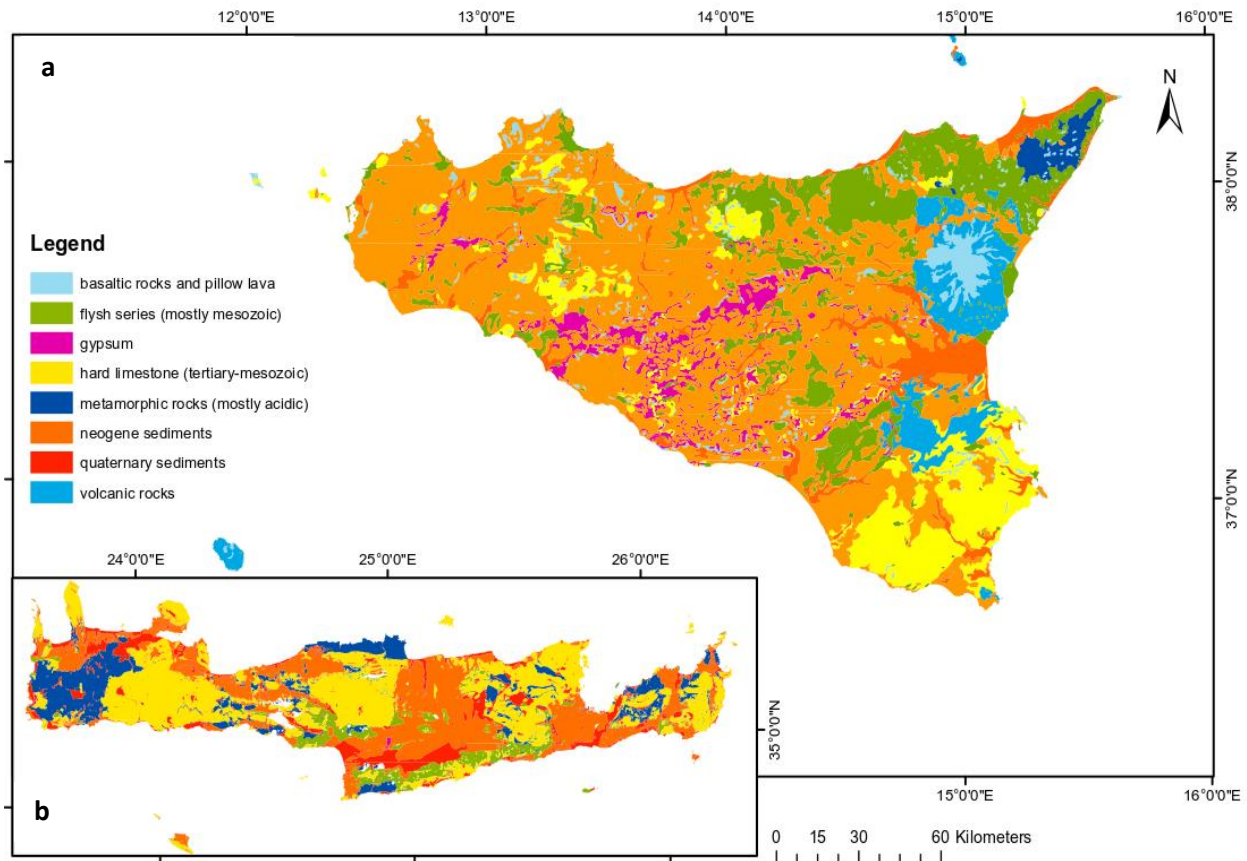


Figure 1.3 Geological maps for Sicily (a) and Crete (b) with a unified and simplified legend, based on published maps (Fierotti 1988; HGME 1959–2002).

plains and valleys, where deeper soils may have accumulated (Jahn and Schönfelder 1995; Venturella 2004). In the lowlands oxidation and long drought periods often hamper soil development, especially where vegetation is reduced and bare soils are exposed. Soils in the Mediterranean are influenced by the special regional climate, the often mountainous topography, significant Saharan dust immissions and long-lasting human impact (Macleod 1980; Suchodoletz et al. 2013; Yaalon 1997).

People have inhabited the Mediterranean area for a long time; through isotope dating the baseline of cultural activities was predated to at least 64,000 years (Hoffmann et al. 2018). The Mediterranean is of high cultural, historical, political and economic importance; several civilisations and empires grew and disappeared around the Mediterranean (Arabian, Cartagan, Egyptian, Greek, Minoan, Ottoman, Roman, Venetian etc.). Landscape and vegetation were thus shaped by millennia of cultivation and settlement (Blondel and Aronson 2010; Grove and Rackham 2001; Quézel 2004). Today coastal zones are densely inhabited, especially where urban centres spread and tourism flourishes. This leads to urban sprawl, land sealing, waste deposition and massive destruction of natural and semi-natural habitats. In contrast many mountainous and hinterland regions with traditional land use were abandoned. Only during the financial crisis of the last years, a reverse trend of people returning to the Mediterranean mountains gets obvious. Intensively irrigated olive and

fruit plantations are extended in some parts of Crete at least. Goat and sheep densities, being high in parts of Crete, not least through EU-subsidies, maintain old open landscapes but also increase landscape degradation (Lorent et al. 2009). Also in Sicily such contrasting trends of land use intensification and abandonment are omnipresent. Intensification and abandonment of land use differ across the Mediterranean but may likewise threaten biodiversity (Caraveli 2000; Kerckhof et al. 2016; Nainggolan et al. 2012; Plieninger et al. 2013; Zdruli 2014).

Hotspots of biodiversity are considered as focal areas of biodiversity protection. The Mediterranean region is such a biodiversity hotspot in a global perspective, with high numbers of vascular plants and vertebrates (Myers et al. 2000). The authors regarded an extant of 2.362,000 km² of primary vegetation with about 25,000 plant species. According to Médail and Quézel (1997, 1999) the Mediterranean basin features 9-10% of the global plant species on only 1.6% of the surface area. Their studies identified strong differences in the distribution of biodiversity within the Mediterranean basin, whereas Sicily and Crete were among the main centres of plant species richness. One reason for this species richness is the high proportion of endemic species. The Mediterranean area hosts strongholds of endemism, i.e. species with local restriction, especially on its islands and in mountain ranges. Endemics and relict stands of plant species are considered to be results of repeated long term environmental changes, which led to spread, retreat, extinction and isolation of species (Greuter 1972, 1979a, 1991, 2001). Environmental conditions in the region recurrently changed in millions of years, e.g. because of macroclimatic changes (Lionello 2012) and pronounced geological dynamics (Faccenna et al. 2014). In this context endemics can be a result of speciation (neo-endemism) or survival of once widespread species (paleo-endemism, definitions see Cox and Moore 2010). For further details on Mediterranean endemics see chapter 4. When the mentioned dynamics were a driving force, there must have been sites of relative stability where taxa could thrive under widely unfavourable conditions. Several such refugial areas were identified within the Mediterranean (Biltekin et al. 2015; Breton et al. 2006; Fuentes-Utrilla et al. 2014b; Gavin et al. 2014; Molina-Venegas et al. 2015; Orain et al. 2013; Petit et al. 2003; Salmerón-Sánchez et al. 2014). Refugial areas may indicate long-term survival of species and they frequently match with biodiversity hotspots (Harrison and Noss 2017; Médail and Diadema 2009).

The high species richness in the Mediterranean is not least featured by the multitude of environmental conditions, forming steep gradients. This allows for organisms with different environmental affinities, and from distinct biomes, to co-occur on small area. Around the Mediterranean basin mountainous areas create topographical and climatical variation, being a key for pronounced gradients and biodiversity (McNeill 1992; Regato and Salman 2008). Other reasons for high taxonomic diversity in the Mediterranean region are influences from neighbouring floristic

regions. The global position of the region at the edges of main continents allowed floristic elements from South-Euro-Siberian, Saharo-Arabian, Irano-Turanian, Macaronesian, and other elements to mix-up in the region (Pignatti 1978; Schröder 1998); e.g. coastal spots in Sicily and Crete, as well as small islets around both islands comprise various African floristic elements (Bergmeier et al. 1997; 2001; 2011; Brullo and Guarino 2000; Pasta 1997a, 1997b); and in the mountains of both studied islands species and vegetation with (cool) temperate preferences exist (Bauer and Bergmeier 2011; Brullo et al. 2012; Marino et al. 2014).

When the big Mediterranean islands are further compared in their species composition, similarities and differences get obvious (Junikka et al. 2006). An ecological comparison for woody species in the Mediterranean region was performed as well (Quézel 1979a; Quézel and Médail 2003). For the biggest Mediterranean islands including Sicily and Crete Quézel (1988) gave a phytogeographical comparison. The latter author also compared the forest communities of Cyprus and Crete and extensively discussed species composition and distribution within the Eastern Mediterranean and beyond (Quézel 1979b); thereby he consulted various studies, e.g. in Southern Greece (Barbéro and Quézel 1976), in Anatolia (Akman et al. 1978) and in the Levant (Barbéro et al. 1976). Brullo et al. (2001b) write about coniferous woodlands in high altitudes for the Central and Eastern Mediterranean. Forest communities in Northern Algeria are related to those with wider Mediterranean distributions (Meddour et al. 2017). An overview to coniferous plant communities across Central and Eastern Mediterranean is given in Brullo et al. (2001b); a wider scale was also addressed for *Quercus ilex* woodlands by Barbéro et al. (1992). The ecology of Cretan woody vegetation and its species are discussed in various studies (e.g. Barbéro and Quézel 1980; Bauer and Bergmeier 2011; Bergmeier and Goedecke 2017; Egli 1998, 2000). For Sicily woody vegetation and its species composition were also described and analysed in various studies (e.g. Badalamenti et al. 2018; Brullo et al. 1995; 1999; Brullo and Marcenò 1985; Guarino and Pasta 2017; Marcenò and Guarino 2015; Marino et al. 2014).

Even though the last paragraphs comprised various studies for woody species, vegetation and ecology in the Mediterranean region, important scientific knowledge gaps for woodlands and beyond exist there (Scarascia-Mugnozza et al. 2000). The Mediterranean, not least due to its outstanding biological and environmental diversity and for its unique biogeographical features, is of high overall significance for the conservation of diversity across scales. The Mediterranean biodiversity is protected by major contracts and conventions (CBD 2012; European Commission - DG Environment 2013) and this gets especially important under globally changing conditions (Heywood 1999; Médail 2017). This thesis aims at contributing to the scientific investigation in the Mediterranean and thus at supporting conservation and management.

Analysed datasets

One main database used (in chapter 2, 4, 5) is the personal floristic database of Ralf Jahn. In it he gathered information on the distribution of plant species in the Cretan area (Crete, Karpathos, Kasos, Saria, and further small islands and islets in the South Aegean). The database is a collection of around 900,000 sets of locations of plant taxa, containing their coordinates and a variety of additional site-based data gathered in the field. The collected information came from field studies and extractions from literature, details in terms of woody species are listed in chapter 2, 4 and 5. Initially, the preparation of the flora of Crete in German language made the author study the region (Jahn and Schönfelder 1995). Further publications of the data of R. Jahn are considered in several peer reviewed articles (Amigues and Greuter 2004; Bergmeier et al. 1997; 2001; 2011; Greuter et al. 2002; Jahn 2003; Mucina et al. 2009) and the data are included in a series of books (Strid 2016; Strid and Strid 2009-2013; Strid and Tan 2003). A second type of analysed datasets is the plot based database of Prof. Dr. E. Bergmeier containing more than 6,500 vegetation relevées, which is included as KRITI (Bergmeier 2012) in the European Vegetation Archive (EVA; Chytrý et al. 2016). It contains plots with all occurring species and their abundance from various vegetation units. For a study on the endemic *Z. abelicea* several records from literature and unpublished collections of records were combined (Table 4.1). For the more global study on the ecology of Cretan woody species the latter sources, were used as well as other published and unpublished data (Table 2.1). For Sicily a database of vegetation relevées was used comprising records from various sources (Table A 5.3). Relevées from all mentioned sources follow Braun-Blanquet methodology and the species are recorded in the extended 9-grade scale (Wilmanns 1998), plot sizes varied within the frame proposed by Chytrý & Otýpková (2003). For one study composition data was analysed (chapter 3). All studies are subjected to woody plants, being selected as elements of potential climax vegetation, for their key role in ecosystems, but also for reasons of data availability and data quality.

Further information for the conservation status of habitats comes from a data survey performed in the framework of the European Union Natura 2000 network and the connected monitoring and mapping campaigns (Directive 92/43/EWG). From 2013 to 2015 a team of foresters and biologists was in charge with the monitoring of the conservation status for the habitats from Annex I of the Natura 2000 directive, which led to an evaluation and quantification of habitat types for all Greece. Also for all Natura 2000 protected areas in Crete and surrounding islets habitat polygons were assigned, which were stored as shape-files in a GIS. The abundance of typical species for each habitat was independently assessed for these polygons and for reference plots within. A specific protocol sheet for each habitat type was filled out during this assessment (Appendix Figure A 3.1; Field protocol for habitat type 92C0 discussed in chapter 3).

Abiotic variables for the two regions Crete and Sicily are as well stored in a GIS environment. Datasets containing precipitation and temperature data on a 1 ArcSec-scale ($\sim 1\text{km}^2$) used in the chapters 2, 3 and 4 were published by the *European Food Safety Agency* (European Commission Joint Research Centre 2012; Hijmans et al. 2005). Chelsa-climate data applied in chapter 5 refer to Karger et al. (2016). Further variables are calculated based on a Digital Elevation Model (DEM) available with a pixel resolution of 30 m at the website of the European Environmental Agency (EEA 2015). Information on the geological substrata was created for Crete using digitized geological maps with a map resolution of 1:50,000 (HGME 1959–2002). These maps were revised and unified for all the maps from different years and mapping institutions sources (Manthey and Goedecke, unpublished). To be able to work on a common geological base map for Crete and Sicily, the latter dataset was further simplified and combined with the digital geological map of Fierotti (1988); a unified legend scheme was produced therefore (Goedecke, Marcenò, Guarino, Jahn and Bergmeier, unpublished).

Chapter overview and problems addressed

This thesis contains studies on different methodological basis, so data base queries, an ecological classification and a vegetation classification were applied as well as species distribution modelling. Therewith the thesis gives examples for analytical approaches applicable for floristic and plant-sociological data bases. It addresses problems in plant ecology, population ecology, vegetation ecology, biogeography and nature conservation. The study region Crete (chapters 2-4) together with Sicily (chapter 5) comprises $35,600\text{km}^2$, and thus this spatial frame allows studies on various scale levels (supra-regional, regional, sub-regional). The diverse spatial frame in combination with different study objects (species, populations, vegetation units) allows to address a multitude of opportunities for the analyses of big datasets of floristic and plant-sociological data and to highlight limitations.

The presented approach in the **second chapter** aims to display spectra of site conditions for a large amount of individual sites for the woody species in a region. The methodology helps to assess species niches, through combining precise coordinates for large numbers of species records with site information in a geographical information system (GIS). Following questions are answered:

Which combinations of landscape-related site parameters (macroclimate, topoclimate and bedrock type) are associated with species and ecological species groups? Do these species groups reflect vegetation patterns?

The case study in the **third chapter** focusses on the regionally diverse vegetation of *Platanus orientalis* woodlands, presents results of a vegetation classification, a classical application in plantsociology and features a data query for a conservation status assessment. Aims of the study are:

To explore the variation in vascular plant species composition and to describe the plant communities of *Platanus orientalis* woodlands in Crete; to provide a survey of the current quality and conservation status and of the impacts affecting the present state and the future of the *Platanus* woodland ecosystems.

In the **fourth chapter** models are used to predict species distribution. In a numerical algorithm locations of the species are combined with digital map data, aiming to extrapolate suitability of sites across the study area. In this context the distinct (meta)populations of the endemic species *Zelkova abelicea* from the main mountain ranges of Crete were ecologically analysed. We ask the following research questions:

How much do isolated populations of *Zelkova abelicea* differ in ecology, as expressed by abiotic variables? Are these differences related to known genetic patterns? Which environmental factors influence species distribution models most? How do predicted distribution patterns relate to known records? Do combined (meta)population samples improve the predictive value for known neighbouring populations?

In the **fifth chapter** species distribution modelling is performed for databases of species records for Crete and Sicily. Woody species from wide-spread maquis vegetation are compared by reciprocal extrapolation, whereby training of models applies for one island and the quality of distribution models is tested on the other island. Therewith following questions are answered:

To what extent can a model be calibrated on one island be a good predictor of the distribution of a given species on another island? Which are the most influential variables in our distribution modeling and are they the same on both islands for a given species? Is the observed shifting ecological behaviour (and related occurrence probability) of a given species more influenced by climatic, by geomorphological or by edaphic drivers?

The final **sixth chapter** concludes the overlapping issues of the four studies. Results are jointly discussed in relation to other studies. Subsections address species ecology, the role of intraspecific differences, ecological species groups in relation to vegetation units, and the assessment of complex environments. Further perspectives and ideas are discussed comprising neighbouring disciplines. Finally limitations concerning species-environment relations, intraspecific genetics and data bias are discussed.

Chapter 2: Quantified ecology and co-occurrence of Mediterranean woody species in a landscape context

Goedecke, F.; Jahn, R. & Bergmeier, E. (2018) Quantified ecology and co-occurrence of Mediterranean woody species in a landscape context. *Plant Ecology* 219: 481–496.

Quantified ecology and co-occurrence of Mediterranean woody species in a landscape context

Abstract

Understanding co-occurrence and ecological affinities of plant species is essential in vegetation and landscape ecology. In a case study, we analysed distribution records with high data density of all commonly occurring tree and shrub species of Crete (Greece) with offshore islands. We present the ecological range of widespread and more range-restricted species in the Mediterranean area, visualising their affinities for macroclimate, topoclimate and geology by means of an ecological heatmap. Complete linkage classification of combined ecological spectra revealed groups of generalist species with broad ecological amplitude, groups related to zonal vegetation and chiefly dependent on elevation, and species of azonal vegetation grouped mainly by topography and substrates. Species and ecological groups with high affinity may be indicative of (a combination of) site features. Our re-evaluation of plant distribution records links plant geographical and ecological information, and thereby complements expert habitat and species assessments. Our case study provides deeper understanding of ecological patterns, and at the same time allows for comparison and extrapolation to other biomes.

Keywords: *ecological heatmap; geospatial data; heatload; location-based geodata extraction; realised niche; topographical wetness index*

Introduction

Understanding plant species-environment relations is fundamental in ecology and in applications such as forestry, nature conservation and restoration. Plant physiological and environmental measures along with records of single species or plant communities in plots and transects are used to assess such relations. However, in situ measurements providing quantitative primary data may be unfeasible or too costly to get in difficult terrain. Alternatively, ecological preferences are often extrapolated from co-occurring species (Abs et al. 2008; Filella and Peñuelas 2003). Field records of site conditions such as soil properties (Ghosh et al. 2016) can be assigned to species that grow on the site. Ellenberg (1974) was among the first to class Central European plant species in ecological groups and to define indicator values, which inspired vegetation ecologists in other regions (Böhling et al. 2002; Guarino et al. 2012; Pignatti et al. 2005). Indicator values were proven and tested by field measures in various attempts (Marcenò and Guarino 2015; Schaffers and Sýkora 2000; Schwabe et al. 2007), but they remain essentially expert-based.

Location-based extractions of site features deliver ecological information about species and thus attempt to determine the realised niche (Hutchinson 1957). The accuracy of this approach depends on scale, quality and quantity of data. Recently, amounts and accessibility of distribution data have continuously increased, not least because niche modelling and distribution modelling are gaining importance (Calabrese et al. 2014; Elith et al. 2006; Reger et al. 2014) and high-resolution environmental datasets are increasingly available (Barry and Blanken 2016; Berry et al. 2016; Byrne and Pickard 2016; Copeland and Harrison 2015). Quantified species-environment relations were assessed in several regions (e.g. Aronson et al. 2015; Birnbaum et al. 2015; Parra-Quijano et al. 2012). Bilton et al. (2016) defined climatic niche groups to predict plant community responses to climate change. The analysis of plant species chorology in conjunction with ecological indicator values revealed coarse-grained landscape patterns (Korsch 1999). The latter approach is an example for quantified landscape classification, just like the study of Bölöni et al. (2011), who used occurrences of habitats within a country-wide grid. In a landscape context Corney et al. (2004) and Olthoff et al. (2016) assessed the ecology of forest species by using forest inventory plots. Both studies evaluated the importance of environmental parameters for woody vegetation and species distribution, the latter study additionally discussed niche separation. The ecology of co-occurring species relates vegetation to environmental variables in manifold ways: vegetation zones are coupled to macroclimatic gradients (Bazan et al. 2015), and vegetation depends on soil, topography and bedrock (Kopecký and Čížková 2010; Kosmas et al. 1993; Kruckeberg 2002). Environmental filtering and biotic interactions may influence patterns of co-occurrences on particular sites (for a review see Kraft et al. 2015). Environmental parameters influence vegetation patterns but reversely woody species have effects on a wide range of environmental conditions and processes such as microclimate, soil

formation and nutrient accumulation (Ludwig and Tongway 1995; Shachak et al. 2008). Our quantifying approach can thus help to understand the formation of vegetation and productivity patterns in a landscape context.

Ecological surveys on woody vegetation exist for the Eastern Mediterranean region on small scale, based on different methods, and for particular species and vegetation types (e.g. Bergmeier 1995; Bergmeier and Goedecke 2017; Matthäs 1988; Søndergaard and Egli 2006). Several papers and reviews discussed woody species and their vegetation in the landscape context of Crete as a result of extensive field surveys (e.g. Barbéro and Quézel 1976, 1980; Bauer and Bergmeier 2011; Greuter 1975; Rechinger and Rechinger-Moser 1951; Zohary and Orshan 1965). A wider scale was applied for the ecological indicator assessment for the South Aegean (Böhling et al. 2002), for which the authors combined vegetation plots with on-site measures and soil analysis. We chose the Aegean island of Crete to quantify woody plant relations to macroclimate, bedrock type and topography. Crete is most suitable for such a case study as it comprises both high environmental and floristic diversity (Fielding and Turland 2005; Jahn and Schönfelder 1995; Rackham and Moody 1996). By visualising ecological spectra of species and by revealing co-occurrence patterns of species groups in a landscape context we add to current plant ecological knowledge. The use of a big dataset of records dispersed along steep ecological gradients allows for an objective quantification of site features across habitats. Our results allow for various applications as we related well-known taxa and mostly apparent site features on landscape scale. We addressed the following research questions: Which combinations of landscape-related site parameters (macroclimate, topoclimate and bedrock type) are associated with species and ecological species groups? Do these species groups reflect vegetation patterns?

Methods

Study area and species addressed

Crete (South Aegean, Greece), with a terrestrial surface area of 8729 km², is the fifth largest Mediterranean island. While annual and local variation is high, the climate characteristics in the lowlands and mid altitudes are typically Mediterranean, with precipitation chiefly in the mild winter half year and a pronouncedly dry and hot summer (Jahn and Schönfelder 1995; Lionello 2012). Longer-lasting snow and frost periods occur in the high mountains. The island's geological uplift at the edge of a subduction zone exposed a variety of rock types and shaped a pronounced relief, with deep gorges and several high mountain massifs, interrupted by Neogene plains (Kull 2011). While woodlands are fragmented and occur mainly in the mountains (Bauer and Bergmeier 2011), shrublands (phrygana and maquis) predominate. About 1800 vascular plant taxa have been recorded, with about 10 % being endemic to the island (Fielding and Turland 2005; Jahn 2003). The woody flora

includes about 53 species of trees and taller shrubs, excluding dwarf shrubs. For this study, we gathered more than 13500 records of all native tree and shrub species present on Crete and its surrounding islets. Data were compiled from databases derived from various types of field surveys (Table 2.1). Older records without precise coordinates were ignored. To remove misplaced records we checked all locations visually using high-resolution satellite imagery (Ktimatologio 2016). Species records closer than 100 m were merged to reduce spatial auto-correlation and sampling bias. We disregarded about 16 rare woody species with 10 or fewer reliable records. After data validation we considered a total of 9692 records from 37 species of trees and higher shrubs (Table 2.2), covering the woody-vegetation in almost all of the islands' landscapes. The biological characteristics of the

Table 2.1 Databases contributing to this study, collector names indicated for > 100 records; with survey time span, related publication, data type, and number of records.

Author	Sampling period	Publication	Data type	Records
Bergmeier, E.	1989-2014	Bergmeier (2012) + Unpublished material	relevées	3172
Jahn, R.	1989-2014	Unpublished material	floristic/ relevées	2728
Natura 2000 team	2013-2015	Unpublished material	vegetation mapping	739
Risse, H.	1981-1986	Unpublished material	floristic	354
Egli, B.	1998-2000	Egli (2000) + Unpublished material	forest monitoring	345
Greuter, W.	1960-1983	Greuter (1967) + Unpublished material	floristic	318
Matthäs, U.	1982-1986	Matthäs (1988)	floristic	253
Zaffran, J.	1964-1967	Unpublished material	floristic	162
miscellaneous	-	-	floristic/ relevées	1621
total				9692

studied species are given in Table 2.2. Despite the large number of records, data deficiencies occur, chiefly in cultivated and urban areas and in inaccessible terrain (Figure 2.1). The nomenclature follows Dimopoulos et al. (2013, 2016). Twenty species have a wide Mediterranean distribution, while eight species are restricted to the Eastern Mediterranean. *Zelkova abelicea* is endemic to the island of Crete. Many species occur as either shrubs or trees, i.e. they have high phenotypical variation depending on site conditions and management.

Environmental data and habitat affinity

Abiotic site variables and their data sources are given in Table 2.3. Map production and the handling of spatial data were performed in ArcGIS (ESRI 2013). Relief indices were calculated using the Geomorphometry and Gradient Metrics Toolbox (Evans et al. 2014). The wetness index (compound topographic index or *cti*) accounts for water movement; for each grid cell the natural logarithm of the quotient of upstream contributing surface area and the tangent of the slope within the grid cell is calculated, resulting in high values for sink areas (Gessler et al. 1995). The heatload index (*heatload*) maximises in steep south-western slopes (McCune and Keon 2002); and the solar radiation index

Table 2.2 Mediterranean woody species sampled on Crete; see Dimopoulos et al. (2013, 2016) for nomenclature and chorology: *Bk* Balkan, *EA* European-SW Asian, *EM* E Mediterranean, *Eu* European, *MA* Mediterranean/ Atlantic, *Me* Mediterranean, *ME* Mediterranean-European, *MS* Mediterranean-SW Asian, *Pt* Paleotemperate; * life form among phanerophytes (P) and chamaephytes (Ch): *N* nano, *caesp* caespitose, *pulv* pulvinate, *rept* reptant, *scap* scapose (Jahn and Schönfelder 1995).

taxon name	abbreviation	family	chorology	life form*
<i>Acer sempervirens</i> L.	Acesem	Aceraceae	EM	P caesp/ P scap
<i>Arbutus andrachne</i> L.	Arband	Ericaceae	EM	P caesp/ P scap
<i>Arbutus unedo</i> L.	Arbune	Ericaceae	Me	P caesp/ P scap
<i>Berberis cretica</i> L.	Bercre	Berberidaceae	EM	NP
<i>Castanea sativa</i> Mill.	Cassat	Fagaceae	Eu	P scap
<i>Ceratonia siliqua</i> L.	Cersil	Fabaceae	Me	NP/ P caesp/ P scap
<i>Crataegus monogyna</i> Jacq.	Cramon	Rosaceae	Pt	P caesp/ P scap
<i>Cupressus sempervirens</i> L.	Cupsem	Cupressaceae	EM	P scap
<i>Erica arborea</i> L.	Eriarb	Ericaceae	Me	NP/ P caesp
<i>Euphorbia dendroides</i> L.	Eupden	Euphorbiaceae	Me	NP/ P scap
<i>Ficus carica</i> L.	Ficcar	Moraceae	MS	P scap
<i>Juniperus macrocarpa</i> Sm. in Sibth. & Sm.	Junmac	Cupressaceae	Me	NP/ P caesp/ P scap
<i>Juniperus oxycedrus</i> subsp. <i>deltoides</i> (R.P. Adams) N.G. Passal. in Bernardo, Passalacqua & Peruzzi	Junoxy	Cupressaceae	EM	NP/ P caesp/ P scap
<i>Juniperus turbinata</i> Guss.	Juntur	Cupressaceae	MA	NP/ P caesp/ P scap
<i>Laurus nobilis</i> L.	Launob	Lauraceae	Me	P caesp/ P scap
<i>Myrtus communis</i> L. subsp. <i>communis</i>	Myrcom	Myrtaceae	Me	P caesp
<i>Nerium oleander</i> L. subsp. <i>oleander</i>	Nerole	Apocynaceae	Me	P caesp
<i>Olea europaea</i> L. subsp. <i>sylvestris</i>	Oleaur	Oleaceae	Me	NP/ P caesp/ P scap
<i>Phillyrea latifolia</i> L.	Philat	Oleaceae	Me	NP/ P caesp/ P scap
<i>Phoenix theophrasti</i> Greuter	Phothe	Arecaceae	EM	P scap
<i>Pinus brutia</i> Ten.	Pinbru	Pinaceae	Me	P scap
<i>Pistacia lentiscus</i> L.	Pislen	Anacardiaceae	Me	NP/ P caesp/ P scap
<i>Pistacia terebinthus</i> subsp. <i>terebinthus</i> L.	Pister	Anacardiaceae	Me	P caesp/ P scap
<i>Platanus orientalis</i> L.	Plaori	Platanaceae	EM	P scap
<i>Prunus prostrata</i> Labill.	Prupro	Rosaceae	Me	Ch rept
<i>Prunus webbii</i> (Spach) Vierh.	Pruweb	Rosaceae	EM	P caesp
<i>Pyrus spinosa</i> Forssk.	Pyrspi	Rosaceae	Me	NP/ P caesp/ P scap
<i>Quercus coccifera</i> L.	Quecoc	Fagaceae	Me	P caesp/ P scap
<i>Quercus ilex</i> L.	Queile	Fagaceae	Me	P caesp/ P scap
<i>Quercus ithaburensis</i> subsp. <i>macrolepis</i> (Kotschy) Hedge & Yalt. in Greuter	Queith	Fagaceae	Me	P scap
<i>Quercus pubescens</i> Willd.	Quepub	Fagaceae	ME	P caesp/ P scap

continued

<i>Rhamnus lycioides</i> subsp. <i>oleoides</i> (L.) Jahand. & Maire	Rhalyc	Rhamnaceae	Me	NP
<i>Rhamnus saxatilis</i> subsp. <i>prunifolia</i> (Sm.) Aldén in Strid	Rhasax	Rhamnaceae	Bk	Ch rept
<i>Salix alba</i> L.	Salalb	Salicaceae	EA	P scap
<i>Styrax officinalis</i> L.	Styoff	Styracaceae	Me	P caesp
<i>Vitex agnus-castus</i> L.	Vitagn	Lamiaceae	MS	P caesp
<i>Zelkova abelicea</i> (Lam.) Boiss.	Zelabe	Ulmaceae	endemic	P caesp/ P scap

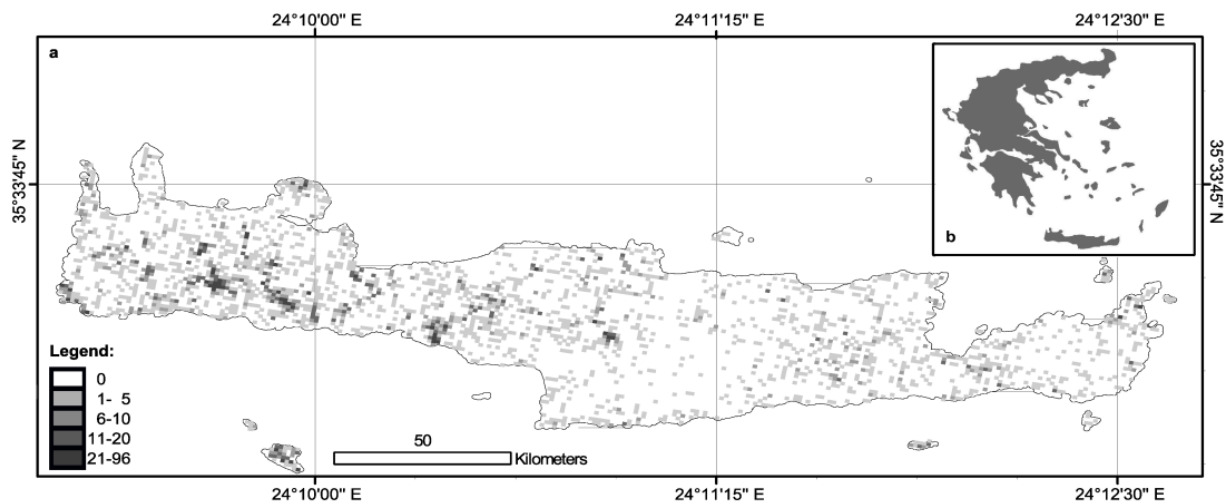


Figure 2.1 The island of Crete with (a) density of woody species records visualised in 1-km-grid cells and (b) its position within Greece.

Table 2.3 Abiotic site parameters and raster data used in this study.

Dataset	Source
(i) <i>altitude</i> , digital elevation model (DEM), based on ASTER satellite data, 30m raster resolution, elevation a.s.l. [m]	EEA (2015)
following derivatives are calculated from DEM:	
(ii) <i>solarrad</i> , point solar radiation for whole year by summed-up monthly values [MW/m ² /yr]	Rich et al. (1994); Fu and Rich (2002)
(iii) <i>cti</i> , compound topographic index [no unit]	Gessler et al. (1995)
(iv) <i>heatload</i> , heatload index, 3 rd equation, constant latitude=35.5° [no unit]	McCune and Keon (2002)
(v) <i>slope</i> [°]	Burrough and McDonell (1998)
worldclim climate data, 30arcsec resolution (≈1km)	Hijmans et al. (2005)
(vi) <i>tmean</i> , mean annual temperatures [°C]	
(vii) <i>prec_ann</i> , mean annual precipitation sum [mm]	

(*solarrad*) sums annual solar energy, with mountain shade (viewshed restriction) causing lowered values (Rich et al. 1994). Geological substrates were digitised from published maps (HGME 1959–2002). Polygons (n=7505) were assigned to twelve major stratigraphic geological units (Table 2.4).

We generalised geological units in accordance with overview maps (Creutzburg et al. 1977; Seidel et al. 1982).

Table 2.4 Geological units in Crete; from digitalisation of geological maps 1:50,000 (HGME 1959–2002), area [km²] and percentages of total island surface are displayed.

Geological unit	Abbreviation	Area [km ²]	%
<i>Neogene sediments</i>	N	2422.6	29.0
<i>Tripolitza limestone</i>	TZ	1264.4	15.1
<i>Phyllite-quartzite</i>	PQ	1076.3	12.9
<i>Plattenkalk limestone</i>	PK	1002.2	12.0
<i>Quaternary sediments</i>	Q	914.3	11.0
<i>Tripali limestone</i>	TR	539.3	6.5
<i>Pindos limestone</i>	PD	314.6	3.8
<i>Pindos flysch</i>	PD-F	292.8	3.5
<i>Tripolitza flysch</i>	TZ-F	290.3	3.5
<i>Ophiolites</i>	O	91.2	1.1
<i>Asteroussia crystalline rocks</i>	AS	71.9	0.9
<i>Asteroussia flysch</i>	AS-F	57.1	0.7

To relate established knowledge and the ecological groups found in the present study, species co-occurrence patterns were compared to widely used phytosociological schemes (Mucina et al. 2016), EUNIS habitats (Janssen et al. 2016), and to Natura 2000 habitat types (European Commission 2013). We assessed the relative frequency of our studied species within the vegetation units of these schemes, addressing four levels of abundance (usually not occurring, occasional, common, (partly) dominant); therefore we used the latter references, our field notes and the works of Barbéro and Quézel (1976, 1980), Bauer and Bergmeier (2011), Bergmeier (1995), Bergmeier and Goedecke (2017).

Statistical analyses

Environmental complexity and its relations to species occurrences were visualised by Principle Component Analysis (PCA), using standard settings in Canoco (Ter Braak and Šmilauer 2012). We used the environmental variables given in Table 2.3 as a basis for the ordination; species and bedrock types were then added as supplementary variables. We calculated the first four canonical axes and applied centering and standardizing of data. All other plots were prepared using R version 3.24 (R Development Core Team 2017). Boxplots were used to display variation of numerical parameters. We produced an ecological heatmap with species grouped by similarity of spectra of environmental data (*heatmap.2()*, *gplots* package, Warnes et al. 2016). Environmental data for this plot comprised means of continuous environmental parameters and frequencies of geological substrates. These values were standardized in a first step [1] to create the heatmap; therewith underlying relative frequencies may increase the relative importance of environmental aspects, e.g. rare geological substrates are

weighed higher in relation to more abundant ones. In a second step [2] we increased simplicity of the plot by grouping very similar bedrock types using a classification (*complete linkage clustering*, dendrogram not shown). Thereafter four pairs of bedrock types with very similar patterns were merged (e.g. Asteroussia crystalline rock (AS) and Tripolitza flysch (TZ-F) to AS_TZ-F). This reduced the twelve geological units to eight columns in the matrix. In a last step [3] species in the final heatmap were grouped using another *complete linkage clustering* based on the reduced set of bedrock types and all continuous environmental parameters. The latter method outperformed several other clustering algorithms, in giving consistent species patterns with little chaining effect. We separated the classification tree along a uniform cut level of similarity, where a clear differentiation between clusters applied.

Results

Ecological species groups

Complete linkage clustering revealed seven groups of woody species, with two to nine species each. While *group [1]* comprises mainly widespread lowland species (Figure 2.2, Figure A 2.1), occurring in a variety of habitats and vegetation units (Figure 2.4), the others often depend on specific and infrequent habitat conditions. *Group [1]* comprises several fruit trees such as olive, carob and fig. The latter grows on exposed slopes, but also as subcanopy tree in alluvial forests. *Pistacia lentiscus* is the most frequently recorded woody plant in the lowlands and occurs in several vegetation units (Figure 2.4). *Pinus brutia*, *Quercus coccifera*, *Rhamnus lycioides* subsp. *oleoides* and *Euphorbia dendroides* grow chiefly on dry limestone slopes with low annual precipitation. *Phillyrea latifolia* and *Rhamnus* occur usually in mixed evergreen woodlands and shrublands and have raised relative affinity to *tripolitza* limestone. *Group [2]* includes two species with a regional preference for low *heatload* and a relative affinity to ophiolites. While *Quercus pubescens* is a woodland tree, *Crataegus monogyna* is a shrub often associated with these oak woods. *Group [3]* contains deciduous *Pyrus spinosa*, *Prunus webbii* and *Vitex agnus-castus*, being frequent on various kinds of flysch and on Asteroussia crystalline rock.

All species tolerate disturbance and are common in anthropogenic habitats. *Vitex* occurs chiefly in (dry) river beds, on alluvial fans and other disturbed sites down to the coastline (Figure A 2.2). *Group [4]* comprises two drought-tolerant extensive-rooted junipers, which occur scattered on sandy and other permeable substrates along the Cretan coasts and on a few of the small islands. *Group [5]* comprises seven riparian species – as indicated by the highest *cti* values – as well as *Quercus ithaburensis* subsp. *macrolepis*, a non-riparian species growing on deep soils. *Platanus orientalis* and *Salix alba* are riparian trees, the latter in wide stream beds, as indicated by low slope angle and

high solar radiation. *Nerium oleander* and *Myrtus communis* are riparian shrubs in the undergrowth of *Platanus* gallery wood or without tree canopy in seasonally dry valleys. *Styrax officinalis* and

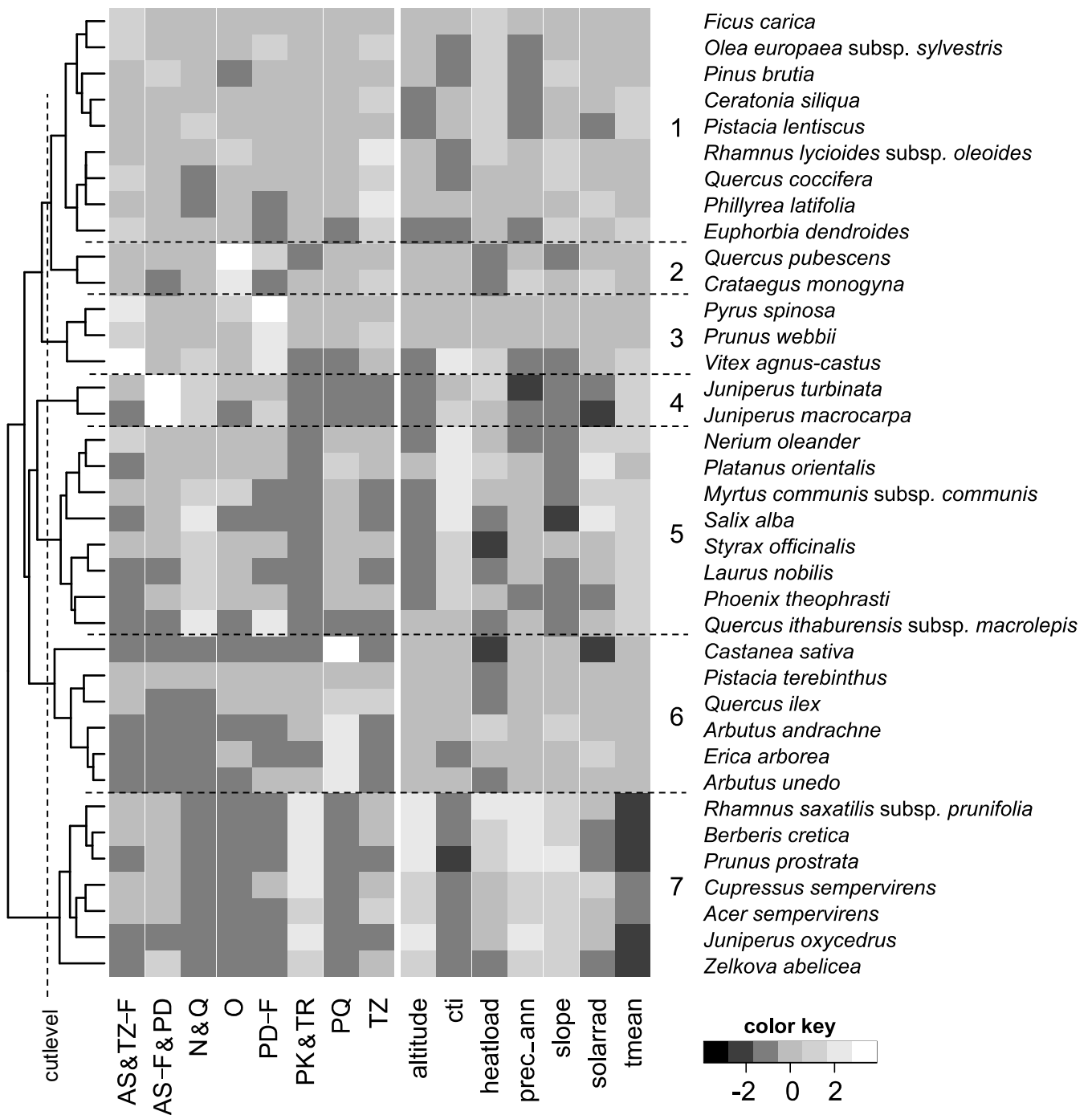





Figure 2.2 Ecological heatmap for Mediterranean woody species on Crete; based on complete linkage clustering of scaled values for environmental parameters and scaled percentage frequencies of geological substrate units (abbreviations in Table 2.4); group numbers 1-7, dashed lines indicate separation of dendrogram.

Laurus nobilis occur infrequently in wooded valleys with low *heatload*, avoiding high insolation. The only native palm *Phoenix theophrasti* occurs scattered along the coasts with groundwater supply,

Fig. 2.4 The matrix contains relative frequencies of 37 woody species from Crete in the units of three classification schemes (European Vegetation Classification, EUNIS Classification, Natura 2000 habitats (Annex I)).

Fig. 2.4 The matrix contains relative frequencies of 37 woody species from Crete in the units of three classification schemes (European Vegetation Classification, EUNIS Classification, Natura 2000 habitats (Annex I)).

 occasional
  common
  (partly) dominant

European Vegetation Classification

code	syntaxon name (class/order/ alliance; description)																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																											
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continued

EUNIS Classification		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37		
code	habitat																																							
B1.6b	Mediterranean and Black Sea coastal dune scrub																																							
E7.3	Mediterranean wooded pasture																																							
F5.1	Mediterranean maquis and arborescent matorral																																							
F5.5	Thermo-Mediterranean arid scrub																																							
F6.2	Eastern garrique																																							
F7.3	Eastern Mediterranean spiny heath (phrygana)																																							
F7.4c	Eastern Mediterranean mountain hedgehog-heath																																							
F9.3	Mediterranean riparian scrub																																							
G1.3	Mediterranean and Macaronesian riparian woodland																																							
G1.7b	Mediterranean thermophilous deciduous woodland																																							
G2.1	Mediterranean evergreen <i>Quercus</i> woodland																																							
G2.4	<i>Olea europaea-Cerastonia siliqua</i> woodland																																							
G2.5a	South-Aegean <i>Phoenix</i> grove																																							
G3.7	Mediterranean low land to submontane <i>Pinus</i> woodland																																							
G3.9b	Mediterranean Cupressaceae woodland																																							
H3.2d	Mediterranean basaltic inland cliff																																							
Natura 2000 habitats (Annex I)																																								
code	habitat, *priority																																							
2250	* Coastal dunes with <i>Juniperus</i> spp.																																							
3280	Constantly flowing Mediterranean rivers with Agrostoid species and hanging curtains of <i>Salix</i> and <i>Populus alba</i>																																							
4090	Endemic oro-Mediterranean heaths with gorse																																							
5210	Arborescent matorral with <i>Juniperus</i> spp.																																							
5310	<i>Laurus nobilis</i> thickets																																							
5330	Thermo-Mediterranean and pre-desert scrub																																							
5420	<i>Sarcopoterium spinosum</i> phryganas																																							
5430	Endemic phryganas of the Euphorbia-Verbascum																																							
8210	Calcareous rocky slopes with chasmophytic vegetation																																							
9260	<i>Castanea sativa</i> woods																																							
9290	<i>Cupressus</i> forests (Acero-Cupressum)																																							
9200	<i>Platanus orientalis</i> and <i>Liquidambar orientalis</i> woods (Plantation orientalis)																																							
9200	Southern riparian galleries and thickets																																							
9310	Aegean <i>Quercus brachyphylla</i> forests																																							
9320	<i>Olea</i> and <i>Cerastonia</i> forests																																							
934A	Greek Kermes oak forests																																							
9340	<i>Quercus ilex</i> and <i>Quercus rotundifolia</i> forests																																							
9350	<i>Quercus macrolepis</i> forest																																							
9370	* Palm groves of <i>Phoenix</i>																																							
9540	Mediterranean pine forests with endemic Mesogeic pines																																							

species group patterns were supported by a distinct distribution of most groups (Figure A 2.1) and by boxplots showing variation of raw data (Figure A 2.2).

Discussion

Quantifying ecological affinities

Our study quantified and confirmed ecological affinities (macroclimate, topography, geology) of the woody species of Crete. A sufficiently high number of reliable records enabled us to attribute sound ecological information to common species and to display the niche width of the species in landscape and regional context. This standardises and validates expert knowledge (Böhling et al. 2002; Fielding and Turland 2005; Jahn and Schönfelder 1995). Therewith our study supports the (re)assessment of ecological indicator values of species, regarding macroclimatic parameters. We generated novel datasets for species affinities to established topographic indices and displayed spectra of occupied geological substrates. Both aspects were poorly regarded in ecological indicator systems. Thus this type of data may substantiate new ecological indicator values for a couple of site features. Olthoff et al. (2016) compiled similar ecological spectra for woody species in a Palencia region, Spain. They covered different ecological gradients and a set of forest species. In contrast, we worked on an environmentally diverse island with longer (and steeper) ecological gradients (humid to arid, coastal to mountain ecosystems, etc.). Our selection of species is not restricted to forests and thus describes general woody vegetation patterns. Olthoff et al. (2016) displayed ecological response curves along the main axis of multivariate space including the results of compositional data, while we concentrated on the spectra of environmental conditions. By the similarity of these site spectra, species interactions can be indirectly discussed, although species composition and direct species interactions are not available from our dataset.

Other studies quantified macroclimatic preferences for continental endemics (Crisp et al. 2001) or reviewed multiple scales (Suggitt et al. 2017). Bilton et al. (2016) defined macroclimatic niches for species groups and assessed climate-change effects. Miller and Knouft (2006) characterised sites spectra of a fruit tree using environmental data extractions for a wide species range. Major climatic parameters of various trees were displayed on European level (San-Miguel-Ayanz et al. 2016). While the latter study improves our understanding of species niches and continental-scale distribution, it does not support local-scale applications of the information. In contrast our study addresses the regional level and allows for various applications. For the management of woodlands especially for rugged mountain landscapes relief parameters are important (Barry and Blanken 2016; Guisan et al. 1998). According to Fois et al. (2017) topography explains best the distribution of endemic plants in the island of Sardinia (Italy). The topographic position of sites may also control soil parameters, e.g. soil moisture, ground water level, pH-values, etc. (Kopecký and Čížková 2010; Kosmas et al. 1993;

Sørensen et al. 2006). Accordingly, topographic indices have been used for landscape-based modelling (Jones et al. 2010; McGarigal et al. 2009; Slavich et al. 2014). Our study is probably the first to relate bedrock types to woody species on a wider scale and across diverse habitats. The full spectrum of geological units has only been analysed for relatively few species (Austin et al. 1990; Leuschner et al. 2006), and many ecological studies merely compare siliceous and calcareous bedrock or address a single type of bedrock (Alvarez et al. 2009; Safford et al. 2005; Salmerón-Sánchez et al. 2014). Geological units are fundamental to site conditions, but alone, they are insufficient to predict plant distribution. In Crete, as elsewhere, chemical and structural bedrock and relief features, erosivity, (micro)relief, soil formation and topoclimate also play a role (Neff et al. 2006; Wang et al. 2004; for general information on rock type and plant relations see Kruckeberg 2002). We found that the range of bedrock types, along with other parameters related to climate and topography, were the main factors affecting variation in niche width.

Ecological groups and co-occurrence patterns

The ecological species groups found in the present study reflect azonal and zonal vegetation. Zonal patterns follow chiefly macroclimatic parameters that vary (mostly linearly) along the altitudinal gradient (Bergmeier 1995). Climatic events such as frost, known to limit altitudinal species ranges (Larcher 2006), are likely to differentiate groups of mountain plant species. Apart from extreme temperature ranges, altitudinal gradients vary in water supply. As water trickles away in the Cretan karst mountains (indicated by a low *cti*), trees and shrubs are subjected to decreased topographic water availability despite increased precipitation. Some species occupy rather distinct niches, made visible by their ecological spectra. *Zelkova abelicea*, a tertiary relict species and regional endemic (Kozłowski et al. 2014), turned out to be a tree of shady mountain slopes, which confirms field observations (Egli 1997; Søndergaard and Egli 2006). Species in *groups* [2] and [3] mostly occupy medium altitudes of west, south-central and central Crete; for *group* [6] medium altitudes apply. Species of the lowest vegetation zone, adapted to a pronounced Mediterranean climate, are represented by *group* [4]. Altitudinal zonation patterns in tree distribution are not always clearly visible. For instance, *Cupressus sempervirens* has a wide elevation range but occurs as a prevalent native forest tree only in the western mountains and scattered in the lowlands (Bauer and Bergmeier 2011). Even generalist species form distinct groups; especially *group* [1] comprises many widespread species, mostly found at low altitudes, where beside the Mediterranean climate (Aerts 1995; Larcher 2006; Mitrakos 1980), millennia of human impact favoured species resilient against drought, fire, cutting and browsing (Greuter 1975; Groves and Di Castri 1991; Jouffroy-Bapicot et al. 2016). Consequently, species such as *Pistacia lentiscus* and *Quercus coccifera* are common in various habitats. The latter is dominant in various shrub communities (Tsiourlis et al. 2009) but is also a tree of woodland remnants in a South Aegean habitat type of national significance (Dimopoulos et al.

2006). Other species groups are restricted to specific rock types even though the limited resolution of geological maps may blur the picture; for instance, base-rich outcrops with *Arbutus andrachne* scattered in phyllite-quartzite areas were disregarded, as were sandy soils suitable for *Juniperus macrocarpa*. Present records do not always reflect potential distribution. For instance, *Quercus ilex* thrives as dominant forest tree in some phyllite-quartzite areas in western Crete (Bauer and Bergmeier 2011), but frequent burning and cutting has transformed most such woodlands into maquis of *Arbutus unedo*, *Erica arborea* and a variety of (dwarf) shrubs. In our dataset *Q. ilex* records on these latter siliceous rocks are outnumbered by those on various limestones, where single trees can be found on cliffs or in deep valleys along shaded streams. This example shows that complex interactions of environmental variables and parameters that could not be recorded such as land use influence the overall validity of our results. A few ecological species groups comprise related taxa suggesting phylogenetic niche conservatism (Prinzing et al. 2001), e.g. junipers in *group [4]* with extensive root-systems and reduced leaves or the Ericaceae of *group [6]*, which share specific mycorrhiza giving advantages on base-poor soils. *Group [5]* features the highest *cti*, usually with water table up to the rooting zone and azonal vegetation dominated by *Nerium*, *Platanus* or *Phoenix*, representing some of the rarest and most vulnerable woodland types (Bergmeier and Goedecke 2017; Décamps and Décamps 2001).

The ecological species groups found in the present study were largely in accordance with units of the widely applied European habitat schemes, EUNIS and Natura 2000, and with phytosociological systems. Most woody species groups belong to Mediterranean pine and oak woodlands and associated maquis, Quercetea ilicis (Mucina et al. 2016; Figure 2.4), corroborating the indicator values of species for abiotic site attributes. Our ecological species groups also support the unique character of low-level vegetation units, e.g. a downy oak forest type on profound soils was described as phytosociological association Oenanthe pimpinelloidis-Quercetum brachyphyllae (Zohary and Orshan 1966) Barbéro and Quézel 1980, which comprises the two species of *group [2]*. The authors treat these two species as distinct regional taxa (*Quercus brachyphylla*, *Crataegus azarella*), whereas in the taxonomic reference we used they are merged to more widely circumscribed taxa. Our methodology in conjunction with genetic analyses, applied to vegetation in a wider area, could address unsolved taxonomic and syntaxonomic issues related to oak woods and beyond.

EUNIS habitats are characterised, at various levels, by a wide array of parameters (biogeography, abiotic environment, vegetation structure, prevailing plant life form, land use, etc.). A crosscheck with our woody species groups revealed 16 EUNIS level 3 habitats, most of which being in fact habitat complexes with several co-occurring woody species (Figure 2.4). Land use-related units (e.g., wooded pastures) feature various ecological species groups, indicating varying significance of abiotic

parameters. Natura 2000 habitats, defined in an expert-based (and political) process, are also based on multiple parameters of which plant species composition is arguably the most important one. Several of the twenty Natura 2000 habitat types to which we assigned Cretan trees and shrubs were narrowly defined with only few co-occurring woody species (Figure 2.4). The species groups revealed by our approach correspond to habitat schemes significant for land management and conservation. Zonal differentiation was only partly supported by our approach, as rather widespread generalists and specialists are separated and because the restriction to all woody species neglects differentiating low shrubs and herbs. The use of further plant species with clear altitudinal limits may improve zonal separation. Bazan et al. (2015) related classified compositional data with macroclimate and could support zonal patterns. Vegetation plot data in conjunction with environmental variables and management information may uncover (a)biotic interactions in relation to vegetation units (Corney et al. 2004). We confirmed general vegetation patterns although our approach was based on species records. Its application in other regions and across regions, especially where plot data are unavailable, could help to understand vegetation patterns on various scales.

Conclusion and outlook

Our quantification of environmental parameters provides a methodology for the ecological description of woody species distribution patterns in the South Aegean. We generated detailed spectra of occupied geological substrates and new data on macroclimatic and topoclimatic affinities. Our ecological species groups are influenced by the selection of environmental variables, by the generalisation level and by the classification method. The co-occurrence patterns found in the present study complement and summarize ecological findings and corroborate expert systems. As woody species are part of succession series and of climax vegetation, a quantified ecological characterisation improves our understanding of present-day (potential) natural vegetation and vegetation dynamics, setting the stage for a geobotanical characterisation and landscape description (Blasi et al. 2000; Bölöni et al. 2011; Lechner et al. 2016). Our data can only supplement niche and distribution models, where (a)biotic interactions apply (Austin et al. 1990; Guisan and Zimmermann 2000), but the present results provide an approximation of species-environment relations. Beyond this, interactions between environmental variables and between co-occurring species are not directly addressed by our approach. Unlike in most above mentioned models, we used simplified ecological spectra for presence-only data, which hardly allows for the quantification of interactions. For comparison of ecological spectra and co-occurrence we consider ecological heatmaps particularly helpful, because this plot type effectively summarises large amounts of information, can be understood intuitively and may include a classification tree. For widespread woody species, our study deepens the understanding of common and deviating abiotic affinities. Ecological differences of widespread and locally restricted species can be underlined using ecological spectra (Hand et al.

2017; Lavergne et al. 2004). Apart from trees, which are generally well-known, the approach is expandable to other groups of organisms. An extension of the approach beyond the study area, or to isolated metapopulations, especially in conjunction with genetic analyses, may reveal ecotypes, speciation processes and even cryptic taxa (Goedecke and Bergmeier 2017; Rissler and Apodaca 2007; Sattler et al. 2007).

Acknowledgements

EB and FG were supported by the Greek Ministry of Environment and the European Commission in the Natura 2000 mapping and monitoring project, thanks to all contributing authorities and co-workers. RJ was funded by Deutsche Forschungsgemeinschaft (DFG: Scho 2-1, 2-2). Ktimatologio SA gave permission to use their satellite-image service. Prof. W. Greuter (Berlin) generously contributed distribution data of his working group (1981-1987), funded by DFG (Gr 676/3-1). Locations of mountain species were delivered by B. Egli (Schaffhausen, Switzerland) and L. Fazan (Fribourg, Switzerland). Processing of geological data was supported by C. Manthey (Bochum), C. Kalaitzidis (MAICh, Chania) and Prof. U. Kull (Stuttgart). P. Mahdavi, I. Schmiedel and L. Sutcliffe (all Goettingen) commented on an earlier manuscript version. The critical comments and suggestions of the editor P. le Roux and three unknown referees helped us to improve the final version of the manuscript significantly.

Chapter 3: *Platanus orientalis* woodlands of Crete – diversity, distribution and conservation status

Bergmeier, E. & Goedecke, F. (2017) *Platanus orientalis* woodlands of Crete – diversity, distribution and conservation status. In: Achille, G. (ed.) Scritti in onore di Franco Pedrotti. Collana Natura e aree protette 31: TEMI, Trento, pp 29-45.

***Platanus orientalis* woodlands of Crete – diversity, distribution and conservation status**

Abstract:

Platanus orientalis, the Oriental plane, forms the most prominent riparian woods in Crete and the Aegean. The woodlands represent a Natura 2000 habitat type (92C0) of which Greece hosts by far the major part in Europe, both in terms of area and number of sites. The present paper provides a survey of the variation of *Platanus* woodlands in Crete, with respect to species composition, distribution and ecology. A total of 81 relevés have been distinguished into three plant associations, two of them described as new: *Euphorbio characiae-Platanetum orientalis* and *Hyperico hircini-Platanetum orientalis*. The former comprises woodlands of rocky stream valleys and alluvial fans without or with periodical surface water flow. The latter is restricted to shady ravines and valleys with seasonal or permanent water in schistose landscapes of western Crete. The third association, *Equiseto telmateiae-Platanetum orientalis*, is the most widespread and was found in valleys with seasonal or permanent water flow, chiefly associated with calcareous rock and base-rich sediments. Based on an assessment of the quality and conservation status of 74 *Platanus* woodlands throughout Crete, about one third turned out to be in good condition, and two thirds in unfavourable conservation status. Widespread and far-reaching adverse effects were water abstraction (noticed in 54 % of the woodlands), water and soil pollution including waste and garbage disposal (32 %), further the effects of fragmentation and disturbance of the riparian woods through plantations and roads (69 %) and invasive plants (42 %, chiefly *Arundo donax* and *Oxalis pes-caprae*). Widespread but less significant impacts were disturbances caused by non-intensive grazing, local erosion and leisure activities.

Keywords: Greece, habitat type, Natura 2000, phytosociology, plane, plant association, riparian vegetation, vegetation classification

Introduction

Platanus orientalis, the Oriental plane, is the well-known broad-canopy tree providing shade to numerous *platías* in villages of Greece and elsewhere in the eastern Mediterranean. As a native tree, it occurs from eastern Sicily through the southern Balkan Peninsula, the islands of the Aegean and Anatolia to the Caucasus, N Iran and further east to central Asia and Afghanistan. In Italy it is considered an archaeophyte (Rosati et al. 2015). *P. orientalis* forms woodlands near springs and as gallery forest along streams, often in ravines and at the bottom of valleys where water supply is not constrained by the Mediterranean summer drought. *Platanus* seedlings may be abundant in suitable places but the establishment of the seedlings depends on a number of fortunate circumstances such as the local topography with occasionally flooded but not severed or eroded fluvial terraces, moist soil, shady ground, proper weather, and the absence of overgrazing, conditions that, if unsuitable, will prevent successful regeneration from seeds in years. On the other hand, *P. orientalis* is well adapted to the riparian environment. The trees resprout readily if damaged by flood, storm or cutting, and thus withstand mechanical disturbance caused by torrential waters, landslides, or through pollarding, a treatment formerly common to harvest leaves at times when other fodder for livestock was unavailable.

According to the IUCN Red List of Threatened Species *Platanus orientalis* is considered to be endangered in parts of its range because of changing water courses for irrigation purposes and the increased expansion of agriculture (World Conservation Monitoring Centre 1998). *Platanus* woodlands have been listed as habitat type 92C0, “*Platanus orientalis* and *Liquidambar orientalis* woods (*Platanion orientalis*)”, in Appendix I of the Habitats Directive of the European Union (European Commission - DG Environment 2013). Within the EU, the habitat type occurs in S Bulgaria, Cyprus, Greece and Italy (where it is presently restricted to rather small areas in Sicily; Brullo and Spampinato 1990; Pedrotti and Gafta 1996). Greece accounts for by far the largest number of sites and surface area of this habitat type. Although the official area estimates for the habitat type in Greece appear much exaggerated (according to the European Environment Agency (2015), an area of 866 km², but with an average width of gallery forest of 25 m the given forest area would amount to a total length of 34640 km!), Greece bears prime responsibility for the habitat type and its conservation among the member states and Europe-wide (Dimopoulos et al. 2006).

In the island of Crete (S Aegean, Greece), *Platanus orientalis* occurs as a native tree throughout the island but is much more common in the west and scattered in the east. It is found in Crete up to over 1000 m (Jahn and Schönfelder 1995), and to 1300 m in the southern mainland of Greece, but occurs at higher altitudes chiefly as small groups of trees or as single trees. Although *Platanus* forms impressive woods in the Aegean the species composition of the woodland ecosystems has not yet

been studied on the basis of a sufficient number of sample plots. Five relevés of plane woodland with the rare wetland endemic *Carex cretica* from W Crete were published by Bergmeier and Abrahamczyk (2007). Further floristic and ecological notes with reference to *Platanus* woodlands from Crete were provided by Rechinger and Rechinger Moser (1951), Gradstein and Smittenberg (1977), Fielding and Turland (2005), and Bergmeier and Abrahamczyk (2008).

The *Platanus* woods of Crete are mainly riparian and arranged in continuous or frequently discontinuous 5-25(-40) m wide bands of some hundreds of meters, typically along V-shaped valleys and ravines, or on coastal plains, accompanied by rangelands with phrygana or by macchia, deciduous or evergreen woodland, or cultivated land (Figure 3.1). The water flow of the streams may be seasonal or permanent, or there may be no surface waters except for events of torrential rainfall. Groundwater flow, however, permanently accessible to the tree roots, is a precondition for plane woodlands. Alluvial deposits are sandy or silty, or commonly rocky on talus fans, in steeper valleys,



Figure 3.1 *Platanus orientalis* woodlands in Crete: a) in a ravine, b) pollarded trees in a valley pasture used for pig grazing, c) along a stream with adjacent *Citrus* plantations, d) along a lowland stream with *Arundo donax*; all photos from April 2015 by F. Goral (a), I. Schmiedel (b, d) and C. Barnick (c).

and along permanent streams. Boulders may be carried in torrents. *Platanus* woods occur in environments of calcareous and siliceous rock, near springs, on alluvial plains and in valleys deepened in landscapes of marble and marl, schist, and sandstone (Dimopoulos and Bergmeier 2008).

Many Cretan *Platanus* woodlands are situated in sites of the Natura 2000 conservation network and are thus under statutory protection (Bergmeier et al. 2006; Dimopoulos et al. 2005, 2006). Nevertheless, the distribution and present conservation status of the riparian woods is not well known, neither which impacts affect the ecosystems and their species composition and to what extent. The aims of the present paper are therefore

- to explore the variation in vascular plant species composition and to describe the plant communities of *Platanus orientalis* woodlands in Crete;
- to provide a survey of the current quality and conservation status and of the impacts affecting the present state and the future of the *Platanus* woodland ecosystems.

Franco Pedrotti dedicated a lifelong scientific interest to the ecology, phytosociology and conservation of riparian forests (e.g. Pedrotti 1984, 1995; Pedrotti and Gafta 1996). This paper is devoted to our friend Franco on occasion of his 80th anniversary, trusting that it will be acknowledged by the jubilarian, and conducive to the knowledge and conservation of the riparian woodlands of Crete and Europe.

Materials and methods

Relevés of *Platanus orientalis* woodlands were extracted from the database of Cretan vegetation (Bergmeier 2012). *Platanus* woodlands were represented in the database by 81 relevés recorded mostly between 1999 and 2015, incidentally or mainly within the frame of a number of projects, among them the documentation and mapping of Natura 2000 sites. Specifically, the relevés resulted from fieldwork carried out by E. Bergmeier (33 relevés), S. Abrahamczyk (25), G. Ilgenfritz (11), W. Wolf (8), and F. Goedecke (4).

Extraction criteria were a *Platanus* canopy of at least 35 %, completeness and reliability of species recording, of the assessment of structural details, and the availability of precise geographical data of the plots with latitude and longitude coordinates. Obviously planted *Platanus* groves were not included. The plot size of the relevés was generally about (60-)100-300 m², with a few smaller plots included due limited accessibility of the sites, and larger plots accepted provided that scale-dependent homogeneity criteria were fulfilled. Plant species cover-abundance data were estimated

using the extended Braun-Blanquet scale (e.g. Dierschke 1994). The nine scale values were later transformed in mean cover percentage values (1, 2, 3, 4, 8, 18, 38, 63, 88 %). Bryophytes were deleted from the dataset prior to analysis, as this plant group had been considered only in a subset of the relevés. The 81 relevés were exported from the vegetation database management system Turboveg (Hennekens and Schaminée 2001) and classified by means of the divisive cluster analysis tool Two-way Indicator Species Analysis (TWINSpan; e.g. Gauch and Whittaker 1981). TWINSpan was run under JUICE 7.0 (Tichý 2002), using four “pseudospecies cut levels” (0, 2, 8, 38). Of the four relevé clusters resulting from the hierarchical subdivision of the dataset at the second level, the first two were re-combined (i.e. to first subdivision level) in order to improve the interpretability of that entity and the floristic distinctness of the clusters. Hence, three relevé clusters were maintained which are easily distinguished by differential plant species. A synoptic table was generated to show the three clusters and their species composition. The nomenclature of the vascular plants follows Dimopoulos et al. (2013).

The local conservation status for the habitat type 92C0 (“*Platanus orientalis* and *Liquidambar orientalis* woods (*Platanion orientalis*)”) was assessed in 74 *Platanus* woods throughout Crete in 2014 and 2015 using threshold quality criteria of the plant species inventory, habitat structures, and adverse effects. Adverse effects on forest habitats were grouped to (1) Damage to the water regime, (2) Pollution of the habitat, soil and water resources, (3) Disturbance of the forest vegetation and damage to the structure, (4) Occurrence of invasive species, (5) Fragmentation and overuse of the habitat. The conservation status per polygon of *Platanus* woodland was assigned to one of three classes: good, inadequate, bad. The latter two classes may be combined as ‘unfavourable’. If any of the adverse effects were significantly affecting the quality of a polygon of *Platanus* woodland, the overall conservation status for the polygon was considered inadequate. Two or more serious negative impacts resulted in a bad conservation status. The conservation status assessment was carried out mostly in Natura 2000 sites, in the framework of the mapping and monitoring project of Cretan habitat types listed in Appendix I of the Habitats Directive, here specifically of the habitat type 92C0).

Results and Discussion

Plant communities and diversity

Most of our relevés of riparian *Platanus* woodlands were from the provinces of Chania and Rethimno in W and WC Crete, respectively (Figure 3.2). Our records range from about sea level to 780 m, at thermo- to meso-mediterranean, or planar to submontane levels, thus representing much of the altitudinal range of *Platanus* woodland in Crete. Almost 90 % of the plots were situated in between 20 and 500 m. Our dataset of 81 relevés comprised well over 2000 species records, with an average of 25.8 species per relevé. Species numbers varied widely between 8 and 70, reflecting the variation in area and continuity of the ground colonizable by vascular plants. The high total number of recorded plant species (360) comprised to more than half species occurring in one (127) or two (77) relevés only. These were mostly casual plants from adjacent lands.

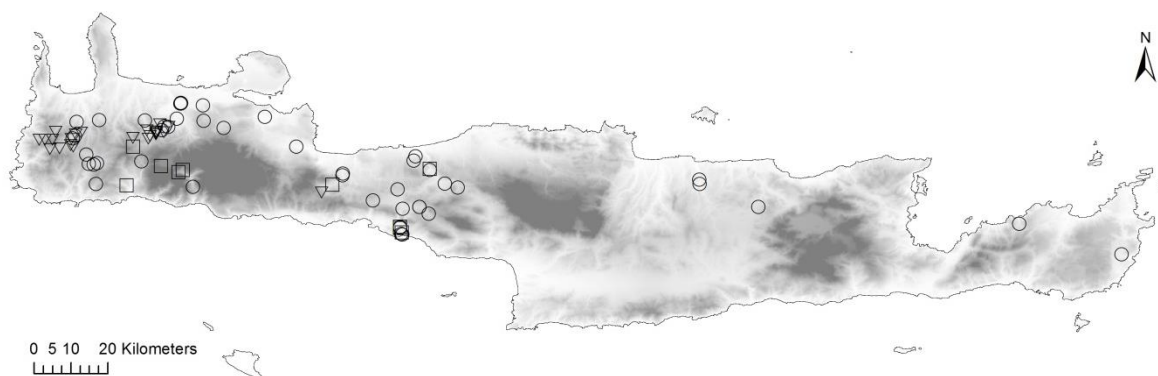


Figure 3.2 Distribution of vegetation records of *Platanion orientalis* in Crete. The records are grouped and identified as associations 1) *Euphorbio characiae-Platanetum orientalis*, square □, 2) *Equiseto telmateiae-Platanetum orientalis*, circle ○, 3) *Hyperico hircini-Platanetum orientalis*, triangle ▽.

Apart from *P. orientalis* itself only few species occurred in more than 50 % of the relevés (*Hedera helix*, *Nerium oleander*, *Dioscorea communis*, *Rubus sanctus*), and 76 species occurred in 10 % or more of the relevés (Table 3.1). Among the 20 most common species were two trees, both deciduous (*Platanus orientalis*, *Ficus carica*), two shrubs (*Rubus sanctus*, *Myrtus communis*), three woody lianas (*Hedera helix*, *Smilax aspera*, *Vitis vinifera*), two of which evergreen, and the rest mesic herbs with a high proportion of much-branched climbing or trailing vines (*Dioscorea communis*, *Galium aparine*, *Rubia peregrina*), and tuberous (*Arisarum vulgare*, *Arum concinatum*, *Cyclamen creticum*, *D. communis*, *Oxalis pes-caprae*) or rhizomatous (*Melissa officinalis*, *Pteridium aquilinum*) perennials.

The classification of the dataset resulted in three unequally represented woodland types (Table 3.1), here interpreted as phytosociological associations

- (1) *Euphorbio characiae-Platanetum orientalis* ass. nov.
- (2) *Equiseto telmateiae-Platanetum orientalis* Bergmeier 1990
- (3) *Hyperico hircini-Platanetum orientalis* ass. nov.

Table 3.1 Synoptic table of Cretan *Platanus orientalis* woods, based on 81 relevés, distinguished into the associations *Euphorbio characiae-Platanetum orientalis* (1), *Equiseto telmateiae-Platanetum orientalis* (2) and *Hyperico hircini-Platanetum orientalis* (3). Frequencies of species are in per cent. High frequencies of 40 % or more in an association are in bold print. Non-differential species occurring in 8 or fewer relevés (< 10 % absolute frequency) were omitted. Woody plants in the herb layer are indicated hl, in the shrub layer sl.

Association	1	2	3
No. of relevés	10	48	23
Trees, shrubs and woody vines			
<i>Platanus orientalis</i>	100	100	100
<i>Nerium oleander</i> sl	80	81	48
<i>Hedera helix</i>	.	73	78
<i>Smilax aspera</i>	30	29	48
<i>Vitis vinifera</i>	20	33	35
<i>Ficus carica</i>	.	35	22
<i>Platanus orientalis</i> sl	20	33	13
<i>Myrtus communis</i> sl	10	27	26
<i>Styrax officinalis</i> sl	10	19	.
<i>Vitex agnus-castus</i>	20	15	.
<i>Arbutus unedo</i> sl	10	.	30
<i>Phillyrea latifolia</i> sl	10	.	26
<i>Laurus nobilis</i> sl	.	8	13
<i>Salix alba</i>	.	13	4
<i>Ceratonia siliqua</i>	20	6	4
Differential species of the <i>Euphorbio characiae-Platanetum</i>			
<i>Rhagadiolus stellatus</i>	80	2	4
<i>Euphorbia characias</i>	70	15	9
<i>Catapodium rigidum</i>	50	4	9
<i>Aetheorhiza bulbosa</i>	50	4	9
<i>Leontodon tuberosus</i>	40	.	4
<i>Galium murale</i>	40	.	.
<i>Phlomis fruticosa</i>	40	4	.
<i>Dracunculus vulgaris</i>	40	2	.
<i>Satureja thymbra</i>	40	2	.
<i>Bromus sterilis</i>	40	4	.
<i>Geranium molle</i>	40	.	.
<i>Hypochaeris achyrophorus</i>	40	.	.

Continued on next page.

Association	1	2	3
Differential species of the <i>Hyperico hircini</i>-<i>Platanetum</i>			
<i>Pteridium aquilinum</i>	10	17	83
<i>Athyrium filix-femina</i>	.	6	65
<i>Rubia peregrina</i>	.	21	61
<i>Selaginella denticulata</i>	20	8	57
<i>Hypericum hircinum</i> subsp. <i>albimontanum</i>	.	6	57
<i>Crepis fraasii</i>	20	10	52
<i>Erica arborea</i>	.	.	48
<i>Ranunculus neapolitanus</i>	10	13	43
<i>Castanea sativa</i> hl	.	.	39
<i>Osmunda regalis</i>	.	6	35
<i>Primula acaulis</i>	.	2	35
<i>Asplenium onopteris</i>	.	2	35
Diagnostic species of the <i>Platanion orientalis</i> and the <i>Populetalia albae</i> in Crete			
<i>Melissa officinalis</i>	30	46	48
<i>Parietaria judaica</i>	.	48	13
<i>Arum concinnum</i>	30	38	13
<i>Dorycnium rectum</i>	.	33	35
<i>Adiantum capillus-veneris</i>	.	25	43
<i>Carex pendula</i>	.	35	13
<i>Platanus orientalis</i> hl	.	25	30
<i>Equisetum telmateia</i>	.	33	13
<i>Rumex conglomeratus</i>	20	23	17
<i>Lecokia cretica</i>	10	17	35
<i>Ficus carica</i> hl	10	15	35
<i>Scirpoides holoschoenus</i>	.	13	35
<i>Equisetum ramosissimum</i>	.	19	17
<i>Orobancha hederæ</i>	10	19	9
<i>Carex divulsa</i>	.	17	17
<i>Helosciadium nodiflorum</i>	.	13	17
<i>Plantago major</i>	.	19	4
<i>Campanula cretica</i>	.	4	30
<i>Nasturtium officinale</i>	.	13	4
<i>Cirsium creticum</i>	.	10	9
<i>Smyrniolus olusatrum</i>	.	15	.
<i>Cyperus longus</i>	.	8	9
<i>Carex remota</i>	.	4	13
<i>Carex cretica</i>	.	.	22
<i>Carex idaea</i>	.	.	13

Continued on next page.

Association	1	2	3
Other species of more than 10 % frequency in the dataset			
<i>Hedera helix</i> hl	30	77	83
<i>Dioscorea communis</i>	60	56	91
<i>Rubus sanctus</i>	20	65	78
<i>Geranium purpureum</i>	60	44	39
<i>Galium aparine</i>	40	35	43
<i>Cyclamen creticum</i>	40	13	70
<i>Oxalis pes-caprae</i>	40	42	4
<i>Arisarum vulgare</i>	50	21	43
<i>Asparagus aphyllus</i> subsp. <i>orientalis</i>	40	19	39
<i>Piptatherum miliaceum</i>	40	29	9
<i>Poa trivialis</i> subsp. <i>sylvicola</i>	20	25	26
<i>Oenanthe pimpinelloides</i>	10	19	43
<i>Arundo donax</i>	20	21	4
<i>Petromarula pinnata</i>	20	17	9
<i>Drimia maritima</i> s. l.	40	4	26
<i>Arum creticum</i>	10	4	39
<i>Nerium oleander</i> hl	10	15	13
<i>Veronica cymbalaria</i>	40	13	4
<i>Theligonum cynocrambe</i>	40	6	17
<i>Myrtus communis</i> hl	10	10	22
<i>Epilobium hirsutum</i>	.	19	9
<i>Samolus valerandi</i>	.	10	26
<i>Aristolochia sempervirens</i>	20	8	17
<i>Muscari comosum</i>	10	2	35
<i>Ficaria verna</i>	10	13	13
<i>Lamyropsis cynaroides</i>	40	2	17
<i>Anagallis arvensis</i>	30	13	.
<i>Crataegus monogyna</i>	20	6	17
<i>Quercus ilex</i> hl	.	4	30
<i>Polypogon viridis</i>	.	10	17
<i>Ruscus aculeatus</i>	10	13	4
<i>Allium subhirsutum</i>	20	.	26
<i>Laurus nobilis</i> hl	10	10	9
<i>Lythrum junceum</i>	.	10	13

All three associations may be assigned to the alliance of riparian gallery forests of the eastern Mediterranean (*Platanion orientalis* I. Kárpáti et V. Kárpáti 1961), the order *Populetales albae* Br.-Bl. ex Tchou Yen-Tcheng 1949, and the class of Eurosiberian and Mediterranean riparian gallery forests (*Alno-Populetea* P. Fukarek & Fabijanić 1968).

The ***Euphorbio characiae-Platanetum orientalis*** is an association of rather open or disintegrated tree canopy, mainly along streams with episodic or periodic water flow. The association is considered rather common in Crete and more widespread than the present number of records suggests (Figure 3.2). The trees were found to be comparatively low (9.5 ± 5.4 m) and showed commonly signs of disturbance by former pollarding and lack of tree rejuvenation. A layer of higher shrubs was not particularly prominent and consisted, if present, of *Nerium oleander* or scattered *Ceratonia siliqua* and *Pistacia lentiscus*. By contrast, heliophilous subshrubs such as *Euphorbia characias*, *Phlomis fruticosa* and *Satureja thymbra* were common and diagnostic for the plant community type. Other differential species of the association included common annual herbs which tolerate moderate shade such as *Rhagadiolus stellatus*, *Catapodium rigidum*, *Galium murale* and *Geranium molle*, and drought-resistant geophytes (*Aetheorhiza bulbosa*, *Leontodon tuberosus*, *Dracunculus vulgaris*). Other herbs common in the *Euphorbio characiae-Platanetum* include *Geranium purpureum*, *Drimia maritima* s.l. and the thistle *Lamyropsis cynaroides*. All differential species may be considered grazing indicators and indeed, the recorded stands of this association were all found to be frequented by flocks of sheep and goats. The following relevé constitutes a typical example of the association; it is published here as type relevé of the *Euphorbio characiae-Platanetum orientalis*: Collector: W. Wolf, 1 May 2000, 100 m²; SW Crete, Province of Chania, N of Sougia, 220 m a.s.l., 35°16'26" N 23°48'07" E; Aspect N, Slope 5°, Tree layer 70 %, Shrub and subshrub layer 40 %, Herb layer 10 %. Tree layer: *Platanus orientalis* 4; Shrub layer: *Pistacia lentiscus* 2b, *Ceratonia siliqua* 2a, *Arbutus unedo* 2a, *Nerium oleander* +, *Phillyrea latifolia* +, *Quercus coccifera* +, *Pinus brutia* r; Subshrub and herb layer: *Euphorbia characias* 2a, *Phlomis fruticosa* 2a, *Salvia pomifera* 2a, *Oxalis pes-caprae* 2a, *Galium aparine* 2m, *Piptatherum miliaceum* 2m, *Aetheorhiza bulbosa* subsp. *microcephala* 1, *Allium subhirsutum* 1, *Arisarum vulgare* 1, *Dioscorea communis* 1, *Muscari comosum* 1, *Cyclamen creticum* 1, *Geranium purpureum* 1, *Orlaya daucoides* 1, *Phelipanche mutelii* 1, *Anemone coronaria* +, *Aristolochia sempervirens* +, *Calicotome villosa* +, *Dracunculus vulgaris* +, *Drimia maritima* s.l. +, *Gladiolus italicus* +, *Leontodon tuberosus* +, *Olea europaea* +, *Ornithogalum narbonense* +, *Prasium majus* +, *Quercus coccifera* +, *Satureja thymbra* +, *Asparagus aphyllus* subsp. *orientalis* r, *Bituminaria bituminosa* r, *Cistus creticus* r, *Ebenus cretica* r, *Lathyrus annuus* r, *Ranunculus neapolitanus* r, *Rhagadiolus stellatus* r, *Rumex conglomeratus* r.

The ***Equiseto telmateiae-Platanetum orientalis*** comprised most of the relevés of our dataset (48). It was found widespread between sea level and 600 m in calcareous areas in western and central Crete, and rarely in eastern Crete (Figure 3.2). The association comprises riparian *Platanus* woods with various but mostly high canopy cover (66.8 ± 14.7 %). The shrub layer averages about 20 % but much denser shrub canopies are not uncommon. The mean tree height was 14.0 ± 7.5 m, with a maximum of 25 m. The water flow in streams of the *Equiseto telmateiae-Platanetum orientalis* was mostly

permanent which is why the association is rare in valleys of southward direction except locally in ravines in the southwest of Crete. Apart from the prevailing *Platanus*, other trees such as *Ficus carica* (not uncommon in the subcanopy) and *Salix alba* (infrequent, sometimes overtopping *Platanus*) occurred but scattered. *Nerium oleander* is a regular and often dominant constituent of the understorey. *Hedera helix* is also common and climbs frequently up to the canopy. Other lianas (*Smilax*, *Vitis*) are rather infrequent. Diagnostic for the *Equiseto telmateiae-Platanetum*, and in contrast to the *Euphorbio characiae-Platanetum*, is the presence of wetland plants such as *Carex pendula* and *Equisetum telmateia*. Table 1 shows that, if compared to the two other associations, own differential species of high frequency are lacking, but the association is nevertheless easily distinguished and the species composition is typical with a combination of plants characteristic of riparian forests in general, such as *Melissa officinalis*, *Brachypodium sylvaticum*, *Carex pendula*, *Equisetum telmateia*, as well as plants of shady nutrient-rich habitats such as *Parietaria judaica* and *Arum concinatum*. The *Equiseto telmateiae-Platanetum orientalis* as defined here encompasses rather degraded stands which do not reflect the core of the association, hence the relatively low frequencies of the above-mentioned differential species.

The ***Hyperico hircini-Platanetum orientalis*** is restricted to the phyllite-quartzite schist areas in western Crete (Figure 3.2). The region is known for relatively high amounts of precipitation. Many rare species of oceanic general distribution have been recorded Bergmeier and Abrahamczyk 2007, 2008; Blockeel 2007, 2012; Fielding and Turland 2005. The association was recorded between 140 and 780 m a.s.l. In terms of average tree canopy cover (70.22 ± 11.2 %) and mean tree height (15.4 ± 6.6 m) the *Hyperico hircini-Platanetum* exceeds the other associations. Apart from occasional trees of *Quercus ilex* and *Castanea sativa* almost no other trees co-occur with *Platanus*. In the shrub layer, *Nerium oleander* is less common, and is almost missing above 300 m. Evergreen shrubs of the adjacent maquis such as *Arbutus unedo*, *Myrtus communis* and notably *Erica arborea* are frequent. Differential species of the ground layer are the tall ferns *Pteridium aquilinum*, *Athyrium filix-femina* and *Osmunda regalis*, and hygrophilous herbs such as *Hypericum hircinum* subsp. *albimontanum*. Other herbs of the *Hyperico hircini-Platanetum* typically occurring in shady or humid habitats include *Arum creticum*, *Campanula cretica*, *Carex distans*, *Cyclamen creticum*, *Primula vulgaris*, *Rubia peregrina*, and another fern – *Asplenium onopteris*. Two significant invasive plants, the giant grass *Arundo donax* and the ubiquitous weed *Oxalis pes-caprae*, are much less common in the *Hyperico hircini-Platanetum* than in other *Platanus* woods. The *Hyperico hircini-Platanetum* provides an important habitat for rare regional endemics such as *Carex cretica* (Bergmeier and Abrahamczyk 2007) and *Scilla cydonia*. The following relevé which is a typical example of the association; is selected here as type relevé of the *Hyperico hircini-Platanetum orientalis* (see also Bergmeier and Abrahamczyk 2007: Relevé 3 in their Table 2):

Collector: S. Abrahamczyk, 17 May 2005, 150 m²; W Crete, Province of Chania, between Langos and Nea Roumata, 330 m a.s.l., 35°23'58" N 23°52'23" E; Aspect SW, Slope 5°, Tree layer 50 %, Shrub layer 5 %, Herb layer 60 %, Moss layer 1 %. Tree layer: *Platanus orientalis* 3, *Smilax aspera* 1; Shrub layer: *Arbutus unedo* 1, *Erica arborea* +, *Ficus carica* +, *Myrtus communis* +, *Platanus orientalis* +; Herb layer: *Dorycnium rectum* 2b, *Carex pendula* 2a, *Hypericum hircinum* ssp. *albimontanum* 2a, *Brachypodium sylvaticum* 1, *Carex cretica* 1, *Dioscorea communis* 1, *Juncus effusus* 1, *Osmunda regalis* 1, *Pteridium aquilinum* 1, *Rubia peregrina* 1, *Rubus sanctus* 1, *Scirpoides holoschoenus* 1, *Athyrium filix-femina* +, *Blackstonia perfoliata* +, *Campanula cretica* +, *Carex idaea* +, *Chamaecytisus creticus* +, *Crepis fraasii* +, *Cyclamen creticum* +, *Cyperus longus* subsp. *badius* +, *Epilobium hirsutum* +, *Hedera helix* +, *Melissa officinalis* +, *Poaceae* (spec. indet.) +, *Polypogon viridis* +, *Rumex conglomeratus* +, *Selaginella denticulata* +, *Sibthorpia europaea* +, *Adiantum capillus-veneris* r, *Asplenium onopteris* r, *Ficus carica* juv. r, *Galium debile* r, *Sonchus asper* r; Moss layer: *Eurhynchium hians* +, *Bryum* species +, *Funaria* species +, *Pellia endiviifolia* +, *Rhynchostegiella tenella* +, *Fissidens taxifolius* +

Conservation status assessment

The quality evaluation of 74 patches (polygons) of *Platanus* woodland (60 inside Natura 2000 sites and 14 outside) revealed that about one third of the stands (34 %) were in a good conservation status, and approximately one fourth (24 %) in a bad. The conservation status of 42 % of the stands was considered inadequate. There was no geographical pattern of habitat quality (Figure 3.3).

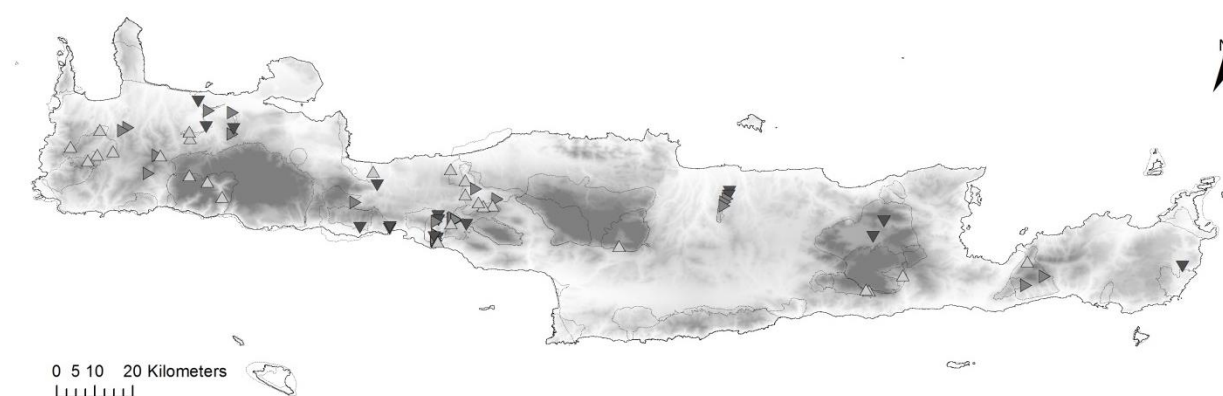


Figure 3.3 Natura 2000 habitat quality assessment of Crete in 2013-2015, distribution of sites of the habitat type 92C0 “*Platanus orientalis* and *Liquidambar orientalis* woods (*Platanion orientalis*)” with quality evaluation: good - bright upright triangle Δ , inadequate – grey turned triangle \triangleright , bad – dark upside-down triangle ∇ ; grey lines indicate protected areas.

Damage to the water regime was registered in 40 forest patches, equal to 54 % of the total. It includes dams and water abstractions mainly for agricultural use. Pollution of the habitat, soil and water resources accounted for 24 polygons (32 %). Disturbance of the woodland vegetation

and damage to the structure of the forests was found in half of the surveyed stands. This includes effects of grazing, erosion and fire. Occurrences of invasive species with significant negative effects were observed in 31 plots (42%). This refers almost exclusively to *Arundo donax* and/or the non-native *Oxalis pes-caprae*, locally *Eucalyptus*. A total of 51 forest polygons, equal to 69 % of the surveyed stands, were affected by fragmentation and overuse of the habitat, caused by roads and cultivation of riparian ground (chiefly *Citrus* plantations). Such adverse effects on *Platanus* forests accumulated frequently and thus resulted in an unfavourable (inadequate or bad) conservation status of about two thirds of the surveyed stands. In only 11 woods (15 %) no visible adverse effects and pressures were detected (Figure 3.4).

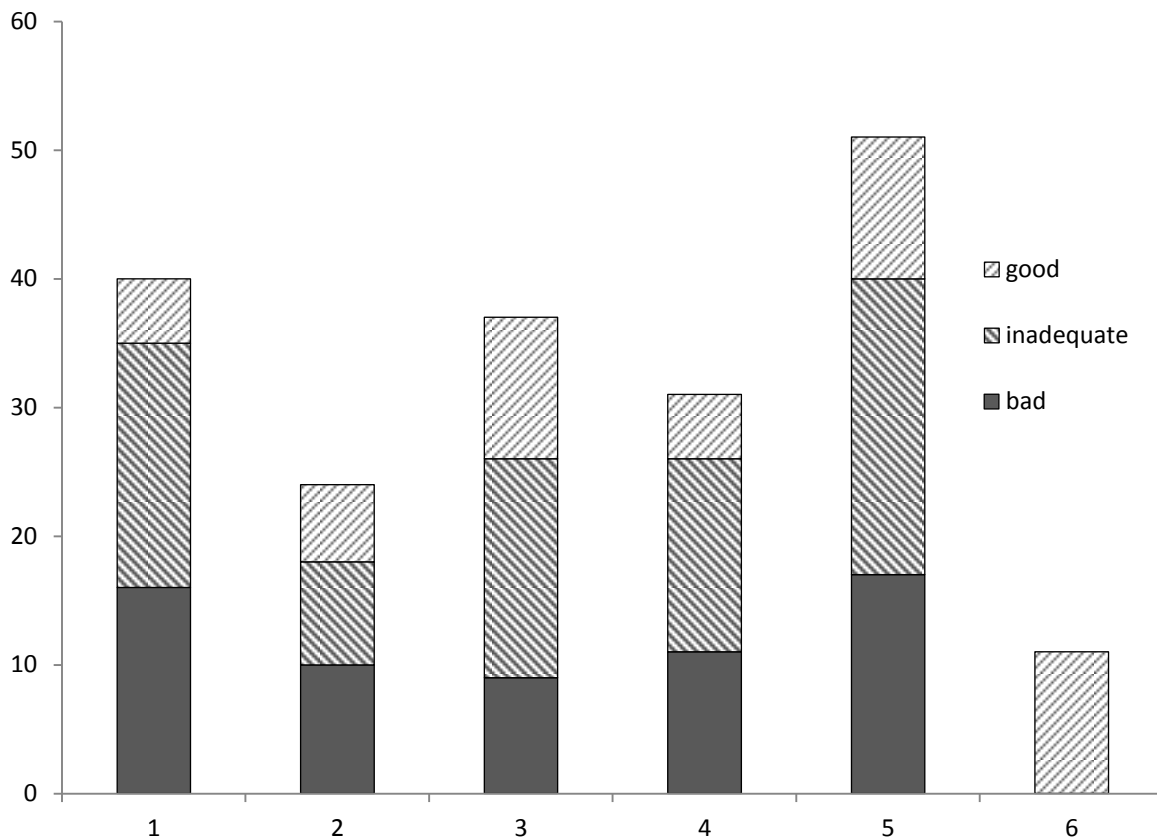


Figure 3.4 Numbers of surveyed sites of *Platanus orientalis* woodlands in Crete with observed pressures and threats in the categories: (1) Damage to the water regime, (2) Pollution of the habitat, soil and water resources, (3) Disturbance of the forest vegetation and damage to the structure, (4) Occurrence of invasive species, (5) Fragmentation and overuse of the habitat, (6) no pressure and threat recorded. The survey was carried out in 74 sites of *Platanus* forest; hatchings display the present quality and conservation status of the sites (good, inadequate, bad).

Conclusions

Pedrotti and Gafta (1996: 147) listed a number of pressures to riparian vegetation in Italy of which, several, to a variable extent, are also relevant for riparian woodlands in Crete. The most serious impact for *Platanus* forests and for Cretan wetlands in general is the abstraction of surface and subsurface waters from springs and streams. The water is piped away to irrigate olive and *Citrus* plantations, and to fill troughs and wells to water sheep and goats. Water consumption by households and touristic infrastructure may also account for some of the water exploitation. To our knowledge, no details on amounts of abstracted water or proportions of its use are available, and there is probably no way of telling. *Platanus* itself is not at risk though, as the trees will survive, provided the groundwater flow remains accessible for the deep-rooted trees. The three *Platanus* woodland associations described above are, however, not equivalent from an ecosystem service and ecological point of view. Woodlands of the *Euphorbio characiae-Platanetum* are characterized by a lower groundwater level and shorter periods of surface water flow per year, if there is surface water at all (personal observations and according to species composition). The assumption seems justified that the proportion and total number of sites of the *Euphorbio characiae-Platanetum* may increase with increasing water abstraction from springs and headwaters, to the cost of the ecosystems of the *Equiseto telmateiae-Platanetum* and the *Hyperico hircini-Platanetum*. The latter two associations both depend on the permanence of surface waters or at least on seasonal flow of water well into springtime.

Qualitative decline and degradation of *Platanus* woodlands and of the habitat type 92C0 in Crete is indicated by the invasive plants *Eucalyptus camaldulensis*, *Arundo donax* and *Oxalis pes-caprae*, the latter two being particularly common in the lowland and foothill stands which are in the immediate vicinity to villages, arable fields and plantations. *Oxalis* was introduced decades, *Arundo* centuries ago. Both species occur now abundantly throughout Crete. *Oxalis pes-caprae* may occupy considerable parts of nutrient-rich soil in *Platanus* woodlands. As a spring geophyte it will leave the ground bare and erosion-prone from late April. The rhizomatous bamboo-like grass *Arundo donax* is much planted and commonly found in disturbed *Platanus* woods (Figure 3.1d). It collapses in torrential floods, littering large tracts in ravines with thick stem and leaf debris and thus preventing other plant growth. Although the two species are pernicious to riparian woodlands and may cause structural damage through erosion, once established it would be a utopian aim and an obviously useless effort to fight them. Nevertheless, it would be important not to lay out clearings and plantations on slopes above *Platanus* woodlands, first to prevent soil erosion and, second, to prevent *Oxalis* bulbils being washed into the valley grounds where the plants would readily establish. *Eucalyptus* trees of all ages exist locally near fruiting planted trees, on river banks and gravel bars, e.g. at the bridge of Keriti near Alikianos. Although widely planted, *Eucalyptus* is not as pervasive in

Crete as it is in the Iberian Peninsula (Andreu et al. 2009) but groups of planted trees should be carefully monitored and controlled.

Another reason why plantations and arable fields should not border *Platanus* ravines, streams and water courses is to prevent agrochemicals to be washed down and pollute soil and water of the riparian ecosystems. The effect of agrochemicals especially on sensitive plants such as riparian and aquatic bryophytes is already obvious – many streams lack such mosses as a result of water pollution. Pollution and eutrophication may also be caused by solid and organic agricultural waste as well as industrial or chiefly household garbage dumped into ravines and in riparian wood.

A potential threat to planes which has not yet observed in Crete is the dieback of trees caused by the pathogenic fungus *Ceratocystis platani*, a native to *Platanus occidentalis* in North America and currently spreading in Europe. Dieback of planted trees of Oriental plane through *C. platani* has been reported from western and southern Europe. The pathogen recently reached the Peloponnese (Ocasio-Morales et al. 2007) and is likely to spread further.

Platanus orientalis is an unusually popular and familiar tree in the Eastern Mediterranean, every child is able to recognize it. It is the scenery of weddings and many open-air feasts. This popularity makes it a perfect flagship species for nature conservation. *Platanus* woodlands provide lots of ecosystem services, such as erosion prevention, water conservation and pollution control, and last but not least shade and recreation. They are now declining and vulnerable due to various impacts which are caused just by people who benefit quite essentially from the services of the riparian forest ecosystems. Public awareness must be raised, and water manipulation of the springs and headwaters efficiently controlled to save the diversity and quality of the *Platanus* woodlands and the services provided by riparian ecosystems.

Acknowledgements

Special thanks are due to S. Abrahamczyk, G. Ilgenfritz and W. Wolf who collected a considerable proportion of the relevés, and to C. Barnick, U. Bergmeier, F. Goral, P. Mahdavi, I. Schmiedel and W. Wolf who contributed substantially to the site-specific assessment of the conservation status of the habitat type. Mapping and monitoring of the habitat type were part of projects funded by the European Union and the Greek Ministry of Environmental Affairs. The digital elevation model used on the map (Figures 3.2 and 3.3) was kindly provided by the Mediterranean Agronomic Institute of Chania (MAICh, Greece).

Chapter 4: Ecology and potential distribution of the Cretan endemic tree species *Zelkova abelicea*

Goedecke, F. & Bergmeier, E. Ecology and potential distribution of the Cretan endemic tree species *Zelkova abelicea*. Journal of Mediterranean Ecology, manuscript accepted 11th October 2017 (letter of acceptance in Appendix)

Ecology and potential distribution of the Cretan endemic tree species *Zelkova abelicea*

Abstract

Mediterranean mountain forests feature woody species relics such as *Zelkova abelicea*, an endemic tree species confined to six spatially and genetically distinct populations in Crete (S Aegean, Greece). We used species distribution modelling to predict the potential distribution of *Zelkova abelicea*. Comparison of coordinate-based geodata extractions for climate and topography revealed pronounced environmental differences for the metapopulations. Main factors for species distribution models were altitude and temperature seasonality (proxy for west-east gradient) whereas topographic conditions had surprisingly little influence on our models. While the most extensive *Zelkova* metapopulations were found to occur under locally fairly mesic conditions and comprising a wider ecological spectrum, the smaller populations comprising narrower ecological range occurred at lower elevations and further east. For further extrapolation with similar models for known populations, only similar site conditions allowed for a prediction. Differentiated site conditions in the mountains, genetic distinctness and possible environmental adaptations of isolated populations are to be considered in conservation and management.

Introduction

A particularity of Mediterranean forests is the conspicuous rate of endemic tree taxa, some of which are considered as relics of a widespread and rich tertiary flora (Mai 1987). As especially isolation by topography is a driving factor for endemism (Steinbauer et al. 2013; Steinbauer et al. 2016; Trigas et al. 2013), Mediterranean mountains and the major Mediterranean islands host many relic tree and shrub populations. For instance, *Cedrus libanii* subsp. *brevifolia* is restricted to Cyprus; *Abies nebrodensis*, *Celtis tournefortii* subsp. *aetnensis* and *Rhamnus lojaconoi* occur only in the Sicilian mountains (Quézel and Médail 2003). Other prominent examples refer to the genus *Zelkova* (Ulmaceae). Widely distributed under favourable pre-Quaternary climate conditions (Garfi 1997; Quézel and Médail 2003), *Zelkova* died out in Central Italy in late Pleistocene, after repeated increase and decline along glacial-interglacial cycles (Follieri et al. 1986; Magri 1999). Today two out of six species of the genus worldwide are represented in the Mediterranean basin: *Zelkova abelicea* in the mountains of Crete and *Zelkova sicula* in south-eastern Sicily (Di Pasquale et al. 1992; Garfi et al. 2011). Chloroplast and nuclear marker analyses revealed close relation of the two Mediterranean species (Christe et al. 2014). *Z. abelicea* is listed Endangered by IUCN (Kozłowski et al. 2012), and *Z. sicula* which occurs in only two single spots is considered Critically endangered (Garfi 2006). Depending on browsing impact and climatic constraints (Garfi et al. 2002), they may grow as tree, treelet or shrub. Compared to co-occurring woody species, both *Zelkova* species take up a rather distinct ecological niche (Garfi et al. 2011; Sørensgaard and Egli 2006). Local climate seems to be crucial, as *Zelkova* populations of both species are restricted to topographically or edaphically relatively favourable sites where evapotranspiration is rather low and water-supply satisfactory (Garfi et al. 2011; Sørensgaard and Egli 2006). Cretan *Zelkova abelicea* grows in several isolated mountains between 900 m a.s.l. up to the tree line at about 1800 m a.s.l. (Kozłowski et al. 2012); *Z. sicula* occurs at lower elevation (320 to 520 m a.s.l.) but is confined to gullies, suggesting that this microtopographic position compensates for inadequate rainfall amounts and helps the species to withstand seasonal water stress (Garfi et al. 2011).

Isolated narrow-range plant populations may be genetically impoverished (Booy et al. 2000; Honnay and Jacquemyn 2007) or may show (unexpected) genetic diversity (Bucci et al. 1997; LaBonte et al. 2017; Liu et al. 2006; Mousadik and Petit 1996; Parducci et al. 2001). For example, Spanish populations of widespread European *Ulmus* species show high genetic variation compared to northern occurrences (Fuentes-Utrilla et al. 2014b). This is interpreted as indicating relict populations, with higher genetic diversity compared to those originating from post-glacial colonisation. Relict populations are thus important for genetic diversity conservation and underline the need to protect glacial refugia in the Mediterranean and elsewhere. Broad genetic diversity also applies to *Zelkova abelicea*. Isolated subpopulations were found to be genetically differentiated

(Christe et al. 2014). Haplotypes, the haploid genotype of individual samples, show distinct intraspecific patterns with a strong separation of lineages from different mountain ranges. This supports the assumption of long-term geographical isolation.

This study aims to illuminate the relation among ecology, distribution patterns and isolation of *Z. abelicea* through species distribution modelling. Toolsets for species distribution modelling can support a clearer understanding of species ecology on landscape scale. This approach helps to assess potential and actual distribution areas of species and can be used to explain past and recent range patterns (Elith et al. 2006; Svenning et al. 2011). Furthermore modelling allows to predict suitable sites under changing climate conditions (Garcia et al. 2013; Keenan et al. 2011; Skov and Svenning 2004). Species distribution modelling may complement molecular research or support targeted sampling; it is also useful for conservation and restoration and may even help to reveal hitherto unrecorded populations and cryptic taxa (Dick et al. 2003; Rissler and Apodaca 2007; Sattler et al. 2007). The present study addresses the following questions: How much do isolated populations of *Zelkova abelicea* differ in ecology, as expressed by abiotic variables? Are these differences related to known genetic patterns? Which environmental factors influence species distribution models most? How do predicted distribution patterns relate to known records? Do combined metapopulation samples improve the predictive value for known neighbouring populations? Consequences for biogeography and management are discussed.

Study area

Crete is among the largest islands of the Mediterranean and topographically outstanding with alternating high mountain ranges and lowland plains. Three mountain ranges rise over 2000 m and all are rather isolated, in the geological past even separated by shallow seas. Hard Triassic metamorphic limestones prevail in the high mountains. Mediterranean lowland climate, with mild winters and hot and dry summers, is modified in the mountains, with precipitation increasing, temperatures decreasing, and evapotranspiration reduced (Barry 2008). This favours hardy species adapted to rather mesic conditions. The prevailing westerlies bring about moist air masses which, in combination with a pronounced relief, cause rain shadow effects on the east sides. Northern strong dry etesian winds, called meltemi, occur regularly during summer. The rugged relief, shaped by tectonic events and erosion, promotes mesoclimatic variation (Barry and Blanken 2016). Sheltered sites in poljes, dolines, gorges and below cliffs support a specialised flora (Egli 1989; Egli et al. 1990; Hedderson and Blockeel 2013). Such local-climate conditions in otherwise sun- and wind-exposed environments favour xero-mesic taxa such as *Zelkova*.

Methods

Coordinates of *Zelkova abelicea* individuals were obtained from collections and field surveys (Table 4.1). Identical coordinates were reduced to one. Occurrences of *Zelkova* in isolated mountain ranges were considered as (meta)populations. Most records by far are in the west of Crete (Figure 4. 1, Table 4.2). The majority of records are from the western Lefka Ori (W), fewer from the eastern Lefka Ori (E), including the lowest known site near Imbros. The Kedros population (K) is isolated on a single mountain massif in the western central part of Crete. Further east, on Psiloritis (P), only one small population occurs in the Rouvas forest. The east central mountain Dikti (D) harbours the second largest population, comprising 31 scattered records of one to few trees.

Table 4.1: Data collection for *Zelkova abelicea* populations of Crete. From all collectors additional unpublished records are included.

Collector	Publication	Timespan	Number of records
L. Fazan et al.	(Fazan et al. 2012; Fazan 2014)	2010 - 2016	218
B. Egli	(Egli 1998, 2000)	1993 - 1999	50
E. Bergmeier	(Bergmeier 2012)	1999 - 2012	13
R. Jahn	-	1988 - 2014	11
various	Literature + herbarium specimen	1988 - 2014	39
total			331

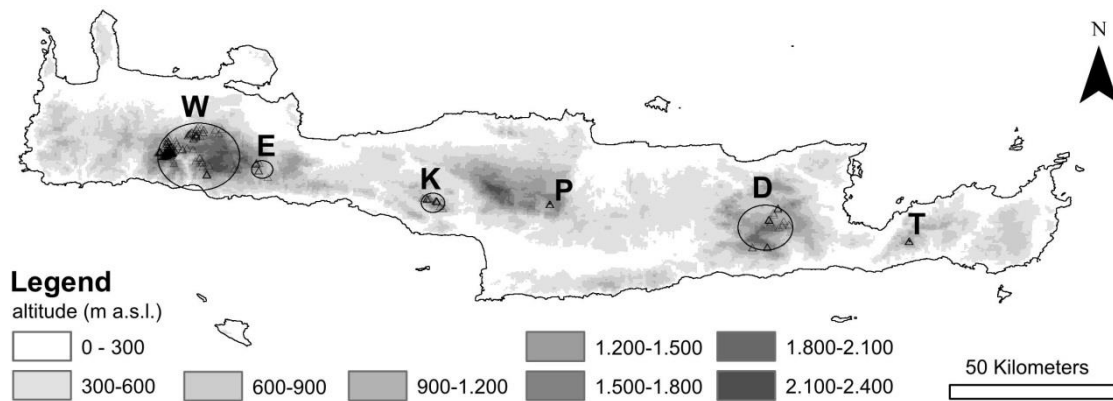


Figure 4.1 Map of distribution and altitudinal patterns for the *Zelkova abelicea* metapopulations in Crete. Circles circumscribe areas with records, but records in P and T are given as single points.

Table 4.2 Populations of *Zelkova abelicea* in the Cretan mountain ranges with spatial extent, number of records and occupied grid cells (397 m x 397 m).

Population	Mountain range	Longitude	Latitude	Records	Grid cells
W	West Lefka Ori	23.88-24.06°	35.26-35.39°	256	114
E	East Lefka Ori (East Imbros)	24.09-24.18°	35.25-35.29°	14	5
K	Kedros	24.59-24.64°	35.17-35.20°	18	11
P	Psiloritis	24.93°	35.18°	7	1
D	Dikti	25.47-25.57°	35.06-35.17°	31	18
T	Thrypti	25.89°	35.08°	6	3

The smallest number of records is from Thrypti (T), the easternmost mountain range. Coordinates from GPS measures as well as raster data for climate and geomorphology were processed in ArcGIS (ESRI 2013, Table 4.3). A grid resolution of 397 m was used for modelling, amounting to about 102,000 grid cells. Multiple records per grid cell were used. Further plotting of results and statistical tests were performed in R 3.4.0 (R Development Core Team 2017). For initially 30 environmental variables Spearman correlations were applied (Table A 4.1, *psych* package, Revelle 2017). Collinear pairs were reduced to one for $R^2 > 0.6$ with priority on geomorphology and mean values, leaving 7 variables for final analysis (Table 4.3). For these variables coordinate-based geodata extractions were calculated for all records and plotted for populations. Additionally, Kruskal-Wallis tests were performed to reveal significant differences (*pgirmess* package, Giraudoux 2016).

MaxEnt software version 3.4.0 was used to compute species distribution models (Phillips et al. 2006). Models based on multiple correlations were compiled for a set of environmental variables, resulting

Table 4.3 Environmental factors used to predict species distribution.

Data source	Original resolution	variables
Chelsa climate data Version 1.1 (Karger et al. 2016)	30 ArcSec = ~1 km	1. <i>mean annual precipitation</i> (mm) 2. <i>Bio2/ temperature mean diurnal range</i> (standard deviation *100) 3. <i>Bio4/ temperature seasonality</i> (mean of monthly (max - min))
Digital Elevation Modell over Europe (EEA 2015)	30 m	4. <i>altitude</i> (m a.s.l.) derived thereof: 5. <i>slope</i> (°, Burrough and McDonell 1998) 6. <i>heatload</i> (McCune and Keon 2002) 7. <i>cti</i> (compound topographic index, Moore et al. 1993, Gessler et al. 1995)

in relative habitat suitability for each grid cell, with or without prior *Zelkova* records. We applied standard settings which provided results similar to when manually modified. Models were improved by jackknife tests, therewith quantifying the contributions of single variables in models. This resulted in the exclusion of *mean annual precipitation*, as the latter data layer was covered by other values, and did not add further value to the models. Cross-validation with geographically distinct metapopulations was preferred to random test sample selection. One species distribution model was performed using all known records, to achieve a robust evaluation of the present *Zelkova* distribution. Extrapolation performance was tested further with combined metapopulations, leaving out the test population. Combinations resulting in sample sizes of $n < 80$ were excluded, as such sample numbers constrain internal handling of environmental features in MaxEnt and therefore render model outputs hardly comparable (Morales et al. 2017; Phillips and Dudík 2008). As for some populations only few records were available, metapopulation W with the largest sample number was always included. The general modelling performance according to Area-under-the-Curve (AUC) test was high, with values close to the maximum, but the measure was not suitable to predict extrapolation performance (Lobo et al. 2008). Hence regularised sample predictions were used for the evaluation of test data, the values of which maximize towards 1, and to describe environmental suitability (Merow et al. 2013). These values were visualised in maps; with values above 0.6 species occurrence is likely.

Results

Environmental comparison of populations

In total 332 *Zelkova* records were used, from (meta)populations ranging between 6 (T) to 256 (W) trees. The six metapopulations of *Zelkova abelicea* differed in their environmental characteristics (Figure 4.2). As revealed by the amplitude of abiotic values, within the Lefka Ori the largest metapopulation (W) displayed the broadest ecological range. The smaller metapopulations covered narrower ecological amplitudes. Steep sloping terrain was a characteristic of *Zelkova* populations in the western Lefka Ori (W), Kedros (K) and Dikti (D). *Heatload* differed among the metapopulations, with lowest values for K. Compound topographic index (*cti*), indicating relief position preferences, was indifferent among metapopulations. The diurnal range of temperatures was highest in the populations of central Crete, while daily differences were attenuated for the two eastern populations. Temperature seasonality was higher in the three eastern populations Psiloritis (P), Dikti (D) and Thrypti (T). From the western to the eastern populations *mean annual precipitation* according to rain shadow effects decreased from 900 - 1000 mm to 700 - 800 mm per year.

Models and prediction values

In jackknife tests *altitude* and *temperature seasonality* were influencing models most, followed by *temperature diurnal range*, while the other variables contributed to a lesser extent. For a model that included all *Zelkova abelicea* records the maximum prediction value for any single metapopulation was found for W (Table 4.4). The wide environmental range of the W metapopulation was nevertheless not fully covered by this general model.

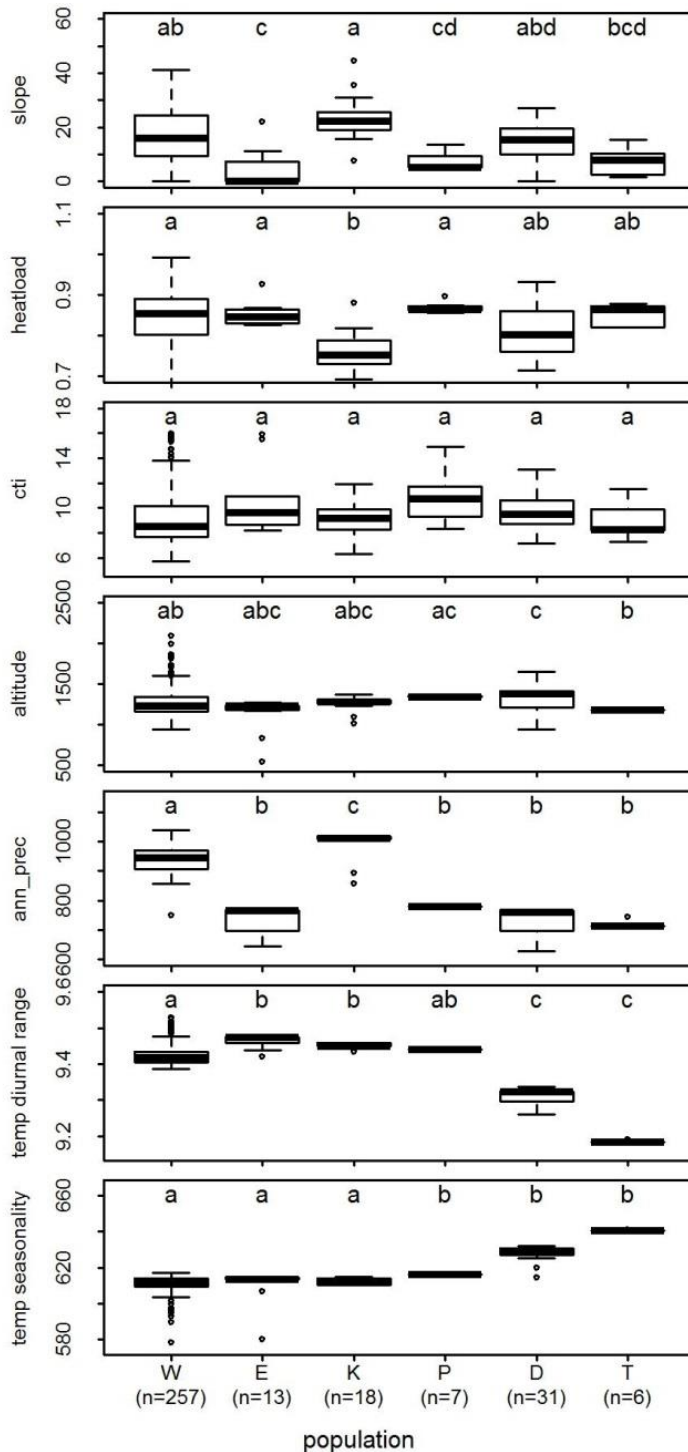


Figure 4.2 Site conditions for six populations of *Zelkova abelicea*. Values from coordinate-based geodata extractions; populations: W= W Lefka Ori, E= E Lefka Ori (E Imbros gorge), K= Kedros, P= Psiloritis (Rouvas Forest), D= Dikti, T= Thrypti; dissimilar letters (a, b, c, d) indicate significant differences in ranks of the Kruskal-Wallis-Test (p-value = 0.05).

Table 4.4 Sample predictions with tested populations for a species distribution model for all records (mx=maximum, mn=mean, sd=standard deviation).

population	W	E	K	P	D	F
mx	0.963	0.730	0.863	0.642	0.406	0.652
mn	0.723	0.578	0.717	0.596	0.332	0.516
sd	0.234	0.242	0.153	0.029	0.081	0.060

Table 4.5 Sample prediction values for combinations of populations (rows) excluding the tested population (columns; mx=maximum, mn=mean, sd=standard deviation); prediction values >0.6 in bold; *as map in Figure 4.3.

Pop- ulation	E			K			P			D			T		
	mx	mn	sd	mx	mn	sd	mx	mn	sd	mx	mn	sd	mx	mn	sd
W*	0.463	0.247	0.119	0.778	0.550	0.113	0.505	0.499	0.010	0.060	0.020	0.008	0.000	0.000	0.000
WE				0.764	0.575	0.118	0.492	0.467	0.016	0.067	0.022	0.009	0.000	0.000	0.000
WK	0.596	0.282	0.151				0.496	0.481	0.025	0.053	0.017	0.007	0.000	0.000	0.000
WP	0.463	0.247	0.119	0.778	0.550	0.113				0.060	0.020	0.008	0.000	0.000	0.000
WD	0.491	0.250	0.116	0.795	0.560	0.129	0.439	0.432	0.010				0.007	0.006	0.001
WT	0.452	0.244	0.111	0.779	0.539	0.129	0.441	0.433	0.012	0.083	0.034	0.019			
WEK							0.535	0.515	0.012	0.057	0.018	0.008	0.000	0.000	0.000
WEP				0.773	0.598	0.120				0.065	0.022	0.009	0.000	0.000	0.000
WED				0.814	0.630	0.137	0.553	0.500	0.034				0.006	0.006	0.001
WET				0.790	0.604	0.131	0.545	0.493	0.033	0.090	0.035	0.021			
WKP	0.612	0.298	0.161							0.050	0.016	0.007	0.000	0.000	0.000
WKD	0.648	0.307	0.159				0.516	0.509	0.011				0.006	0.006	0.001
WKT	0.624	0.310	0.159				0.510	0.504	0.010	0.076	0.032	0.017			
WPD	0.534	0.284	0.133	0.810	0.598	0.133							0.007	0.006	0.001
WPT	0.483	0.270	0.124	0.795	0.562	0.123				0.094	0.036	0.023			
WDT	0.499	0.256	0.118	0.794	0.564	0.136	0.447	0.441	0.010						
WEKP										0.056	0.018	0.008	0.000	0.000	0.000
WEKD							0.638	0.588	0.032				0.006	0.006	0.001
WEKT							0.564	0.532	0.021	0.079	0.033	0.018			
WEPD				0.821	0.655	0.139							0.006	0.005	0.001
WEPT				0.797	0.627	0.134				0.098	0.036	0.024			
WEDT				0.806	0.633	0.142	0.546	0.503	0.027						
WKPD	0.651	0.322	0.165										0.007	0.007	0.001
WKPT	0.639	0.330	0.168							0.065	0.031	0.014			
WKDT	0.648	0.316	0.159				0.526	0.520	0.009						
WPDT	0.534	0.286	0.133	0.810	0.605	0.138									
WEKPD													0.006	0.006	0.001
WEKPT										0.065	0.029	0.015			
WEKDT							0.595	0.548	0.030						
WEPDT*				0.844	0.708	0.146									
WKPDPT	0.655	0.332	0.166												

As some records were poorly predicted (minimum values), a lower mean prediction value resulted. The best mean values for the extrapolation tests added up for population K (Table 4.5). With only few good predictions with values above 0.6, and all other populations below this prediction threshold, the model poorly qualified. W was included in all extrapolation models, thus it could not be tested and its overall influence remained high. Combinations with neighbouring metapopulations modified the extrapolation performance slightly. The best results in mean and maximum sample prediction values were obtained from the combination WEPDT, followed by WEPD, WEDT and WED. The poorest results were from WT.

Predicted populations in maps

Mapped distribution patterns visualise the model-specific site conditions and their suitability for *Zelkova* (Figure 4.3). Favourable conditions and thus high occurrence probability of *Zelkova* were indicated by higher values (0.6 is frequently used as presence-absence threshold). The three maps exemplify repeatedly occurring predictions for modelled metapopulation combinations: while the distribution patterns of W and K, derived from W, were well predicted, the others were not (Figure

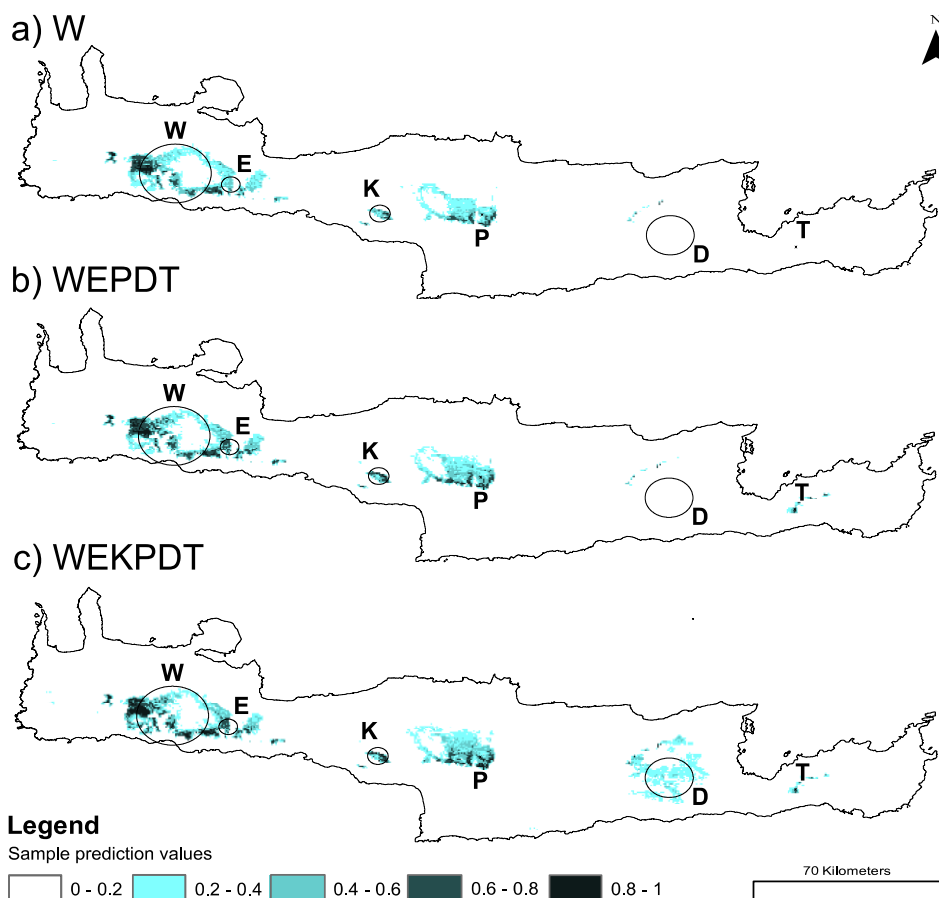


Figure 4.3 Result maps of species distribution modelling (regularized training gain) based on changing combinations of neighbouring populations by using the same set of environmental variables; model based on W a), WEPDT b) and all six populations in c); values > 0.6 imply favourable site conditions according to model parameters and likely occurrence.

4.3a). The map in Figure 4.3b, based on WEKPT, did not predict population D but it predicted population T, though with rather low values. With all populations included (Figure 4.3c), rather different prediction values applied, some of which were low (D). Populations E, D and T were predicted with low to very low sample prediction values in all three maps. Also in all maps predictions of the *Zelkova* range were locally overestimated and did not correspond to recent records, for example areas neighbouring west (Apopighadhi range) and east (around Kastro mountain) of the main Lefka Ori metapopulation (W), topmost Agathes mountains east of E and large parts of the Psiloritis range.

Discussion

Ecology of populations

Zelkova abelicea needs specific environmental conditions typical for high altitudinal woodlands (Bauer and Bergmeier 2011). Fairly mesic conditions are crucial (Søndergaard and Egli 2006). Such environments are common in the west but less so eastwards due to decreasing rates of precipitation. Beside elevation, a longitudinal gradient is regarded by *temperature seasonality* in distribution models. We assume less favourable climate conditions towards east to be responsible for scattered or small populations, with frequently dwarfed *Zelkova* plants. Thus topography-driven climate conditions (topoclimate, mesoclimate) may compensate for less than perfect macroclimatic conditions by mitigating, e.g., irradiation and water stress (Lipscomp and Nilsen 1990a, 1990b; Scherrer et al. 2011). *Zelkova abelicea* is known for a general preference for such woodland sites (Søndergaard and Egli 2006). The present study even revealed pronounced affinity to low *heatload* values for the eastern *Zelkova* populations. As long as there are locally favourable conditions, environments with raised *temperature seasonality* and lower *mean annual precipitation* are occupied. The closely related *Z. sicula* is linked to specific topoclimate too (Garfi et al. 2011). Low *heatload* values as found in Kedros are induced by the orientation of the mountain range, hosting the main population on the windward northern side. The vital Kedros population grows in evergreen woodlands on steep shaded slopes with relatively high precipitation and high potential water run-off (or rather raised percolation). The main *Zelkova* metapopulation in the western Lefka Ori, an area which receives more precipitation than the other Cretan mountains, is associated with the widest spectrum of site conditions among all populations. Precipitation can be high and steep slopes are colonised there as well. It may be deduced that, together with generally more humid environments, slopes with high potential run-off and permeable soils are preferred by *Zelkova abelicea*, supporting sizable populations and a broader environmental niche. In drier environments, in contrast, usually moderately sloped or flat terrain, with consequently lower

potential water run-off and shaded mountain sides, are preferred. As a general rule, populations of *Zelkova abelicea* were found to be associated with complex but predictable environmental gradients but site condition spectra differ between metapopulations.

Ecological and genetic patterns

Knowledge about regional ecological and genetic variation is required for many applications (Khadari et al. 2005; Petit et al. 2004; Vander Mijnsbrugge et al. 2010) and may inspire biogeographic and evolutionary research (Thompson 1999). Along environmental gradients, differentiated physiological reactions were recognised for distinct populations of Mediterranean *Quercus ilex* (Martin-StPaul et al. 2013) and high-Andean pines (Sáenz-Romero et al. 2013), assuming relations between ecology, physiology and genetic variability. Other studies showed that geographic isolation is a driver for species evolution, followed by ecological adaptations of isolated populations (Peterson et al. 1999; Wiens 2004). For *Zelkova abelicea*, indeed, several genetic markers suggest local patterns of isolated populations (Christe et al. 2014). The authors found that western populations (W, E) are genetically heterogeneous, central populations (K, P) are different but share similarities with that of D, and the easternmost population (T) is genetically more pronouncedly separated. We assume that the individual genetic structure of populations may be linked to environmental adaptations. High genetic diversity of the western population corresponds to high diversity of the occupied sites, and a strong genetic separation of the eastern populations comes along with their relative ecological distinctness. Conceivable may be either *in situ* adaptation to local site conditions or ancient colonisation from genetically and ecologically different lineages. Further research on comparative ecology and functional genetics within and between metapopulations of *Zelkova abelicea* are necessary.

Environmental variables in models

Main factors for species distribution models were *altitude* and *temperature seasonality*. Topographic conditions had surprisingly little influence on our models; their importance for general distribution was low, though populations showed individual differences. The clear preference of *Zelkova abelicea* for high elevations supports model compilation. In Mediterranean high mountains specific environmental factors act upon plants, such as low temperatures, snow cover, etc. (Körner 2014), supporting many hardy xero-mesic species such as *Zelkova abelicea*, many of which being narrow endemics and absent from the lowlands (Bergmeier 2002). *Temperature seasonality* is known for its fundamental influence on biological processes (Vazquez et al. 2017) and, within the models, expresses an east-west gradient. *Annual mean precipitation* is based on extrapolation of climate station records and the algorithm comprises a correction for elevation and topographic lee-side effects, but it reduces model performance and was outperformed by the two above mentioned parameters. A reason could be low relevance of overall precipitation patterns for *Zelkova abelicea*,

perhaps due to its preference for topoclimatic (mesoclimatic) conditions with factors such as cloud and dew formation, water condensation, snow cover, frost protection, etc. Another reason for weak performance of the dataset can be unreliable or unsuitable *annual mean precipitation* values for the study area. Climate stations for data extrapolation in the mountains of Crete are lacking. Poor data quality can also be due to underestimated terrain complexity in the algorithm or variability in origins of climatic influences. Coarse grained climate data have been criticised as unsuitable for fine-scale studies like ours (Nadeau et al. 2017).

Distribution maps and extrapolation performance

Suitable habitats for *Zelkova abelicea* are scarce in the Cretan mountains and the species is probably declining, boosted by human impact (Egli 1997). Its range may have been less fragmented during more humid periods in the past. In our models the potential distribution range of *Zelkova abelicea* appears to be overestimated, as especially in western to central Crete some mountains without actual records have been assigned high occurrence probability. Local prediction errors such as near population E may be due to dry lee-side conditions. Further, erroneous distribution gaps cannot be ruled out. Near Imbros *Zelkova* has only recently been recorded, and especially dwarfed and browsed individuals are easily overlooked. The Psiloritis distribution gap, however, is likely to be actual, and is supported by our models that predict low occurrence probability for most of the mountain range, except for the south-eastern part (Rouvas), where population P occurs in mixed and sheltered stands with *Acer sempervirens* and *Quercus coccifera* (Bauer & Bergmeier 2011).

Heikkinen et al. (2012) reported for MaxEnt models high prediction accuracy for range extrapolations over large areas. This is only partly confirmed by our local study. Scale differences clearly matter, and while the tested model with all records is fairly close in predicting the general distribution pattern, extrapolations fail for populations with markedly different environmental conditions. We assume that marginal ecological conditions deviate too much from the mean and thus hamper model extrapolation. Low prediction accuracy can be due to unbalanced sampling or too simplistic model, as few parameters were included. Our model approximates site conditions but only roughly, while complex environmental conditions may influence mountain plants in many ways, such as by acting upon seedling growth through frost damage (Viveros-Viveros et al. 2009). Low prediction accuracy can thus be due to a lack of environmental as well as biotic data such as of soil parameters, mist and cloud cover frequency, surrounding vegetation, wildfires, grazing intensity and other historical and recent land management.

Biogeographical implications

Due to repeated climate change during the Pleistocene and Holocene, changes in plant population numbers, species range and vegetation composition occurred throughout Europe and the Mediterranean (Huntley 1990). As a result of cyclic climate development Mediterranean forests expanded and declined (Combourieu-Nebout 1993). For *Zelkova abelicea*, as a consequence of changing growth conditions during these cycles, shifts in altitudinal range, retreat to refugia and forest expansion may be assumed. Even so, distinct genetic patterns suggest long-term isolation and limited genetic exchange between metapopulations to the present day (Christe et al. 2014). Similarly, our results show, underlined by prediction patterns, metapopulations in each mountain range to be rather varying in terms of occupied site conditions. Specific abiotic combinations even for nearby metapopulations support the hypothesis of their long-term isolation. This corresponds with the concept of elevation-driven ecological isolation (Steinbauer et al. 2013), enhanced by mountain-specific conditions.

Concluding remarks

Along an east-west gradient in Crete, *Zelkova abelicea* shows surprising genetic and site variation. As spectra of site conditions vary among mountains inhabited by *Zelkova*, metapopulations differ in the range and degree of abiotic parameters. From a methodological point of view, the mountain-specific habitat heterogeneity of *Zelkova* metapopulations hampers good overall performance of species distribution models. In all *Zelkova* sites specific topoclimatic conditions are involved that mitigate to some extent unfavourable macroclimatic conditions. Suitable sites are rather rare and require special attention in conservation and forest management. In the Cretan mountains, as emphasised by Bauer & Bergmeier (2011), current woodland and rangeland degradation as a result of overgrazing is arguably the most fatal impact and counter measures are urgently needed. In spite of the patchy distribution of *Zelkova*, it is crucial to protect mountain ranges in total, covering complex abiotic conditions, thereby taking account of distributional shift under climate change.

Acknowledgements

The authors thank L. Fazan, G. Kozłowski, B. Egli and R. Jahn for generous data supply. S. Pasta, L. Fazan and R. Jahn supported this work with lively discussions. N. Kirchhoff and R. Pätsch read an earlier manuscript. Comments by guest editor C. Wellstein and two unknown reviewers brought significant improvements.

Chapter 5: Geological data significantly reduce the model performance of species distribution models on broad spatial scales. A GIS – based approach from two Mediterranean Islands

Goedecke, F.; Marcenò, C.; Guarino, R.; Jahn, R. & Bergmeier, E. Geological data significantly reduce the model performance of species distribution models on broad spatial scales. A GIS – based approach from two Mediterranean Islands

Manuscript planned for submission to *Diversity and Distributions*

Geological data reduce the model performance of species distribution models on broad spatial scales. A GIS – based approach from two Mediterranean Islands

Abstract

Extrapolation of species distribution models is frequently performed for mainland regions, therewith predictions for e.g. unrecorded occurrences of plant species or for difficult terrain can be made. We extended the methodology to isolated regions and applied it to the Mediterranean islands Sicily and Crete. The islands share woody species of the widespread maquis vegetation, belonging to the class *Quercetea ilicis*. We trained species distribution models in MaxEnt on one island and extrapolated to the other island to test. Precise coordinates were used for 12 woody species, of which four are edaphic specialists and eight are generalists. Additionally bedrock type, topography and macro-climate parameters are included in the models. For these widely-used environmental parameters we describe a selection process, which helps for extrapolation. Models work well chiefly for substrate specialists, while predictions for some species elude from extrapolation. Ecologically and thus spatially restricted specialists perform better than generalists. We discuss several advantages and issues for method; e.g. distinctly different site-conditions for species of the (meta)populations in two isolated regions can hamper extrapolations. Models performed well when climate data and relief were included, whereas performance was lowered for models comprising bedrock types. Differences in the affinity to bedrock types, in the isolated test region can be a reason.

Introduction

Islands are important model systems, enabling to understand general biological processes and isolation-related patterns, for sharing “the hard boundary of the sea” (Bramwell and Caujapé-Castells 2011). Mayor evolutionary and biogeographic theories were developed with by investigating island organisms and they still offer research perspectives. Also the Mediterranean basin comprises islands to study, hosting at the same time differentiated floras and common generalists. These common species facilitate ecological comparison and are crucial for manifold applications. To compare ecological patterns species distribution models are an important method. Therefore various algorithms exist (Elith and Leathwick 2009) which usually predict distribution using records of organisms combined with abiotic data such as soil, bedrock type, topography or land use. But modeling distribution in isolated regions can be difficult, i.e. due to varing landscapes configuration across regions. Such environmental variations affect e.g. susceptibility for invasive neophytes (Lambdon et al. 2008).

While niche conservatism is a basic paradigm of species distribution modeling (Peterson et al. 1999; Wiens et al. 2010), Morphologically similar isolated populations can differ in ecological niche but even in genetic constitution (Broennimann et al. 2007; Christe et al. 2014; Violle et al. 2012), particularly effecting evolution and ecology (Johnson and Stinchcombe 2007). To differentiate species environment relations extrapolations are increasingly used in ecological research (Miller et al. 2004). In this context reciprocal extrapolation for split datasets applies for methodological optimization. Several authors modeled distributions of isolated subpopulations of species, e.g. mammals for spatial bins in South America (Radosavljevic et al. 2014) and amphibians in Australia (Elith et al. 2010). Heikkinen et al. (2012) tested reciprocal extrapolation for Finnish forest plants in neighbouring regions. Extrapolation was performed using continental bird data to test predictive performance (Bahn and McGill 2013; Peterson et al. 2007); but also on global scale too detect fungal diseases patterns (Escobar et al. 2014). Martínez-Meyer and Peterson (2006) addressed temporal extrapolation for recent and Last Glacial Maximum tree pollen taxa and discuss niche evolution. Similarly temporal scales were compared in further studies (Maguire et al. 2015; Svenning et al. 2011). The latter examples comprised successful approaches of extrapolations. But when species distribution models are extrapolated outside training regions fundamental issues apply. Especially differences in environmental parameters cause trouble in predictions (Stohlgren et al. 2011; Young et al. 2012).

A complex interplay of various environmental parameters limits the growth conditions of plants and their occurrence; to account therefore a set of environmental variables is usually combined. Climate datasets are mostly integrated therin. They cover different spatial and temporal scales and various

resolutions; having their pros and cons (García-López and Real 2014; Suggitt et al. 2017). Many ecological studies used climatic data for global scales for modelling. These frequently used high-resolution data are based on interpolation of climate station data e.g. Worldclim which integrates elevation to generate climate data surfaces (Hijmans et al. 2005). Karger et al. (2016) improved high-resolution calculations using various parameters from global digital terrain models and cross checks with reliable alternative climate data. We aim to support the test of the dataset with this study comparing islands. The two studied islands share the biogeographic region, are similar in general site conditions and comprise a well-studied species-rich flora. Even if environmental conditions overlap, we propose strategies of parameter selection helping to extrapolate species distribution models for isolated populations. The complexity of ecological interactions comprising topography and substrate features (e.g. Copeland and Harrison 2015; Helman et al. 2017; Kessler 2002; Kopecký and Čížková 2010; Meentemeyer et al. 2001), should be regarded in this study as well. Thus we test the influence of topography and bedrocks on extrapolation performance. Following questions are intended to be answered: I) To what extent can a model calibrated on one island be a good predictor of the distribution of a given species on another island? II) Which are the most influential variables in our distribution modeling and are they the same on both islands for a given species? III) Is the observed shifting ecological behaviour (and related occurrence probability) of a given species more influenced by climatic, by geomorphological or by edaphic drivers?

Materials and methods

Study area

We chose two of the largest Mediterranean islands as study area. Sicily is located in the Central Mediterranean, while Crete is located in the South-Aegean Sea about 750 km eastwards. The first has an area of 25,500 km² while the second covers almost one third of the big neighbour and stretches from east to west for about 250km. Sicily (Meulenkamp and Sissingh 2003) and Crete (Meulenkamp et al. 1988) are considered to be islands during most of the Tertiary. Therewith sea level and geological uplifts were important factors. Today Sicily's shortest distance to the mainland coast is 3 km at the strait of Messina, thus biogeographical connection to the Italian mainland applies. Crete is more isolated with a distance of about 100 km to Peloponnese-Peninsula, whereas arc-forming islands are virtually reducing the distance as stepping-stones for migrating organisms. While volcanism contributes markedly to the Sicilian landscape, on Crete volcanic rocks and basalts are merely absent. Hard limestones and metamorphic rocks prevail in the main Cretan mountain massifs, but have minor proportions on Sicily. Flysch series, Quaternary and Neogene sediments form vast areas in the lower altitudes of both islands. For the island regions coastal areas are facing pronounced Mediterranean summer drought. With higher altitudes precipitation rises and mean

temperatures decrease, which allows Euro-Siberian taxa to thrive (e.g. *Berberis*, *Betula*, *Populus*). A general climatic gradient is formed within the Mediterranean study region by decreasing precipitation from West to East.

Species data

Published Atlas Flora Europaea volumes 1-13 show 35% floristic similarity for the two islands (Junikka et al. 2006). High endemism rates apply for both regions: So Crete hosts 10.4% (Jahn and Schönfelder 1995) and Sicily even 11.6% (Brullo et al. 2004). Similar is likewise the set of woody species within the vegetation class Quercetea ilices for both regions. This Vegetation unit comprises woodlands and scrubs, commonly dominating landscapes in the Mediterranean Basin. It is often altered by historical or recent anthropogenic land use (Pignatti 2003; Quézel 2004). Therewith species have particular relevance for climax vegetation of mostly lower altitudinal belts. Thus for 12 Mediterranean woody member species of this syntaxon we collected 4311 geographically resampled records (Table 5.1). These records derive from plot data and floristic data from Crete (Bergmeier 2012; unpublished material) and relevées from Sicily (Appendix Table A 5.2). We applied a broad taxonomic concept merging closely related taxa, which are treated as subspecies or even different species in literature; nomenclature follows (Euro+Med 2006-2017). Subsets of the same species in two regions are considered as (meta)populations. Ecological specialist species and generalist species among the woody species were distinguished based on expert knowledge.

Table 5.1 Taxa used in this study and their records for each island, Nomenclature follows (Euro+Med 2006-2017)

Taxon name	Plant family	Records from Sicily	Records from Crete
<i>Arbutus unedo</i> L.	Ericaceae	57	60
<i>Ceratonia siliqua</i> L.	Fabaceae	116	116
<i>Erica arborea</i> L.	Ericaceae	135	135
<i>Euphorbia dendroides</i> L.	Euphorbiaceae	166	166
<i>Juniperus oxycedrus</i> subsp. <i>macrocarpa</i> (Sm.) Ball	Cupressaceae	20	20
<i>Juniperus phoenicea</i> subsp. <i>turbinata</i> (Guss.) Nyman	Cupressaceae	34	34
<i>Olea europaea</i> L. subsp. <i>europaea</i> (no cultivars)	Oleaceae	298	298
<i>Phillyrea latifolia</i> L.	Oleaceae	251	251
<i>Pistacia lentiscus</i> L.	Anacardiaceae	433	433
<i>Pistacia terebinthus</i> subsp. <i>terebinthus</i> L.	Anacardiaceae	133	133
<i>Quercus coccifera</i> L.	Fagaceae	59	59
<i>Quercus ilex</i> L.	Fagaceae	452	452
Records per island		2154	2157
Number of all records		4311	

Data handling in the GIS

In ARCGIS 10.2 (ESRI 2013) coordinates of species records are handled as point data and environmental data as a raster format. The program was also used to create maps for species distributions and prediction results from MaxEnt models described later. For environmental data a 1-km-grid was used with 35,634 cells covering both islands (EEA 2012). Climate data were obtained from CHELSA (Karger et al. 2016) for annual mean temperatures (*t_mean*) and annual precipitation sums (*ann_prec*). Additionally slope angle (*slope*) and *compound topographic index* (*cti*) were calculated from a digital elevation model (EEA 2015) using the GIS extension by Evans et al. (2014). *CTI* is a wetness index, which accounts for slope position and the upstream contributing area of the watershed (Gessler et al. 1995, Moore 1991). As proxy for substrates geological maps were integrated. Simplified stratigraphic and lithological units follow map legends (Fierotti 1988; HGME 1959–2002): a) Quaternary and Neogene sediments, b) hard limestones, c) flysch series, d) gypsum, e) volcanites including basalts and pillow lava, and f) metamorphic rocks mostly causing acidic soil reaction. In the GIS the percentage of each geological unit was quantified for the grid cells resulting in individual data layers for each unit. All environmental data layers were handled in the same extent and the same projection. For their import in MaxEnt they were transformed to ASCII-files.

Variable selection

Environmental differences exist in the study area, but extrapolation of species distribution is problematic for unequally distributed values of abiotic variables on the two islands. To overcome such difficulties only those environmental parameters with a comparable range of values on the two islands were used, according to Anova tests (Figure 5.1, IBM SPSS Statistics for Windows, Version 22, Armond, NY). Secondly, to avoid collinearity only those with $R^2 < 0.6$ in Pearson correlations were included (Appendix Figure A 5.1; R Development Core Team 2017; Revelle 2017). Area Under the Curve (AUC) was used as unreflected usage (Lobo et al. 2008), it remains a measure frequently applied for model evaluation, allowing the comparison of models for the same species in the same area. The proposed order of selection steps gives higher and thus better AUC-values compared to the reverse one. The following variables were used in this study: *ann_prec* annual precipitation, *t_mean* annual mean temperatures, *slope* angle, *cti* compound topographic index; and the bedrock types: *meta* metamorphic rocks, *lime* limestones, *basa* volcanic and basaltic rocks, *sedi* Quaternary and Neogene sediments, *flys* flyschs, a measure for model evaluation. Despite the fact, that AUC is criticised for *gyps* gypsum. All further available climate variables (for a list see Karger et al. 2016), *altitude*, *heatload index* (McCune and Keon 2002) and *solar radiation index* (Rich et al. 1994) did not fulfil the filtering criteria.

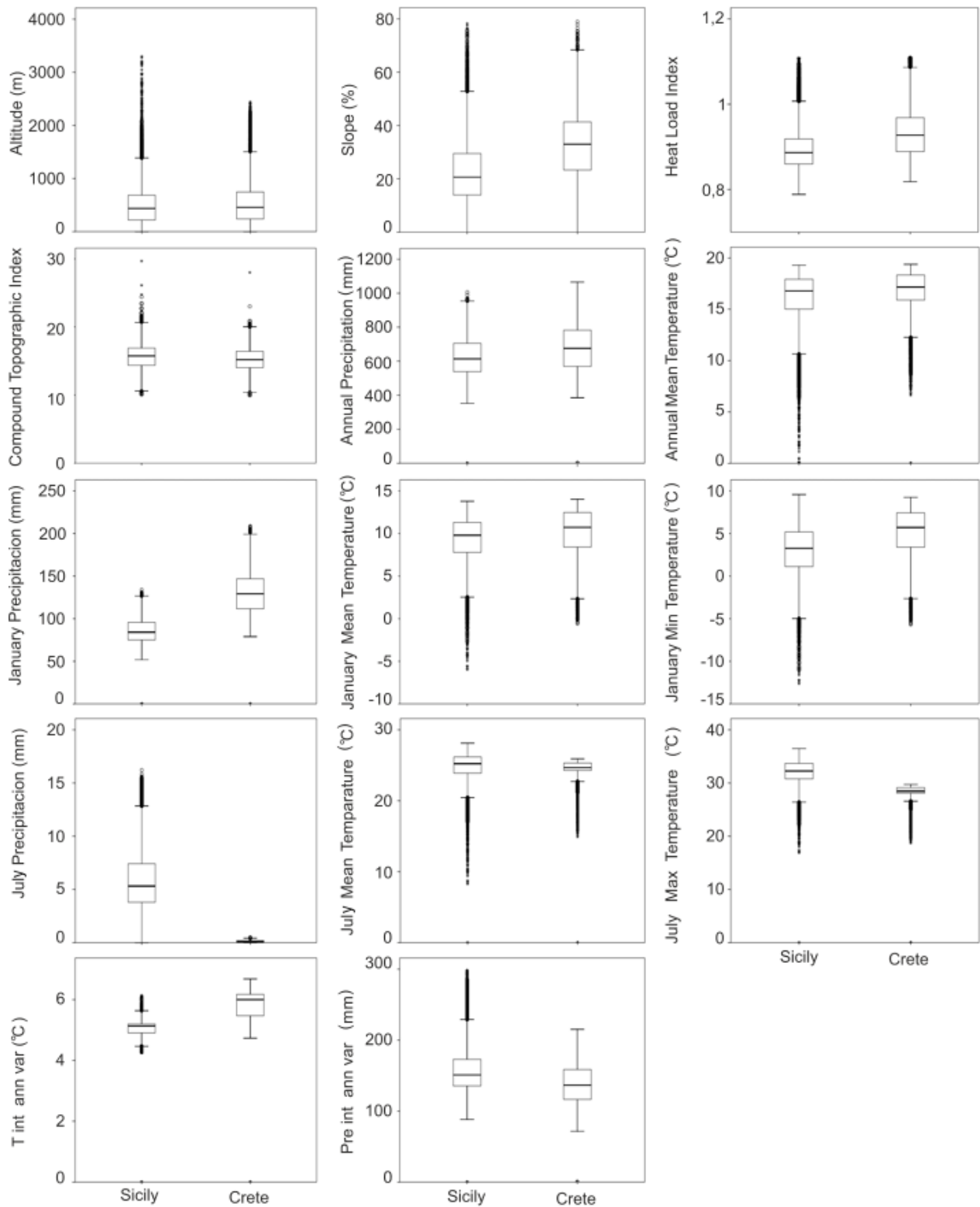


Figure 5.1 Range of environmental variables for the two study regions Sicily (left) and Crete (right) based on values from 1 km grid cells; *Pre int ann var* Interannual variation of Precipitation, *T int ann var* interannual variation of Temperatures.

Modeling

For the calculation of species distribution models we used MaxEnt Software version 3.3.4 (Phillips et al. 2006). It gives predicted probabilities of occurrence for the species in raster cells by combining point distributions of species and abiotic raster data for these cells. We calculated two MaxEnt-models for every species, each one trained on either Crete or Sicily. Those records from the second island which were not used for training served as test data. This reciprocal testing allowed the comparison of the prediction values and to infer differences in model performance. AUC-values were used to evaluate extrapolation quality of models, but should as well serve as an indirect measure of the difference in the realised ecological niche. We expect that minor AUC-differences apply, when species are equally extrapolated to the respective test region. Hence a varying AUC-value between regions is related to diverging abiotic conditions in the training and test region. Additionally different combinations of the three factors climate, topography and geology were tested in models. These environmental factors represent groups of environmental variables: *rel* relief comprises *slope* and *cti*; *cli* climate contains *ann_prec* and *t_mean*; and *geol* summarises the joint influence of the six distinguished geological units. Single factors and their combinations are used in models and tested according to AUC-values. The individual influence of the 10 environmental variables is evaluated as well by using jackknife tests. They account for relative importance on the test gain of the models.

Results

In their affinity to bedrock types the selected species differ on both islands (Table 5.2). Further the edaphic specialists from the Ericaceae family *Arbutus* and *Erica* occupy metamorphic rocks on Crete in about 70% of their sites, while in Sicily they cover a wide bedrock spectrum comprising also flyschs. The two *Juniperus* species growing near the coasts of both islands on predominately sandy sediments are specialists as well, but in Crete they additionally occupy limestones to larger extent. These limestones are frequently overblown by sands in Crete, which disregarded in the geological basemaps. Generalist species covering similar bedrock spectra on islands are *Ceratonia siliqua* and *Pistacia lentiscus*. Generalists cover a wide range of bedrock types on both islands, but some differ markedly in covered substrates. On Crete 60% of sites where *Euphorbia dendroides* thrives are on limestones and 25% on sediment rocks, while in Sicily it occurs on the latter substrate in highest proportions but additionally on limestone, flysch and volcanic rocks. Volcanic rocks are a particularity in Sicily without analogues in Crete. Almost one fifth of Sicilian records of *Olea europaea* and *Phillyrea latifolia* are on volcanic rocks; for *Quercus ilex* this rock type makes 35% of all sites and for *Pistacia terebinthus* even 45%. Pronounced differences apply for occupied substrates of *Quercus coccifera*: 81% of sites for Sicily are on sediments, stretching merely near the

southern coast, while in Crete the species is omnipresent with two third of records on wide-spread hard limestones. But also relief and climatic variables differ for the studied maquis species (Figure A 5.2). *Q. coccifera* is outstanding for its affinity to high *cti* and low *slope* angle; and this species grows in a dry environment with lower annual precipitation and higher temperatures in Sicily compared to Crete. Sicilian juniper sites appear to be similar with high *cti*, low *slope* and lowered annual precipitation.

Table 5.2 Woody species on Crete (Cr) and Sicily (Si) with their affinity to bedrock types in % of records: *basa* basalts and volcanic rocks, *flys* mostly Mesozoic flysch series, *lime* hard Tertiary to Mesozoic limestone, *meta* mostly acidic metamorphic rocks, *sedi* Neogene and Quaternary sediments, *gyps* gypsum.

Species	island	bedrock types					
		basa	flys	lime	meta	sedi	gyps
Edaphic specialists							
Arbutus unedo	Cr	0	1	16	67	17	1
	Si	9	33	16	23	19	0
Erica arborea	Cr	0	0	13	71	15	0
	Si	13	38	9	19	22	1
Juniperus oxycedrus subsp. macrocarpa	Cr	0	11	22	0	67	0
	Si	0	0	16	0	84	0
Juniperus phoenicea subsp. turbinata	Cr	0	8	30	6	54	0
	Si	0	5	0	0	95	0
Generalists							
Ceratonia siliqua	Cr	0	3	36	14	45	1
	Si	11	5	32	0	41	11
Euphorbia dendroides	Cr	0	4	61	8	25	0
	Si	20	16	20	0	42	2
Olea europaea subsp. europaea	Cr	0	7	39	18	34	0
	Si	18	14	22	0	42	5
Phillyrea latifolia	Cr	0	2	53	24	20	0
	Si	19	9	26	0	35	12
Pistacia lentiscus	Cr	0	5	33	12	49	0
	Si	14	14	23	0	42	7
Pistacia terebinthus subsp. terebinthus	Cr	0	4	44	21	30	0
	Si	45	2	34	0	19	0
Quercus coccifera	Cr	0	4	63	14	17	0
	Si	0	7	12	0	81	0
Quercus ilex	Cr	0	2	37	44	17	0
	Si	35	14	23	3	23	2

Further species are rather similar in their affinity to the four relief and climate variables tested (Figure A 5.2). In this study also complex ecological interactions are considered, assessed in species distribution modelling for which results of jackknife tests are displayed here (Table 5.3). Percentages of maximum regularized training gain reflect the importance of environmental variables for the fitting of models to training data. Only for two species environmental variables were the same on both islands, for *J. phoenicea* subsp. *turbinata* with annual mean temperatures and for *P. latifolia* the *slope* angle were most relevant an (Table 5.3); in contrast the other species differed in

Table 5.3 Percentages of maximum regularized training gain from species distribution models evaluated in jackknife tests for Crete (Cr) and Sicily (Si) concerning the influence of single environmental variables: *ann_prec* annual precipitation sums, *t_mean* mean annual temperatures, *slope* angle of slope, *cti* compound topographic index, geology follows table 5.2.

species		ann_prec	t_mean	slope	cti	meta	lime	basa	sedi	flys	gyps	maximum regularized training gain
<i>Arbutus unedo</i>	Cr	23.0	11.5	27.6	2.8	78.3	2.8	5.1	10.1	7.8	1.4	2.17
	Si	49.2	3.3	18.0	4.9	31.1	0.0	1.6	21.3	19.7	9.8	0.61
<i>Erica arborea</i>	Cr	33.1	16.5	18.6	4.1	78.5	2.5	4.5	13.6	0.5	2.1	2.42
	Si	42.7	28.2	36.8	7.3	18.2	7.3	6.8	2.5	2.5	2.7	1.10
<i>Juniperus oxycedrus</i> subsp. <i>macrocarpa</i>	Cr	0.0	68.8	3.3	0.0	2.1	0.4	4.6	2.1	0.0	2.5	2.40
	Si	33.9	6.3	53.6	13.5	2.6	3.1	6.3	7.3	0.9	3.1	1.92
<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	Cr	2.6	53.8	4.1	0.0	4.6	5.1	5.6	6.2	8.7	2.6	1.95
	Si	9.8	72.1	0.0	14.8	4.1	10.7	9.0	0.8	0.0	1.2	1.22
<i>Ceratonia siliqua</i>	Cr	1.4	17.9	23.6	1.4	21.4	15.7	8.6	15.7	4.3	4.3	1.40
	Si	32.1	33.7	15.3	8.2	5.6	3.1	4.1	11.2	0.5	6.6	0.98
<i>Euphorbia dendroides</i>	Cr	2.5	16.7	30.3	1.0	7.1	36.9	5.6	14.6	3.0	3.5	1.98
	Si	1.4	7.7	37.5	1.4	5.3	0.0	16.3	8.2	1.4	1.4	1.04
<i>Olea europaea</i> subsp. <i>europaea</i>	Cr	3.9	12.7	31.4	2.0	26.5	28.4	12.7	15.7	2.9	6.4	1.02
	Si	7.8	20.8	15.6	1.3	7.8	1.3	6.5	15.6	1.3	2.6	0.77
<i>Phillyrea latifolia</i>	Cr	16.4	10.2	39.5	5.5	33.2	33.6	10.2	21.9	6.3	5.5	1.28
	Si	9.7	12.9	19.4	1.6	9.7	8.1	6.5	17.7	0.0	1.6	0.62
<i>Pistacia lentiscus</i>	Cr	1.5	9.5	12.4	0.7	11.7	10.2	9.5	13.1	4.4	3.6	1.37
	Si	17.2	25.4	9.0	3.7	6.7	3.0	6.0	11.9	1.5	3.0	0.67
<i>Pistacia terebinthus</i> subsp. <i>terebinthus</i>	Cr	17.8	9.9	34.9	5.3	34.2	23.7	7.9	9.2	4.6	3.9	1.52
	Si	5.3	35.6	3.0	3.0	3.8	12.9	35.6	21.2	3.0	4.5	1.32
<i>Quercus coccifera</i>	Cr	15.4	9.1	42.3	4.9	31.7	55.3	9.8	23.6	36.6	52.8	1.23
	Si	20.0	56.4	23.6	4.3	3.6	5.7	7.9	18.6	1.1	4.3	1.40
<i>Quercus ilex</i>	Cr	27.7	12.8	31.4	6.4	57.4	12.8	6.4	13.8	4.8	3.2	1.88
	Si	6.1	15.3	33.7	4.6	1.5	6.1	30.6	21.4	2.0	4.1	0.98

combinations of variables, so for *A. unedo* and *E. arborea* over 78% of the training gain was explained by metamorphic rocks on Crete, while for Sicily precipitation was the most important variable instead. In this case the magnitude of records found on this bedrock is similar to the magnitude of training gain in models. Situation differs for the junipers, attributed to the group of specialist species, they occupy coastal sediments in both regions, while in models *ann_prec*, *t_mean* and *slope* are most relevant. The major ecological variable for the kermes oak (*Q. coccifera*) was

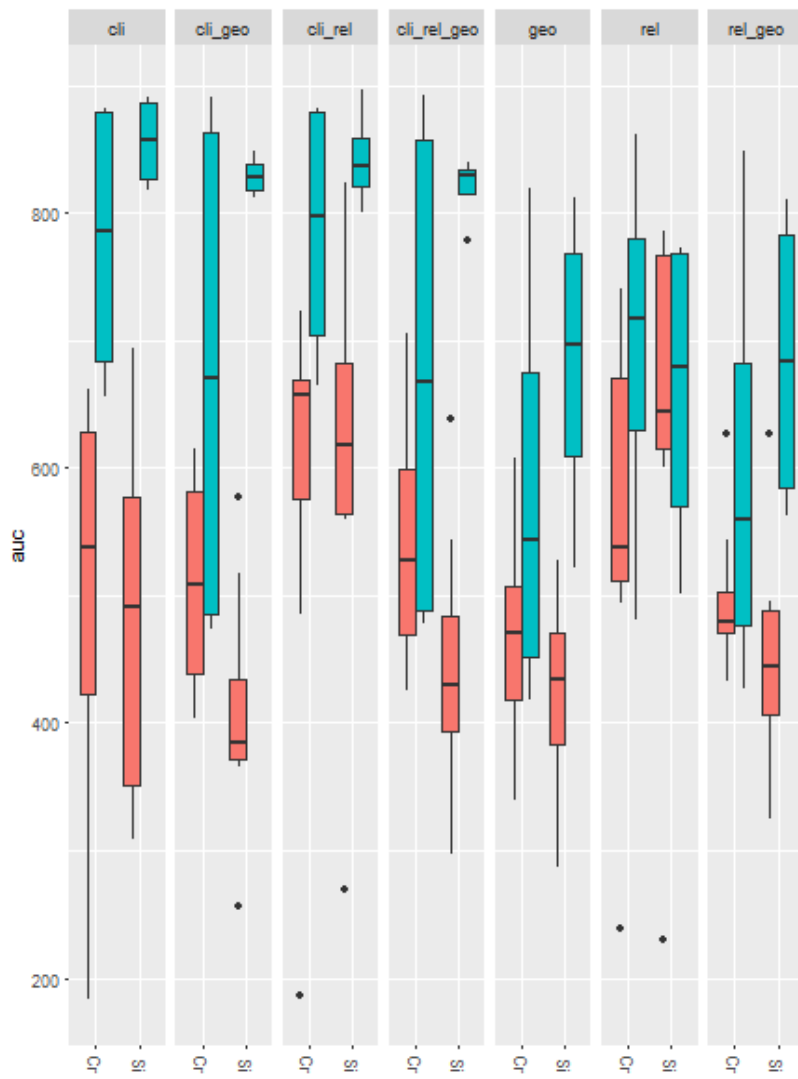
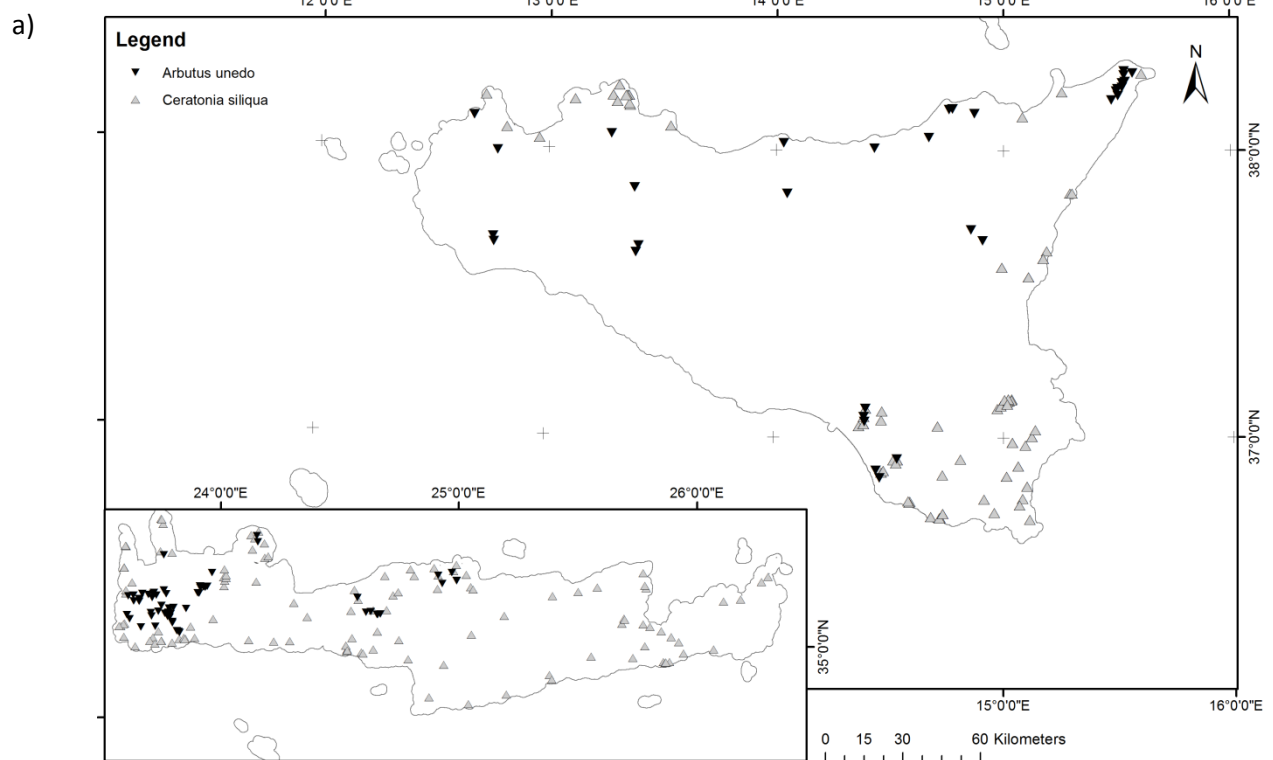
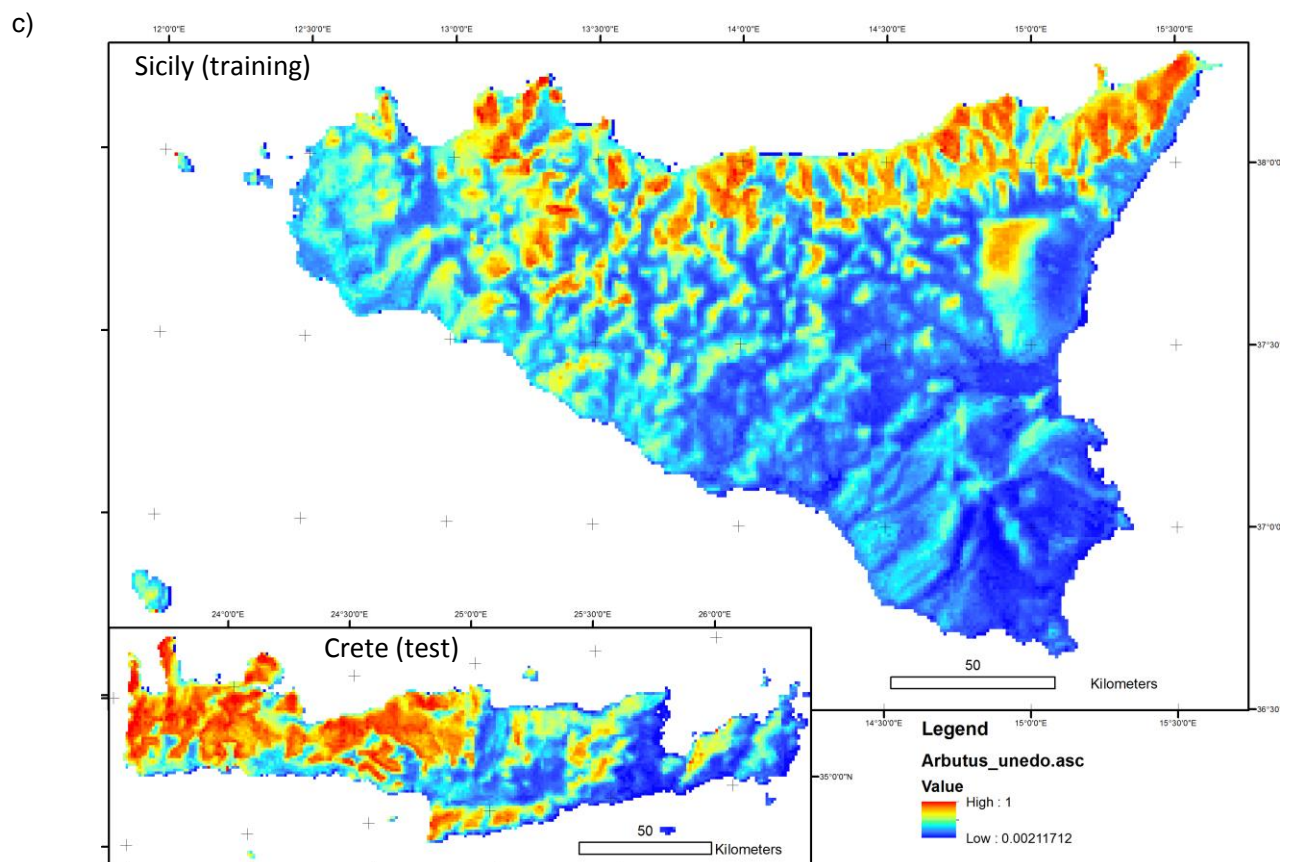
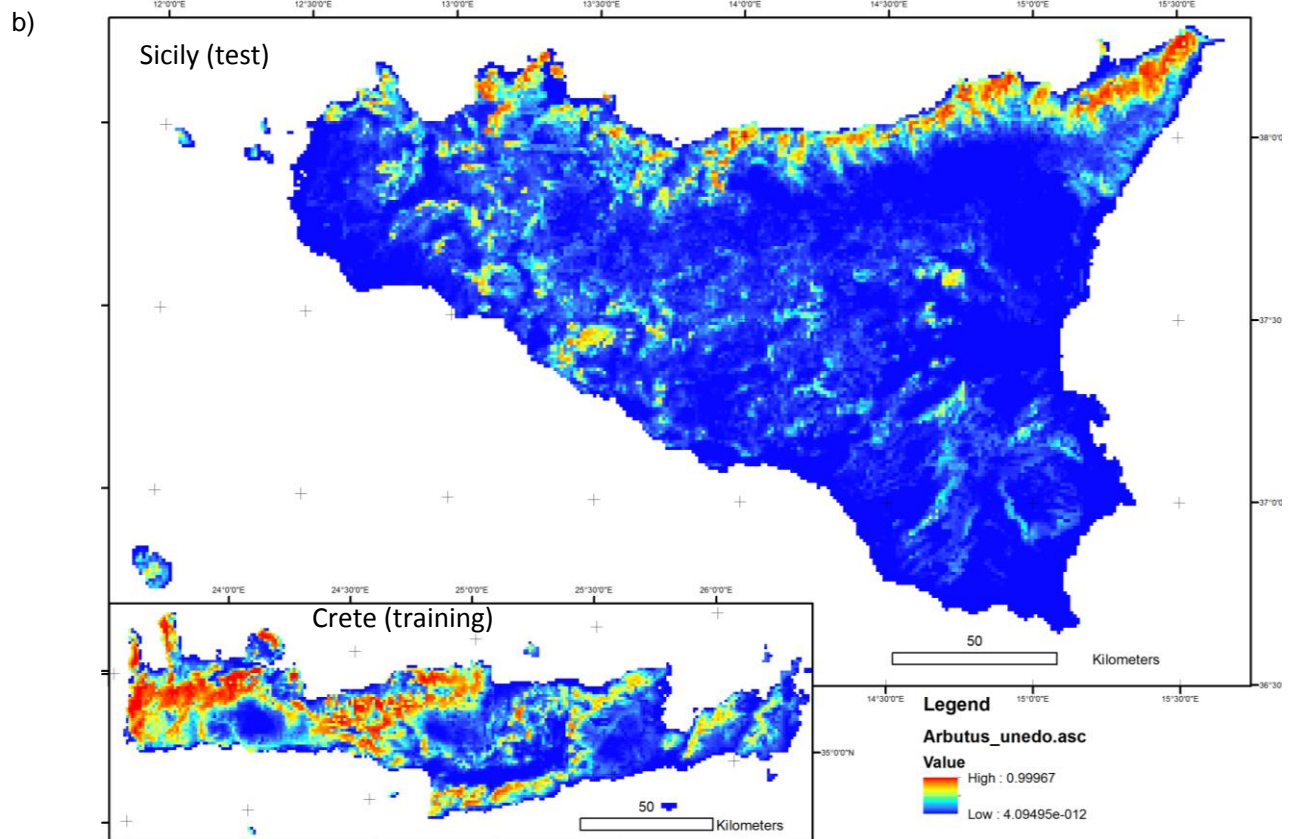


Figure 5.2 Boxplots displaying variation in test AUC-values (x 1000) for woody species trained on Crete (Cr) and Sicily (Si) for 7 combinations of environmental parameters (cli – climate, geo – geology, rel – relief). Blue bars indicate ecological specialist species, red bars comprise models for generalists.



continued



continued

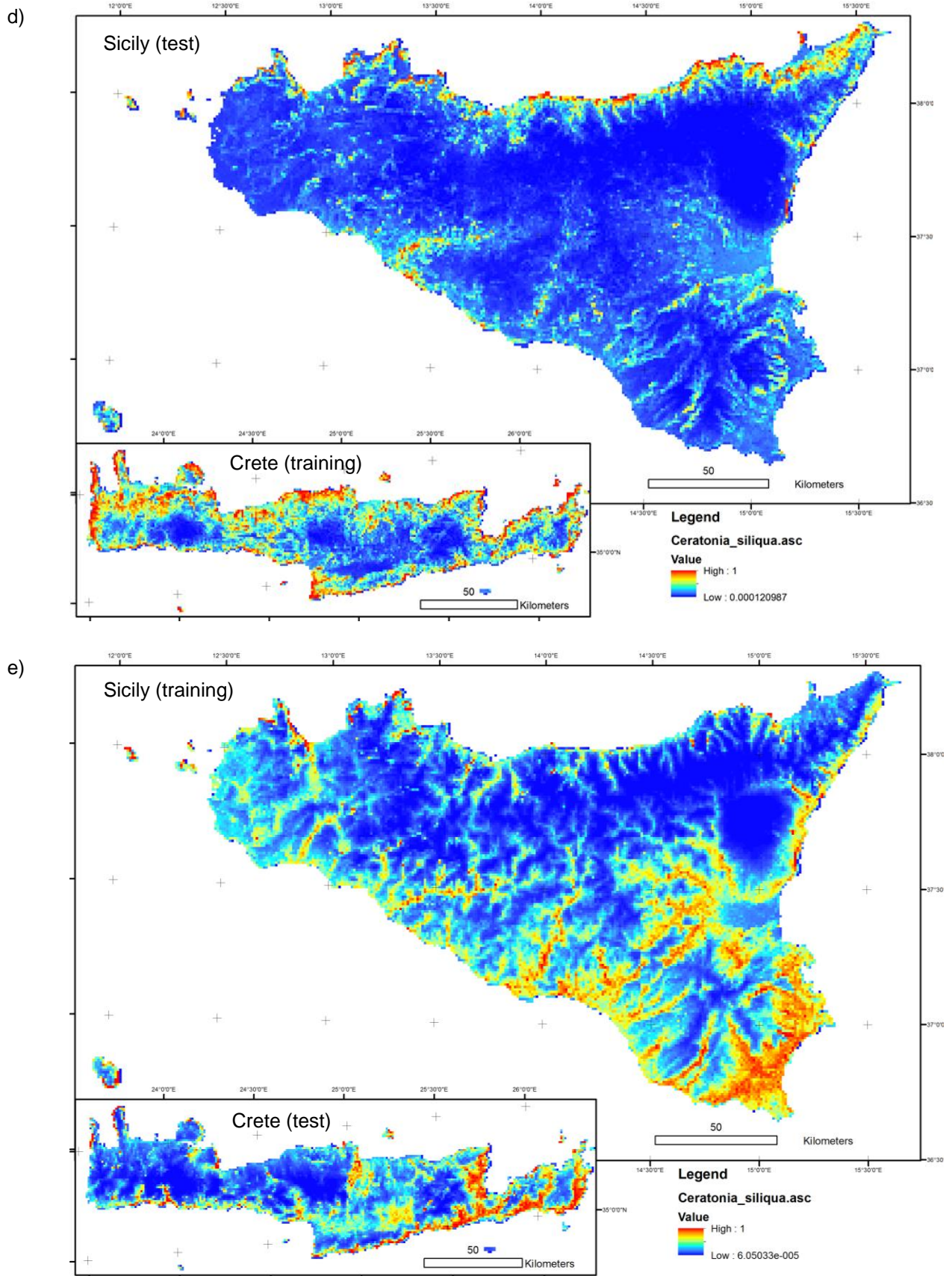


Figure 5.3 Maps for species distribution models trained for Crete (b,d) and Sicily (c,e) and extrapolated to the test island in each case; a, resampled records for both species, b, c: *A. unedo* (edaphic specialist), c,d: *C. siliqua* (generalist); warmer colours indicate higher probability of species' occurrence.

t_mean in Sicilian models, but bedrock types had high influence on the Cretan model. Most of the occupied bedrocks are relevant for its distribution, as the species is so wide spread on the latter island. Metamorphic bedrock best supported Cretan models for the second oak *Quercus ilex* (even though several rock types were occupied), while for Sicily volcanic bedrock and sediments were the most important. Flysch and gypsum generally had low influence on models, but merely the fitting of training data for *Q. coccifera* on Crete and *A. unedo* on Sicily were based on these bedrocks.

Test AUC values were used as an estimate of extrapolation and to compare subsets from the regions as well as ecological generalists and specialists. All tested combinations of environmental variables and maquis species are indicated in the Appendix table A 5.1. Best overall extrapolations are found among the junipers and the two other specialist species. Lowest AUC-values apply for the extrapolation of *Q. coccifera* in the modelling based on “climate” only, “climate+relief” and “relief” only. Among the generalist species *Euphorbia dendroides* featured good AUC values of 0,723 and 0.824 for the extrapolations to Sicily and to Crete respectively, when climate and relief were considered. *Pistacia terebinthus* and *Quercus ilex* performed well in extrapolations using relief features only. The general trends from this table are visualised in boxplots (Figure 5.2); models trained for ecological specialists outperformed those for generalists. Highest mean AUC-values were calculated for specialist’s species including climate data in the models, while lowest AUC-values apply, when geology is used. When combinations of different ecological variables are concerned, models trained on Sicily performed better in the extrapolation of specialist’s species, while generalists are better predicted by Cretan training points; for models applying only relief parameters the reverse was observed.

Exemplary cases of prediction maps display a specialist and a generalist species with their predicted distribution based on all environmental variables for either Cretan or Sicilian records (Figure 5.3). The model trained on Crete for the edaphic specialist *A. unedo* gives robust results but may underestimate some occurrences in the east of the Sicilian test area (Figure 5.3a). The second image is based on Sicilian records and gives a blurred picture of the delineations of the potential species’ distribution (Figure 5.3b), Sicilian and Cretan populations are predicted therewith, but the area is overestimated. Similarly, maps perform well for the training region but extrapolation to the test region is limited for the generalists (Figure 5.3 d + e). For those the potential area in the test region is too small for both extrapolations.

Discussion

Quality of extrapolation

Extrapolation performance for models trained for one island and tested for another island led to good results for few maquis species. Models for taxa with restriction to very particular environments performed best, while other species with a broad ecological niche performed weaker. This is supported by several other studies (Araújo and Guisan 2006; Brotons et al. 2004; Hernandez et al. 2006; McPherson and Jetz 2007). So generally the quality of extrapolation depends on species records and their occupied site conditions. We consider differences in availability of sites to be related to particular ecological environments on individual islands. Together with shifting ecological behaviour it could be a possible reasons for limited extrapolation performance. Technical constraints are connected: because the used MaxEnt algorithm contains a selection procedure, which takes the most suitable ecological variables explaining input distribution of training points; different driving variables apply and extrapolation outputs vary. When the selection of variable combinations is bound too tightly to training data, models may suffer from overfitting, which is a likely reason for the low performance of extrapolation in case of generalists models. Overfitting is especially problematic when ecological conditions vary across the study region. Studied species prefer combinations of site conditions, which do not correspond to those of the training data (Radosavljevic et al. 2014). Additionally overfitting depends on e.g. modeling algorithm, sample selection, complexity of environmental data and their choice. In our study the best prediction results apply for specialist species related to specific coastal conditions. These rather extreme environmental characteristics are restricted in total area and occur on both islands.

Some species, such as *Q. coccifera*, eluded from extrapolation by their very different ecology in the training and the test region. In Sicily the species is restricted to sedimentous substrates near the southern coast (Pignatti 1998) where sites have low *slope* angles and high *cti* mostly according to our results. Macroclimate in the south of Sicily is hot and dry. Thus the oak species may be restricted to those sites, where topography and bedrock compensate water deficits. Contrary to this assumption *Q. coccifera* occurs together with *Juniperus phoenicea* subsp. *turbinata* and is described for sandy substrates with low carbon content and low water holding capacity (Pignatti 1998). On Crete *Q. coccifera* covers various substrates, a wide ecological amplitude and reaches from the coast to almost 1600m a.s.l. (Bauer and Bergmeier 2011; Goedecke et al. 2018; Jahn and Schönfelder 1995; Tsiourlis et al. 2009). Hypothetically also in Sicily the species could have had a wider distribution in earlier times and be reduced to few recent sites due to past extinction events. Alternatively competition could have hindered the spread of the oak species from founder populations along the coast. In a similar way ecological filtering, could constrain expansion of the

species to an unsuitable surrounding. An example for a species captivated under special ecological conditions is *Zelkova sicula*, endemic to southern Sicily (Garfi et al. 2011). The strong affinity of Sicilian *Q. coccifera* for sediments and the completely different ecological variables applying for sites, could suggest distinct ecological or even genetic position of the Sicilian taxon. To test this hypothesis, a detailed genetic analysis is needed.

Our results were partially influenced by the availability of different site conditions on both islands. In Sicily gypsum and volcanic rocks represent in total about 10% of the land surface but are rare on Crete. The exclusion of the records from these two bedrock units could have improved the performance of the model, but this was not the purpose of our approach. Instead, by considering the whole edaphic range of both islands we did not lose the completeness of spatial cover and we accounted for shifts in the species' ecological behaviour.

A crucial point for the extrapolation concerns sampling bias. As Owens et al. (2013) discuss environmental conditions covered by sampled records for the training area do not match the potentially covered ecological range for modeled taxa. The numbers of records per species and island show a wide range (20 to 452). We cannot exclude, that sampled records do not suit to a range of values, which is wide enough for the training and the test region. *Q. ilex* and *P. lentiscus* have the highest sums of records, covering wide ecological spectra and therewith give high site heterogeneity. For the to latter generalists, heterogeneity could hamper model fitting for the training region, and even more ecological heterogeneity and shifted ecological behaviour could decrease extrapolation performance. The fewest records though were available for the two *Juniperus* species, being ecologically specialized and rare. Their distribution models performed well for the two islands and outperformed those of other species with higher numbers of records.

Driving environmental conditions on the two islands

The data from global extrapolation of climate stations (Karger et al. 2016) offer a high resolution and were successfully used on large scales. We showed that on regional level such widely used climate data work well to predict species distributions. Caution applies, as few interpolated climate stations are available for a pronounced mountain relief with complex terrain. The regional application of global climate data was discussed by other authors (Beaumont et al. 2016; Nadeau et al. 2017). Our selection of variables for species distribution models resulted in few independent ones, which were expected to generalise conditions sufficiently for both islands and help for extrapolation. Not least because the study of Peterson & Nakazawa (2008) observing the failure of over-complex bioclimatic variables from global climate models in extrapolations, we preferred simple macroclimate parameters such as mean temperatures and precipitation sums. Other collinear bioclimatic variables were neglected. Beside general applicability in this study and even

though altitudinal and topographic corrections are implemented within global climate models (e.g. Karger et al. 2016), climate data should be further tested for suitability in fine-scale applications. Suchlike was performed by Daly et al. (2010), who installed an array of climate data loggers to correct climate models for complex mountain topography. Their study revealed relative independence of macro-climate and topoclimate, highlighting the importance of topography. Topography is important especially in mountain areas, bearing complex interactions and a wide range of site features. This is frequently underestimated in coarse scale climate models related to climate station records (Barry 2008; Berry et al. 2016; Körner 2014; Scherrer et al. 2011; Scherrer and Körner 2009).

Relief parameters such as *slope* values and *cti* describe only parts of the regional topography but are crucial for the understanding of species ecology. Three modeled species in our study showed best extrapolation performance when only “relief” (*P. terebinthus*, *Q. ilex*) or “relief + climate” (*E. dendroides*) were used. As a part of distribution modeling for Californian woody species topography revealed its importance in contrast to macroclimate (Franklin 1998) and also distributions of grasses and ferns were well predicted by topography (Slavich et al. 2014). Other authors discussed the importance of climate and topography on plant diversity patterns (Fois et al. 2017; Irl et al. 2015) and a meta-study revealed topographic features, such as wind and sun exposure, essential for seedling-survival and species distribution across continents (McIntire et al. 2016). Special cases of topographic complexity apply for karstic landscapes with talus cones, deep valley incisions, poljes, dolines, etc., occurring scattered and on a wide scale on both studied islands (Di Maggio et al. 2012; Egli 1989). Because species thrive there under else unsuitable conditions, such structures can affect predictions. The latter example shows, that the affinity to a certain bedrock can be related e.g. to its erosivity or featured landforms.

Our results revealed that models including geology do not perform well for all species. One reason for the weak performance can be the quality of geological data. Referring to the resolution of the used maps and their focus on stratigraphic units various surface conditions were disregarded. In the West of Sicily and various parts of Crete the formation of soil pockets is not captured in mapping because of their small-scaled distribution. Similarly overblown sand preferred by *J. oxycedrus subsp. macrocarpa* is disregarded. Another difficulty resulting from the application of mapping units: coarse grouping applies for bedrock types in our study, this allowed for a supra-regional application, but led to a high heterogeneity within each of the bedrock types. Such heterogeneity of rocks influences soil conditions for plants (Neff et al. 2006). Partly bedrocks relate to soil types, but alone they are not sufficient for a quantification of substrate parameters (Bockheim and Gennadiyev 2010; Minasny et al. 2008). One important soil parameter is the pH-value in Mediterranean landscape context (Chytrý et al. 2010). Low pH-values and acidic soil conditions can occur over

metamorphic rocks but also over flysch, volcanic rocks and sediments. But also high precipitation as in mountain can cause acidification of substrates through leaching effects. Therewith pH-values can be low in else well-buffered surroundings. Along with aged soils in woodlands low pH-values could develop as well (Wilson et al. 1997). Reversely high pH-values and high phosphorous content can occur over generally poor bedrock when dust immissions apply (Macleod 1980; Suchodoletz et al. 2013; Yaalon 1997). Wide spread species with an affinity to such substrate conditions may thus also occur over else unsuitable bedrocks, especially when dust accumulates in hollows. The diverse Mediterranean study area features a pronounced heterogeneity of soil formation in relation to bedrock, climate and topography. This complexity could reduce the applicability of coarse and simplified geological units as proxies for substrate conditions. Beside quality of base data and coarse mapping units an overfitting to certain bedrocks may hamper extrapolation in models.

The role of shifting ecological behaviour of species in models

For the studied species a flexible selection of variables was applied within the MaxEnt algorithm, but rarely the same variables were selected as important for the independent training regions. The variables selected should describe the range of ecological conditions covered by the training data. When these variables vary between regions, the site conditions applying for the set of training records are different. Strong driving variables feature the occurrence of specialists' species, e.g. high *t_mean* and low *ann_prec* in the case of the two coastal junipers led to best extrapolations for both regions. For generalists diffuse patterns for environmental variables apply, this makes the algorithm to select several suitable variables for the models; for the training region this helps to fit the ecological range of values, as prediction maps display; but for deviating ecological conditions in the test region, this kind of overfitting disables extrapolations. Thus MaxEnt-models may capture the range of environmental conditions for the training region. But these models are only suitable for extrapolation, when strong driving variables describing site conditions apply for the training and the test region.

Geological units applied in models reduced their extrapolation performance across all species tested. Available and occupied bedrocks are different for both islands, which involves overfitting effects and disables extrapolation. Differences are pronounced for *Q. coccifera*, *P. latifolia* or *E. dendroides*, which also led to low AUC-values in models for both training regions. The vague affinity to bedrocks is indicated by percentages of featured bedrocks but also by their role in models represented by jackknife tests. For specialist species such as *A. unedo* and *E. arborea* a strong edaphic affinity applies only for the fitting of training points from the Cretan region. The records on Sicily are better represented by annual precipitation sums. The species distribution models for *A. unedo* is a special case, because it is frequent on metamorphic rocks on Crete, where sufficient

water is available. Various locations in the Sicilian mountains are not covered in the distribution model. There the species benefits from high precipitation on mountain tops or good water availability for an affinity to local edaphic conditions. Other studies describe the species for having oceanic preferences. The species is wide-spread in the west Mediterranean and also along the Atlantic coast from Morocco to Ireland, where it thrives on sandstone and limestone bedrock with good water supply (Mesléard and Lepart 1991; Sealy 1949). Volcanic rocks and gypsum are virtually exclusive for Sicily. This hampers extrapolations of some species, for which these bedrocks play a role in models according to jackknife tests.

There can be manifold reasons for the occurrence of distinct ecological site spectra for the tested plant species in the two regions. Phenotypic plasticity of species may be important as well as adaptation to particular site conditions connected to shifts on genetic level. According to their phenotype plant species can adapt to various site conditions without prior genetic changes. This can be explained in many cases by epigenetic processes (Chen 2007; Herrera and Bazaga 2009; Zhang et al. 2013). On the other hand genetic differentiation on intraspecific level is not unlikely and often related to the latter phenomenon (Zhang et al. 2013). For the Mediterranean islands studied the occurrences of many endemic species can be correlated with evolutionary processes (Beierkuhnlein 2007; Steinbauer et al. 2013). For the Cretan study area post-isolation range expansion caused by mountain uplift was successfully tested by Trigas et al. (2013). Therewith the authors indirectly link the potential for ecological and genetic differentiation to the mountain uplift in the region. A reason for limited performance in extrapolations may thus be individual genetic patterns of Mediterranean tree populations, which were revealed by several studies (Fineschi et al. 2004; Fuentes-Utrilla et al. 2014b; Papageorgiou et al. 2014; Petit et al. 2003). According to Christe et al. (2014) haplotypes of *Z. abelicea* differ along isolated mountains within Crete. Because elaborated technical procedures are needed to test phenotypical and genetic patterns, for many species the level of intraspecific differentiation is yet unknown (Zhang et al. 2013).

The mentioned uplift process for Crete may also feature ecological differences for the maquis species in our study: species like *Q. coccifera*, *P. latifolia* and *P. terebinthus* show higher altitudinal ranges on Crete compared to Sicily (indicated here by temperature variability). The mass uplift of Etna is related to specific site conditions and may be unsuitable for some species, exceptions are e.g. *Q. ilex*, *P. terebinthus*. The niche of species may also shift along with an exposure of species to new environmental conditions as Broennimann *et al.* (2007) proved for an invasive species on continental scale. Several studies suggest that changes in altitudinal ranges, occupied bedrocks and a combination of ecological site conditions result in speciation, especially when isolation is involved (Ali and Aitchison 2014; Gillespie and Roderick 2014; Kruckeberg 2002; Steinbauer et al. 2013; Steinbauer et al. 2016; Steinbauer 2017). Similarly, for the studied species we foremost expect an

effect of isolation and individual island conditions on epigenetic and intraspecific genetic differentiation which could disable extrapolation performance.

In conjunction to our study testing ecological generalists and specialists, also range size is considered to be limiting for the accuracy of species distribution modelling, in such a way that wide spread species having a broad ecological amplitude may tend to be more difficult to model, compared to species with a small range and narrow niche (Hernandez et al. 2006; McPherson and Jetz 2007; Stockwell and Peterson 2002). The latter authors propose to enhance performance of species distribution models, by specific geographical resampling of records to obtain more differentiated models for regions. This could also help to extrapolate models within the study setting, e.g. by excluding unsuitable records from isolated sub-populations. Another procedure to improve extrapolation results involves the restriction of the model area, to train the model only on the cells having a common climatic range on both islands, as applied in other studies (Heinrichs et al. 2016; Horsák et al. 2010). We found no significant improvement in the model's predictions, due to data abatement and to loss in the ecological response curves of the training data and therewith support the findings of other studies (Thuiller et al. 2004). Another shortfall in such procedure comes from the limitations of using AUC-values for evaluating the model outputs, because these values are related to all grid cells in the data frame. When the area differs AUC-values should not be compared (Lobo et al. 2008).

Conclusions

The use of species distribution models for reciprocal extrapolation to neighbouring islands allowed for the indirect comparison of species niches across regions. The inclusion of bedrocks in models hampered their performance in comparison to models with climatic and topographic variables only. Especially wide-spread generalists performed weakly. The models for edaphic specialists performed better for each of the islands; but rather for their relation to specific climatic and topographic conditions than their relation to bedrock types. One reason for the general failure in extrapolation is that the geological units are heterogeneous representations of surface conditions. Such conditions could be better covered by soil types. Secondly we suspect interplay of different availability of bedrock types and a broad edaphic niche for species, which is not fully covered by records in the training region. Such niche differences could be explained by phenotype (epigenetic regulation) or genetic variation.

Chapter 6: Synthesis

Analyses opportunities addressed

The last four chapters each presented a case study of data analyses either based on species occurrences or compositional data. In the following section these studies are discussed in a wider context. The first of these sections discusses the several analysis aspects of the performed studies, the subsequent ones addresses their limitations, further analysis ideas and future perspectives.

Approaching plant species ecology

Species' ecological patterns are displayed in manifold ways in this thesis: while in chapter 3 ecology is indirectly assessed through vegetation units, the studies in chapters 4 and 5 comprised information about distinct differences between metapopulations. The overview in chapter 2 visualizes patterns of environmental affinities for the majority of Cretan phanerophytes. For the latter, ecological trends are generally applicable for the whole Mediterranean area. That means regional results reflect patterns on wider scales; e.g. the Mediterranean tertiary relicts *Styrax officinalis* and *Laurus nobilis* (Mai 1987; Schmid 1970) occur in Crete and elsewhere in relatively humid ravines and on lower slopes (Di Pietro and Germani 2007). The chapters 2 and 5 deal with the ecology of wide spread woody maquis species. For example the coastal junipers (*Juniperus macrocarpa* syn. *J. oxycedrus* subsp. *macrocarpa*, *J. turbinata* syn. *Juniperus phoenicea* subsp. *turbinata*) are stress tolerators, well-adapted to low precipitation and co-occur along coasts around the Mediterranean (Baquedano and Castillo 2007; Meddour et al. 2017; Muñoz-Reinoso 2004; Paradis et al. 2014; Pedrotti 2013; Rubio-Casal et al. 2010); *Erica arborea* reaches East African mountain heathlands (Knapp 1973; White 1981); and *Platanus orientalis* occurs eastwards until the Himalaya (Rosati et al. 2015). Therewith the observed ecological patterns for wide spread species may be relevant for practitioners and scientists. On the other hand ecological affinities of some portrayed species differ markedly in Crete compared to other areas, e.g. *Quercus ithaburensis* subsp. *macrolepis* from the small and somewhat isolated local (meta)population has a narrow ecological spectrum compared to the centres of occurrence (Dufour-Dror and Ertas 2004; Pantera et al. 2008). Also other studies shared the observation that marginal metapopulations compared to those with a wider range are limited in niche breadth. Quézel (1979a) portrayed the ecological niches of 54 woody taxa for the Mediterranean region and he frames the narrower ecological amplitude of the French compared to the circum-mediterranean occurrences. The latter study allows for comparison with results in chapter 2 and 5 as it displays a similar set of environmental variables. Ecological niches may differ along with (gradual) changes in site conditions within the wider distribution area; and between isolated populations. Intraspecific differences will be addressed later in this chapter.

Species ecology can be inferred indirectly from vegetation, as done in chapter 3, but also from species distribution patterns and ranges (Cox and Moore 2010; Frey and Lösch 2010). The focus of

chapter 2, 4 and 5 was on landscape-related ecological patterns, whereas site conditions were displayed and compared; species' co-occurrences were displayed. Especially altitudinal patterns may generally mirror ecological affinities on wider scales. For the patterns on Crete though caution applies as probably mass elevation of the Cretan mountains caused an upward shift (see Chapter 5 for details). For many species a shifted ecological range to higher elevations could be observed in comparison to other regions (Steinbauer et al. 2017; Trigas et al. 2013). Niches for some of the mountain species may thus apply rather locally; further studies are needed to quantify altitudinal shifts.

Ecological filtering processes are frequently mentioned as drivers for species patterns in landscapes and in plant community context; thereafter ecological factors hamper the establishments of species and shape their distribution (Catry et al. 2006; Cingolani et al. 2007; Kraft et al. 2015; Steinbauer et al. 2017). Such processes may as well underlie the patterns described the presented studies. Ecological adaptation to extreme conditions, i.e. coastal habitats exposed to salt, drought and high solar radiation are inhabited by few specialised species only. Merely two junipers are included in the group of coastal species (*Tamarix ssp.* could thrive there as well but the genus was disregarded for its unclear taxonomy and deficient data; Villar et al. 2014). Filtering processes could be particularly important in such extreme sites; they would prevent most other seedlings of woody species from establishment. Many planted trees, when watered, may grow in such coastal spots as well, but die off if their roots do not reach ground water and human assistance is stopped. Whenever planting in such coastal spots is necessary, e.g. for wind protection, the use of local taxa with good adaptations should be preferred. Few woody species grow well in high altitudes, some being specialised to specific slope expositions. Especially for sites with extreme conditions, the results of chapter 2 may support practitioners in their choice of appropriate species for ecological restoration.

Plant-environment relations can also feature the assignment of ecological indicator values. Indicator values imply site attributes i.e. soil reaction, affinity to macroclimate and to wetness (Böhling et al. 2002; Ellenberg 1974), but they usually do not feature (micro) topography. Many studies describe the affinity of species (groups) to particular topography (Fois et al. 2017; Hedderson and Blockeel 2013; Schnittler et al. 2010), while an assignment of numerical topographic indices to species was not done. Chapter 2 revealed a strong affinity to extreme topography for some species. Topographic features may thus serve as a basis for specific ecological indicator values. For example the used compound topographic index provides a theoretical quantification of available surface waters and may be used for testing of existing indicator values for moisture or for the assignment of new ecological indicators accounting for topography.

Affinities to rock types are discussed in chapters 2 and 5. According to the study in chapter 2 a group of downy oak and hawthorn appeared frequently on ophiolites on Crete. For some plants a strong affinity to such specific bedrocks was found in our study e.g. to gypsum or ophiolites; which confirms study results from other regions (Kruckeberg 2002; Stevanovic et al. 2003). Among the woody species studied in chapter 2 and 5, none is exclusively constrained to one of these two bedrock types. For gypsum this confirms unpublished results for Sicily (personal communication Riccardo Guarino). Few woody species are good indicators for ophiolites (serpentine) in the wider area, exceptions are *Quercus trojana* subsp. *euboica* and *Genista* spp. (Horvat et al. 1974; Stevanovic et al. 2003). In serpentine areas in the Rhodope mountains other oak species (*Q. pubescens*, *Q. frainetto*, *Q. cerris*) may thrive on serpentine rocks (Pavlova et al. 1998). For the Western Balkan *Pinus sylvestris*, *P. nigra*, *Quercus robur*, *Ostrya carpinifolia*, *Forsythia europaea*, *Syringa officinalis* and several oaks are described on this rock type (Horvat et al. 1974). Interestingly, the affinity of oaks to serpentine/ophiolite, is a phenomenon which applies across continents (Abbate et al. 1993; Ernst 1974; Harrison 1999; Roberts and Proctor 1992; Tyndall 2005). Because soils over serpentines contain heavy metals, a basic tolerance and phylogenetic conservatism can be assumed for the genus. GIS-based assignments of geological substrates, soil types, topographic features, etc. is generally promising for applications on various scales and for datasets of species records (e.g. Paulo et al. 2015; San-Miguel-Ayanz et al. 2016). For the species in chapter 5 a strong affinity to specific bedrocks (edaphic specialists), allows for a better extrapolation. Species covering a wide spectrum of bedrock types, have a broad ecological niche, which reduces the potential of extrapolation when geology does not match in training and test areas. Additionally intraspecific variation could apply, which is discussed in the next paragraphs.

Intraspecific ecological variation

Intraspecific variation is addressed in various studies dealing with plants and plant communities, thereby it may be challenging to distinguish between variation of phenotype or genotype (Herrera and Bazaga 2010; Violle et al. 2012). A good experimental setting is helpful to compare such variation. Thus in chapter 4 we use the isolation of the Cretan mountains, forming a Creto-montane archipelago (parallel to Afro-montane archipelago, see White 1981); for which a separation on floristic level (Greuter 1971; Rikli and Rübel 1923) and on haplo-type level applies for the studied species (Christe et al. 2014). Already Greuter (1972) highlighted the islands' evolutionary significance, because of endemics and wide-spread species being genetically (and ecologically) distinct in the isolated Cretan mountains. In the frame of the study we applied the term *(meta)population* in a sense, that spatially structured and isolated occurrences of taxa are addressed; even though further definitions exist, e.g. related to animal populations and fragmentation (Hanski and Gilpin 2008).

In the Cretan mountains *Zelkova abelicea* differs in its haplotypes in the main mountains (Christe et al. 2014), which stimulated the study in chapter 4. Similar patterns were studied for the endemic *Jurinea pinnata* in the Baetic ranges on the Iberian peninsula by Salmerón-Sánchez et al. (2014), who proposed that geographic isolation in mountain ranges is important for intraspecific genetic structuring. Whereas on a wider scale for the whole Baetic-Rifan complex climate and lithology, were most influential for the distribution of endemic species diversity, and merely climatic variables for the patterns of non-endemic species (Molina-Venegas et al. 2013). Even though various studies describe a high genetic diversity for many Mediterranean woody species (Petit et al. 2003), the high genetic variation of *Zelkova abelicea* is surprising on this small scale. But therewith the study of Criste et al. (2014) confirms results of Papageorgiou et al. (2014), who used dense haplotype sampling for *Fagus sylvatica* in a Greek refugial region, and who related it to fine-scale ecological and topographic isolation barriers. The authors explain the patterns merely by migrations from distinct founder populations and isolation by topography and dispersal barriers (Papageorgiou et al. 2014). Suchlike could suit as well for *Z. abelicea*, as our study in chapter 4 revealed ecological dissimilar sites for the metapopulations. Even though the study of Christe et al. (2014) presented differences in terms of haplotypes for the Cretan mountains, their sampling covered only a selection of sites. Tendencies in spatial separation of haplotypes in the mountain ranges are visible, but denser sampling is needed for sound interpretation.

Spatial patterns of *Zelkova* haplotypes (chapter 4) could also support the concept of Steinbauer et al. (2013; 2016), who claimed altitudinal isolation to be a key factor for diversification and propose topographic features as potential driver. Additionally for each of the Cretan mountains individual abiotic conditions apply (at least in terms of occupied sites for *Zelkova*); thereby the isolated metapopulations face individually differentiated site conditions along natural gradients. Other authors displayed the distribution of endemics in the isolated mountains (Greuter 1971; Jahn and Schönfelder 1995), which can be explained by isolation, ancient migrations along the South Aegean island arc and the ecological gradient. Ecological differences of single mountains could support ecological radiation processes, applying on several scales (Rainey and Travisano 1998; Sudhaus 2004), and could also explain diversification of metapopulations on haplo-type level. A pronounced isolation for *Zelkova* can be explained by dispersal limitations related to low fertility of the seeds; and – even if the fruits are winged – they are not travelling far (Egli 1997; Kozłowski et al. 2014). If dispersal barriers and low fertility are old phenomena, a reduced genetic exchange can be assumed and thus long-term separation of metapopulations. The fact, that isolation of the Cretan mountains happened “recently” in geological and evolutionary terms, and a repeated connection of the isolated peaks during glacial-interglacial cycles, could support the assumption that merely intraspecific genetic differentiation was introduced. Maybe genetic differentiation could also result in distinct

sub-species for some taxa (e.g. Greuter and Grau 1980). The speed of genetic differentiation may vary for taxa (Petit et al. 2005). Population dynamics over time include isolation and reunion, which can be assessed (e.g. for a Chilean Mediterranean tree species by Pérez et al. 2017). Such estimations of times of species isolations are extremely helpful for the reconstruction of biogeographic processes and could be valuable in the Mediterranean study region. Various studies tested haplotypes across populations, sometimes also with a relation to ecological patterns (Hampe et al. 2003; Petit et al. 2003; Petit et al. 2005; Thompson 1999). Approaches in terms of landscape genetics could apply for the studied species and their metapopulations in various regions (Balkenhol et al. 2009) and they could therewith address the genetic component of spatial patterns in a more precise way; additionally eco-physiological measurements, tree ring analysis and the application of functional genetics should be helpful.

In chapter 5 ecological differences between two islands Sicily and Crete were studied for maquis species and the consequences for the regional extrapolation of species distribution models were discussed. Good extrapolation results for specialised species underlined ecological similarities in occupied site conditions for those species on both islands. Distribution of generalists was more difficult to extrapolate for their dissimilar ecological niches. They may occupy different habitats in isolated regions with e.g. divergent climatic and edaphic conditions. This could be explained with a broad phenotypical flexibility of wide-spread species or differentiation on genetic level.

Intraspecific ecological differentiation should be considered for future plant ecological and vegetation ecological studies, especially for isolated metapopulations in the Mediterranean. Genetic diversity is high among ancient Mediterranean species occurrences, especially in comparison to areas occupied in the post-glacial period, as various examples expressed (Petit et al. 2005); in this context several studies revealed genetic diversity in metapopulations of wild species (e.g. Bucci et al. 1997; Ducci et al. 1999; Fuentes-Utrilla et al. 2014b; Fuentes-Utrilla et al. 2014a; Thompson 1999); and among fruit trees and vines (Gristina et al. 2017; Khadari et al. 2005; Zohary and Hopf 2012). The described variation of occupied site conditions, having a genetic basis or not, can hamper results of species distribution models. When ecological differentiation applies, extrapolated predictions of species occurrences should be consulted with caution (chapters 4, 5). The high intraspecific genetic diversity in the Mediterranean is often disregarded but should be considered more frequently in e.g. conservation, restoration, planning and management of protected sites, plant breeding or pest control.

Ecological species groups, vegetation and landscapes

The description and classifications of the land surface has a long tradition in geosciences. Approaches may vary depending on applications, political borders, scale levels, and also used base data can be

quite different: Abiotic attributes apply as data basis on the global scale (Weigelt 2014) and on country or regional scale (Bunce et al. 1996; Drachenfels 2010). The separation to biogeographic units (realms, regions, etc.) on the basis of species distribution is another basic concept (e.g. Kreft and Jetz 2010, Frey and Lösch 2010). In conjunction to such patterns based on species turn-over, floristic dissimilarity and environmental gradients were assessed (König et al. 2017; Rueda et al. 2010). Distributions of species or habitats may also reveal landscape-ecological units and differences across spatial scales (Bölöni et al. 2011; Korsch 1999; Schmiedel 2014; Wasowicz et al. 2014). In chapter 2 the distribution maps of ecologically similar species revealed patterns on a landscape scale (Figure A 2.1). The identified ecological species groups share similar site conditions; species forming these groups reflect patches of contrasting conditions on this regional scale. These patterns do not represent landscape units ready for application, but they allow for an ecological interpretation. The use of high-resolution species distribution data with reasonable density may thus be a good basis for a rather objective ecological landscape classification. On this spatial scale data gaps and sampling bias influence results more than in large-scale analyses. In addition, land use effects are probably more pronounced on finer scales and have to be considered. Korsch (1999) performed a similar analysis but he generated species groups based on ecological indicator values, hemerobic index and similar chorology. This way, just like in chapter 2, the ecological affinity of species to strong ecological drivers found expression in wider landscape patterns. Generally, the approach using clusters of ecologically similar species could serve as a method to classify land surface on various scales.

Zonation patterns of plant species along (climatic) gradients can be explained by ecophysiology and adaptative traits (Körner 1998, 2012; Larcher 2006; Way and Oren 2010). Such traits apply for tree species in relation to e.g. climate change adaptations (Bugmann 1996), ecological strategies such as competitiveness (Swaine and Whitmore 1988) or community ecology and functional assemblies (Cingolani et al. 2007; Kraft et al. 2008; McGill et al. 2006). Even though results of chapter 2 do not allow for a direct interpretation of functional groups, we can assume that functional similarity applies for several species within the proposed ecological species groups, as this is one fundamental basis for the occupation of similar ecological niches. Functional similarity can as well explain shared habitats and species abundance, which can be explained by various studies across ecosystems (e.g. Cornwell and Ackerly 2010, Mahdavi & Bergmeier 2016, Maire et al. 2012). The latter studies approached species groups chiefly by species traits; in contrast the study in chapter 2 integrates site attributes and species' similarity in complex ecological spectra including climate, geomorphology and geology. The initial selection of these variables and the classification of ecological spectra resulted in a restriction to important ecological drivers. The proposed classification was based on a composite of site attributes and not on direct measures of species or species composition from plot data. Anyway, trends in ecological similarity got obvious, which confirmed field experience and habitat schemes.

Woody species were chosen in all presented studies for being frequent elements of climax vegetation. A high species diversity of woody species is an indicator for a high diversity of other organism groups across trophic levels (Barrico et al. 2018; Kati et al. 2004). This implies that the co-occurrence of multiple woody species within a spatial unit (e.g. landscape patch, grid cell, district) is an indicator for biological diversity. Thus for the study in chapter 2 the spatial pattern of ecological groups feature biodiversity patterns. In relation to this it has to be considered, that species groups restricted to extreme environmental conditions are rare in landscapes and thus host fewer but specialised species. In addition, co-occurrence of these groups could serve as an indicator for niche diversity and for biodiversity.

The co-occurrence of plant species is the basis for the description of vegetation units, the latter may thus serve as proxies for a combination of site conditions. Therewith vegetation units are ecologically related to the ecology of comprised species. This relation was displayed by the comparison of ecologically similar groups and units from vegetation and habitat schemes in chapter 2. Moreover, in this context the classification of species composition data from vegetation plots is a common strategy helping to understand ecology and to assess typical species. Chapter 3 covers a numerical classification of *Platanus orientalis* woodlands, revealing two new plant associations and confirming a third one. All three vegetation units have a specific floristic composition and particular ecological properties. This showed the potential to describe vegetation units even in else well-studied Europe. Recently, also the European vegetation classification (Mucina et al. 2016), gave new insights for syntaxa (alliances, orders and classes). Therewith a unified system was established on continental scale. The proposed associations in chapter 3 have relevance for the local differentiation of the alluvial forests and extend this new system as subordinate units within the alliance Platanion.

This alliance is wide-spread and species composition of the Cretan woodlands is similar to other parts of the distribution area, including those with the Tertiary relict *Liquidambar orientalis* (Dimopoulos and Bergmeier 2008; Öztürk et al. 2008; Pedrotti and Gafta 1996); while the northernmost occurrences of this vegetation types comprise more elements of temperate riparian forests (Horvat et al. 1974). A syntaxonomical overview for alluvial forests and alder carrs is given by Douda et al. (2016). This important study for Europe includes the Platanion, whereas two associations from older studies, Petasito-Platanetum and Nerio-Platanetum, were verified; their relation to the proposed types in chapter 3 should be discussed to avoid synonymies as both apply for Crete according to the published maps. Similar to the latter study various reclassifications and re-evaluations of formerly described syntaxa were performed for Europe in the last years, and more are expected (Chytrý et al. 2016; Willner et al. 2018). For the Platanion a wider overview is necessary but should not be limited to the European part of the distribution area of *Platanus orientalis*. Such a study would help to

understand the distribution of associations and vegetation ecology of this frequently threatened vegetation type.

Limitations

Environmental data and their bias

For the understanding of species and vegetation ecology a multitude of environmental variables applies. The presented studies (chapters 2, 4, 5) comprised a selection of available variables from measurements, remote sensing and interpolation. Main driving factors were selected, others were neglected and further environmental aspects remain unrecorded. They may all influence species niches, the quality of extrapolation and analysis options. The reduction of variables to few important ones though can have various reasons. In case of the species-environment heatmap in chapter 2 the set of variables was reduced to a set of few, allowing for a better interpretation of the clustered matrix presented. Redundant information in the matrix was further decreased by merging some categorical variables to similar pairs based on similarity in a classification. A simplified set of environmental conditions was displayed in the heatmap and in a similar way in multivariate plots. The both plots are simplified also in terms of data distributions, e.g. unlike reaction curves which comprise the range of values. Simplification of the heatmap manifests as well in the use of few colours to display ecological affinities. Additional information of SD for each data cell in the heatmap would be an improvement. The grouping of species in the heatmap may suggest strict separation of species in the groups, in reality species occurrences are overlapping. Especially species with wide ecological amplitude may co-occur with species from various clusters, e.g. *Pistacia lentiscus*, a common maquis element, frequently co-occurs with many other lowland species like palms, pines and junipers. The ecological classification in chapter 2 results in a simplification of the complexity of vegetation patterns and groups do not fully match with real world plant communities.

Complex patterns of environmental conditions are indirectly assessed through the classification of vegetation plot data in the study in chapter 3. The use of compositional data has the advantage that the broad spectrum of ecological conditions, covered by the sum of relevées, can be characterised by repeated occurrences of characteristic species. Distinct vegetation units comprise complex environmental conditions, which are not directly assessed by measurements but explained by species ecology and (few) observed or measured site conditions. Thus, this kind of vegetation unit comprises a multitude of information shaping their species composition, including measureable and hardly measurable variables (e.g. land use, extreme events in the past, etc.). Location-based data extractions using GIS for vegetation plots could help to integrate spatially explicit information and therewith substantiate plant-sociological classifications. Such quantifications of site conditions could

improve ecological differentiation of vegetation units; e.g. for the study in chapter 3 mean CTI-values for the three associations could probably support ecological separation, such index values are impossible to assess from header data of the relevées.

The complexity of climate is partly underestimated in presented ecological surveys. For the studies (chapters 2, 4, 5) few climate variables were favoured instead of many collinear ones. The choice of mean temperatures and precipitation sums can be critical as their extreme values are not regarded (Blasi 1998). Partly this was compensated by the study by bioclimatic variables (Hijmans et al. 2005; Karger et al. 2016). Other approaches successfully integrated effects of climatic variation in models (Boulard et al. 2017). Climatic gradients are steep especially in the mountainous Mediterranean study areas and thus global climate datasets can underestimate topographic, regional and local effects (Nadeau et al. 2017). Interpolation of macroclimatic data relies on a small number of stations in the Cretan study area, which further complicates modelling. Instead of downscaled data from global climate models, ecological studies could also use values from climatic indices or bioclimatic stratification, which may better integrate the climatic complexity (Blasi 1998; Soteriades et al. 2017). Generally the use of climate variables outperformed the use of geology, which was discussed in detail in chapter 5.

Datasets created to serve large scale studies, turned out to be useless for ecological assessments in the presented studies. So the high resolution of 500 m for the European LUCAS survey datasets on soil properties (Ballabio et al. 2016) was promising for the performed fine scale studies, but delivered nonsense results for the Cretan study area e.g. high sand content for the topsoil layer in the mountains. The soil attributes assessed by the LUCAS dataset may apply for coarse grained analyses and in other regions, but the failure for Crete shows that an extrapolation from few data points to wider scales is not applicable in every context. Such publicly available datasets need to be tested for study areas. Similarly, derivatives of the DEM can be affected by intrinsic satellite scanning and algorithm bias (Ouédraogo et al. 2014). In pre-processing a sink-fill procedure is used to delete artificial zero values from the DEM; for modeling mean values for each grid cell were used which compensates for single false measurements.

Coordinates and identity of taxa

A major problem for location-based methodologies is imprecision of coordinates. Merging records from different sources and authors needs careful handling in terms of coordinate systems and projections in the GIS. As Budic et al. (2016) displayed, the quality of species distribution models decreases, when projections of raster data are incorrect and do not match coordinates of species records. In all four presented studies (chapter 2, 3, 4, 5) various datasets were handled and

transformed into uniform geographic projections to reduce projection bias. Further reasons for imprecision is temporal disturbance of the GPS signals, which applied for signal jamming in the 1990th during the Balkan wars; this could have corrupted locations of species records for the period. Also weak satellite connection under canopies, in gorges and due to overcast sky can bias coordinates of recorded species and plots. For the Cretan study region coordinates were corrected by strict selection and crosschecks to aerial imagery. Nevertheless, some records may have been attributed to improper sites. This was partly compensated by large numbers of record. However, it is recommended to interpret trends and not single attributions.

Identification skills may also bias results of collections and surveys (Ahrends et al. 2011), which was compensated in the studies by data from experts with local field-experience. Additionally the selection of well-known woody species reduced taxonomic problems: unclear taxa were excluded e.g. *Tamarix spp.*, or treated on species level e.g. *Ulmus minor ssp. canescens* as *U. minor*. Nevertheless, ecological (and genetic) differences could apply affecting ecological assessments and models (which is discussed in this chapter). Another form of data bias may be generated, when sites are repeatedly visited by surveys, e.g. to visit rare species, thus in the presented studies (chapter 2, 4 and 5) sampling strategies were applied (Ahrends et al. 2011; Dormann et al. 2007). Anyway, data gaps appeared as well as areas with denser sampling, which partly reflect the patchy distribution of woodlands in the study areas. Patchiness can be problematic for the quality of species distribution models and the assessment of ecological niches. Environmental conditions in patches with woody plants can be very different in comparison to neighbouring sites, but in models a homogenous extrapolation applies, when such differences are not captured in spatial data in the GIS (Bakkestuen et al. 2009; McInerny and Purves 2011).

Data selection and algorithms

In analysis attempts using models and large species datasets and composition data bases, a main issue applies as over-complex and over-simplified models may be limiting (Merow et al. 2014). The used MaxEnt algorithm (chapter 4, 5) is sensitive to over-complex data input, as thereby interactions and collinearity may disqualify results (Dormann et al. 2013; Syfert et al. 2013; Wisz et al. 2013). It is a limitation of this model type, that (few) independent driving parameters are included, although species and ecological conditions interact for sites in complex way. Results in chapter 4 and 5 also showed that the choice of spatially isolated (meta)populations affects predictions of species distribution models. This is another weak point in models, which often assume homogenous genetic structure and evenly distributed ecological behaviour for organisms. Such fundamental phylogeographical problems were addressed in reviews (e.g. Avise 2009, Weiss and Ferrand 2010).

Other studies conclude, that sample size has a strong influence on models (Wisz et al. 2008). In chapter 4 ecological affinities of metapopulations were assessed for isolated mountain ranges, whereas few records were available for some of them. The MaxEnt algorithm would not deliver comparable modeling results, when too small numbers of records were used. Thus, these few records were added to neighbouring populations, which extended the modeled ecological space of larger metapopulations by smaller (marginal) ones and thus introduces higher heterogeneity. This way, these small populations could not be directly modeled and the quality of overall results is limited. Alternative modelling algorithms could have been used, maybe in combination with repeated random sampling from the bigger populations to allow for even sample numbers. Such a balanced sampling might allow for a more robust analysis of the ecology and potential distribution of small and isolated (meta)populations.

The case studies contained selection procedures for environmental data, which had the aim to set objective criteria for ecological assessments and help for the extrapolation of models. The initial choice though influences the selection, e.g. alternative datasets for climate data are available. Similarly, MaxEnt was the only algorithm tested for modeling, even though a variety of improved algorithms exist. An advantage of MaxEnt is the integration of presence-only records, as well as numerical and categorical data. A promising alternative procedure is the use of multiple modeling algorithms and their combined evaluation, e.g. for small datasets (Breiner et al. 2015; 2018). Besides the choice of the algorithm, the quality and the resolution of data are important for modeling studies (Gotelli et al. 2009; Guisan et al. 2007; Hurlbert and Jetz 2007; Seo et al. 2009), the availability of raster data not least defines the used grid cell size. For Models in MaxEnt a uniform grid cell size must be applied, which was about 1 km for the study in chapter 4, attributable to the original climatic data resolution. Models with a grid size of about 400 m were performed in chapter 4, which was a compromise accounting for the original climatic data resolution and for the fine-scaled DEM of about 30 m resolution. For the mesic species studied, which depend on exposition, finer resolution than 1 km seemed reasonable. Even if the highest resolution was not integrated in the models, it was used to describe site conditions in boxplots. Smaller grid cell sizes are recommended for future studies. The working scale and the size of grid cells may influence the selection of environmental variables in models for species richness and species distributions (Marcantonio et al. 2017; Thuiller et al. 2003). Further theoretical implications on environmental variables acting across landscape scale are addressed by Wu et al. (2000).

Further perspectives

Availability and joint analysis of ecological data

Location-based approaches depend on quality and quantity of species data and environmental data; their amount is constantly growing, and large datasets come from new sources, such as collaborative networks, social media and ecological initiatives. The integration of public data from amateurs bears risks in terms of data quality, but at the same time offers a great potential; e.g. decentralised processing and online crosschecks through experts. Also mobile devices further develop and allow for affordable and easy-to-use applications (Schrader et al. 2017; Teacher et al. 2013). Such technical advances and the interaction of scientists and amateurs may fundamentally change peoples' perception of scientific work and the way data is assessed and handled (Byrne and Pickard 2016; Graham and Zook 2011). Technical developments allow for a new quality of raw data and data products; e.g. by using LIDAR (light detection and ranging) for the assessment of (micro)relief, vegetation structure, etc. (Höfle and Rutzinger 2011; Omasa et al. 2008; Shan and Toth 2009; Suárez et al. 2005). Lift-off perspectives for the assessments of organism record and environmental data come from semi-automated devices like data trackers and drones (Carrivick et al. 2013; Lonneville et al. 2014). Multitudes of available biological and environmental datasets share the fact, that they can be spatially linked on fine scales. This can boost ecological exploration and stimulates new ecological questions; some options are discussed in the following paragraphs.

Metapopulations and community ecology

In the case of *Zelkova abelicea*, ecological site conditions differ between (meta)populations (chapter 4). Isolation of *Zelkova* could be further tested using other trials of genetic and functional genetic analyses. Also in chapter 5 a differentiated ecology of generalist species on the tested islands was assumed. Further genetic analyses may reveal distinct (meta)population structures. Similarly, ecological and genetic differentiations were already investigated for wide-spread European tree species (Köckemann et al. 2009; Papageorgiou et al. 2014; Rose et al. 2009). Details on genetic structure and age estimation for specific mutations, in combination with strong isolation barriers, may reveal insights to ongoing evolutionary processes and likewise to the history of isolation. The impact of marine barriers (Crete, Sicily, other islands, mainland regions, etc.) and orographic isolation on ecology and genetics can be tested. Such isolation effects could be checked also in terms of trait variation of endemics and related non-endemic species, as Hand et al. (2017) did in Mediterranean context. Related to this, measures for endemism rates using phylogeny (e.g. phylogenetic endemism; Rosauer et al. 2009) could highlight centres of endemism, speciation and old refugial areas, but need advances and wider application of genetic sampling and analysis. The assessment of spatial genetic patterns for Mediterranean species is still deficient and further comparative studies are needed. The

conservation of taxa based on proveniences is a major element of *ex-situ* conservation (e.g. handling in germplasm) but for a long time many *in-situ* nature conservation schemes ignored aspects of genetic differentiation; this situation is changing stepwise (Heywood 2014). Both *in-situ* and *ex-situ* conservation can benefit from in-depth analyses of site features (chapters 2, 4, 5), as ecological patterns for taxa reveal insights into regional or landscape-based differentiation. Such genetic and ecological differentiations should be widely considered in terms of global biodiversity protection goals (CBD 2012).

GIS-based approaches could be used to define, modify and substantiate ecological indicator values of species or their local proveniences. An European initiative currently tests and extends ecological indicator values for wider scales (Dengler et al. 2016). Based on universal environmental parameters also new ecological indicator values can be featured, which hitherto eluded from expert assessment for technical reasons. In chapter 2 the affinity of woody plant species to site conditions was assessed in a simple approach using a classification of a matrix of species and environment data. The patterns displayed were related to vegetation units. The approach could be used on wider scales and with various taxa and even (plant) communities; but due to its simplification it is no alternative to modeling approaches, which use advanced algorithms and may integrate interactions between organisms.

Biotic interactions, soils and further ecological factors

Interactions between taxa may appear aboveground and belowground and comprise e.g. competition and facilitation (Cuesta et al. 2010; Das Gupta et al. 2015; Kardol and Wardle 2010; Violle et al. 2010). Interactions are often disregarded in modelling attempts for species; not least because some wide spread algorithms merely use presence-only or presence-absence data. For the analysis of species interactions, more complex modelling approaches and the use of compositional datasets are advantageous (Ashcroft et al. 2017; Gomes et al. 2018). Co-occurring species could compete for resources and thus models could be corrected accordingly (Araújo and Guisan 2006; Cabral and Kreft 2012; Cabral and Schurr 2010; Wisz et al. 2013). High-resolution species records could help to give rough estimates, but there with only virtual co-occurrence and interaction can be assessed and not tested properly (see chapter 2). Positive and negative biotic interactions have impact on the global scale (Wisz et al. 2013). For the Cretan study area Bosque et al. (2014) observed facilitation for woody mountain species. The latter examples underline that the relation between organisms can be rather complicated and simple models may only explain parts of the ecological space.

Also soil related studies consider biotic interactions; e.g. Teste et al. (2017) showed that differences in mycorrhisation and the origin of soils influence plant growth and also drive diversity in species-

rich Mediterranean woodlands. Various species responses may depend on factors related to soil organisms. A study using river corridor plants revealed below-ground interactions and explains distribution patterns by the occurrence of fungi (Nobis et al. 2015). Generally, there are manifold interactions of soil biota and plant cover (Kardol and Wardle 2010; van der Heijden et al. 1998); a North American study even attributes invasive earthworm activity to be a driver of changes in forest vegetation (Hale et al. 2006). In addition to biotic interactions various soil properties can influence plant ecology. Soil properties from maps can deliver good result in combination with climatic data to predict woody species' distribution (Coudun et al. 2006; Leathwick and Whitehead 2001). Models accounting for the complexity of the land surface, addressing other scientific fields such as avalanche and permafrost prediction, can help explaining hidden ecological phenomena connected to topographic features in mountain landscapes (Salzmann 2006). The study of Geroy et al. (2011) found the aspect of slopes to be a crucial factor for soil formation; and organic carbon storage and water availability are affected by bulk density and stoniness of landscapes (Román-Sánchez et al. 2018). Vincent et al. (2018) calculated soil attributes and predicted soil types for complex landscape features. The integration of advanced soil models and soil organisms could improve the application of ecological niche modelling and species distribution modelling; e.g. instead of raw topographic values from DEM robust results of soil models could be included in ecological assessments and models, some mycorrhiza can be integrated in plant species predictions due to symbiotic relations.

Generally the influence of soil reactions on the occurrence of plant species is fundamental; but also reverse relations apply, because vegetation cover has a strong impact on soil formation. Many soil parameters depend on particular species compositions. Such plant-soil feedbacks need more attention in ecology (Jones et al. 1997; Kulmatiski et al. 2008; Shachak et al. 2008). Especially in patchy landscapes the relation between vegetation, soil properties and their age-assessment are important (Badalamenti et al. 2018; Dupouey et al. 2002; Innangi et al. 2015). The examples in this paragraph highlight the dependence of ecological patterns on interactions with other organisms and the environment; better cooperation between separated disciplines could result in improved scientific approaches.

Beside the interactions of taxa, also human impact is a crucial parameter for the understanding of recent distribution of species (Fois et al. 2017). Fine-grain information for human land-use (livestock rates, grazing intensity, urbanisation parameters, etc.) can be helpful when an estimation of anthropogenic land use should be integrated in ecological research, therefore e.g. remote sensing data could help (Carmel and Kadmon 1999; Hostert et al. 2003). For the study area such information was not available but could support management decisions, e.g. by the assessment of grazing impact on species distribution and vegetation. Besides grazing, various aspects of human interference have

shaped vegetation and plant distributions for millennia. Today fast changes in land use take place but also quick climatic alterations (Pachauri and Meyer 2015; Pereira et al. 2004).

Changes in time

Species are considered to react to climate change in various ways: Studies revealed constant dynamics in environmental variables in deep time being major drivers of species extinctions, habitat shift and range shift (Jackson and Overpeck 2000; Rödder et al. 2013; Rodríguez-Sánchez and Arroyo 2008). As the latter study underlined, under widely unfavourable conditions species distribution is often reduced and restricted to particular regions or sites and recent distributions may still reflect regression patterns. Around the Mediterranean several refugial areas exist, where species probably repeatedly survived unfavourable climatic conditions of the past (Bennett et al. 1991; Papageorgiou et al. 2014; Quézel and Médail 2003). Datasets of floristic and plant-sociological data could be used to assess structure and suitability of such refugia. In this context, beside recent climatic data, also paleoclimatic data and future climatic scenarios may be integrated (e.g. Rodríguez-Sánchez and Arroyo 2008). Uncertainty of these climate data must be considered, but predictions may allow for a general understanding of dynamics in species and vegetation (Sinclair et al. 2010). Not only single species change their range in time, but there is also evidence that species assemblages go back to various dynamic events (Kondrakov et al., 2015). However, when past species co-occurrences are analysed caution applies (Grimm et al. 2016; Grimm and Potts 2015). Research in refugia and their conservation must have high priority, when their overall high genetic diversity and long term survival of species are considered (Hampe and Petit 2005). This way in the Mediterranean mountains not only single species are preserved but communities with several rare elements of boreo-temperate distribution (Brullo et al. 2012; Weiss and Ferrand 2010). The protection of refugia also needs high priority, because they are meant to buffer some of the adverse effects of climate change in the future (Harrison and Noss 2017).

While a property of refugial areas is a relative environmental stability in particular sites, other areas can be prone to changes in species composition. Where disturbance applies, e.g. along coasts and on river banks, in urban and in agricultural landscapes, species turnover is likely, with invasive species arriving. The latter may take place within decades or few years (Bardsley and Edwards-Jones 2007; Groves and Di Castri 1991). Invasion patterns and processes based on recent data can be described, analysed and spatially predicted using floristic and plant sociological datasets. Local and wide-scale studies assessed susceptibility for invasive species (Lazzaro et al. 2016; Lloret et al. 2005; Steinbauer 2017; Wagner et al. 2017). Species distribution models including future climate change could also help to understand changes in species ranges, but an over-interpretation should be avoided (Sinclair

et al. 2010). An assessment linking habitats across landscapes to relative stability and susceptibility to invasions is lacking. This could be most relevant for management and conservation.

Habitats and diversity in landscapes

Conservation and management decisions may benefit from results of distribution modelling. In this context the presented studies comprise patterns for the potential distribution of single plant species helpful for applications in the study area. Beside single species, habitat types and plant communities hosting specific species compositions are relevant in the frame of conservation. Distribution models can be used to predict also habitat types supporting mapping and monitoring (Amici et al. 2014; Culmsee et al. 2014; Jiménez-Alfaro et al. 2018; Pottier et al. 2013; Taminskas et al. 2013). The studied woody taxa of this thesis are key species of habitat types. Thus their distribution patterns may already indicate potential habitat distribution. But these data as parts of typical species lists could be integrated as well in more complex habitat models. Stacked results from single species distribution models can also feature biodiversity patterns (Calabrese et al. 2014). Suchlike can be performed based on records from floristic and plant-sociological databases in order to assess phytodiversity on landscape scale. For the study area such phytodiversity patterns can be compared to published maps based on the distributions of records in data bases (Jahn 2003; Raimondo et al. 2003). Biodiversity is often distributed in patches, frequently related to natural or antropogenic fragmentation. Fragmentation and complexity of landscapes influences diversity of species groups and can be analysed in conjunction with large datasets of species (Moser et al. 2002; Schmiedel et al. 2015; Schmiedel and Culmsee 2016). Fragmentation and connectivity of species' (meta)populations and habitat patches is an important issue in conservation. It can be integrated in semi-automated algorithms used for conservation and management planning (Ball et al. 2009; Ball and Possingham 2000). This algorithm may use information from landscape metrics, e.g. accounting for fragmentation, in conjunction with species, habitat and biodiversity distributions to deliver objective delineations for protected areas. However, the fundamentals of such algorithms and of distribution models are field surveys and expert knowledge on various aspects of biodiversity. That means investments in technical solutions in future should not rise at the cost of education and expert training.

Concluding remarks

The Mediterranean study region hosts a high environmental and biological diversity and therewith offers excellent research perspectives to solve ecological and biogeographical questions. This natural wealth supported the investigations of ecological patterns and processes for plant taxa and vegetation in this thesis. All presented studies share the application of floristic or plant-sociological

datasets from the region, and they integrated location-based extractions of environmental data, classification and species distribution modelling. Methodological limitations deriving for example from bias in ecological background data, uncertainty of coordinates and algorithms were discussed. Generally, ecological complexity of sites can be difficult to estimate; models and exact measures may be easily overestimated in their overall meaning within species' ranges and across scales. In this context, the presented studies could show differing site conditions occupied by isolated metapopulations of species, which may involve ecological and genetic intraspecific variation. In addition to the exemplary ecological studies and methodological limitations presented, further analysis options and (near) future developments in this context were discussed for the region, for woodland species and beyond. The produced datasets and results can be used to support such future studies.

Woody species were studied in this thesis, which helped to understand vegetation patterns in landscapes. With numerical methods they support the characterisation and differentiation of Mediterranean woodlands, being of high ecological importance (Merlo and Croitoru 2005). Woodland habitats as those of the studied *Platanion* are examples of vegetation types protected for their high importance. Even if the understanding of the term *habitat* differs, the integration of habitat-concepts helps to assess conservation priorities and to quantify changes (Brooks et al. 2002; Harding et al. 2001; Maes et al. 2012). Parts of the latest results of the conservation status assessment for Crete are presented, comprising only one of dozens of habitats assessed for protected areas. The exhaustive mapping and monitoring results are delivered to the environmental authorities of the Greek state and the European Commission. However, local authorities being in charge with site management, should be more involved, trained and financed, to be able to reduce the diverse adverse effects acting on habitats and species (not just the protected). Therefore also a wide public interest for nature and its conservation is needed, which is hopefully increased through innovative initiatives and projects (e.g. Mediterranean Agronomic Institute of Chania 2018; WWF Mediterranean Programme Office 2018). Natural resources in many parts of the Mediterranean are under pressure by land use change, climate change, expanding urban and touristic infrastructure, etc. – thus, local people, authorities and scientists, as well as stakeholders of industry and tourism must communicate and act responsibly for the sake of nature and man.

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Acknowledgements

This thesis tells a short story, but was written during an awful long period. Thus I thank my supervisors Prof. Dr. Erwin Bergmeier and Prof. Dr. Holger Kreft for their patience and good support.

My wife Nina Kirchhoff and my family suffered from neglect and my occasionally moody behaviour. Nina also helped out during field surveys, when others had holidays. Thanks for supporting and standing by me.

The Department Vegetation and Phytodiversity Analysis hosted me during many phases of my life - a familiar atmosphere accompanied me there through courses, projects, times of writing and coffee breaks. I really appreciated all support and nice words I received by: Naveed Akhtar, Christine Battmer, Viktor Chepinoga, Hartmut Dierschke, Oliver Fried, Parastoo Mahdavi, Alireza Naqinezhad, Ricarda Pätsch, Inga Schmiedel, Michael Schwerdtfeger, Charlotte Seifert, Brigitte Siegesmund Christian Vogt, Ute Wergen, and many more. Nina Kirchhoff, Ricarda Pätsch, Inga Schmiedel and Laura Sutcliffe helped read half-baked manuscripts and text passages. Many thanks to Nina Kirchhoff, Ricarda Pätsch, Inga Schmiedel and Laura Sutcliffe for repeated proof reading during writing phases.

Ralf Jahn deserves special thanks for providing unlimited access to his excellently managed data base. It was a generous gift to allow me the analysis of data deriving from decades of work in the field, on the computer, in libraries and in herbaria. Many thanks also for the good floristic introduction in the field and the opportunity to use the revised unpublished version of the flora. Further important data contributors and collaborators during various writing phases were Bernhard Egli, Laurence Fazan, Werner Greuter, Chalidon Chalaitzidis, Ulrich Kull and Caroline Mantey. I also like to thank my Sicilian co-authors Riccardo Guarino and Corrado Marcenò for offering me a fruitful cooperation and for widening my perspective.

Andreas Traxler I like to thank for excellent planning and funding during excursions and during extended visits in the biological research station "Zora" in Lentas/Dytikos, Crete. Thank you and all participants of the Exkursions for the informative exciting trips to gorges and inhabitat islets, for good live musik and the unforgettable time we had together sharing beer and "Spaghetti à la Dragonada".

I also thank the field work and the back-office team of the Natura 2000 mapping and monitoring project on Crete for the excellent cooperation and the good time namely: Carl Barnick, Panayotis Dimopoulos, Friedemann Goral, Parastoo Mahdavi, Constantia Patelodimou, Inga Schmiedel, Ioannis Tsiripidis, Walter Wolf, Fotios Xystrakis. Many thanks to all the coworkers of the Mediterranean Agronomic Institute (MAICh) and the forest service of the Samaria National Park in Chania for accommodation, support and exchange. Valuable logistic support came from Car Rental Crete in Heraklion, by good offers and an uncomplicated way of changing and repairing broken cars.

Further good advises and ideas during planning, writing and conferences came from: Milan Chytry, Salvatore Pasta, Franco Pedrotti, Fransceco Spada, Helge Walentowski, Camilla Wellstein and Stefan Zerbe. Thanks to everyone who helped me and who I did not mention.

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Scientific steering committee for the wood pasture project *Neue Hute* (Solling)

Scientific contributions

Articles in peer-review journals

- 2018 **Goedecke, F.**; Jahn, R.; Bergmeier, E.: Quantified ecology and co-occurrence of Mediterranean woody species in a landscape context. *Plant Ecology* 10, doi: 10.1007/s11258-018-0810-x
- 2017 **Goedecke F.**; Bergmeier, E.: Ecology and potential distribution of the Cretan endemic tree species *Zelkova abelicea*. *Journal of Mediterranean Ecology*
- to be submitted **Goedecke, F.**; Marcenò, C., Guarino, R.; Jahn, R.; Bergmeier, E.: Geological data significantly reduce the model performance of species distribution models on broad spatial scales. A GIS – based approach from two Mediterranean Islands. planned for *Diversity and Distributions*

Other publications

- 2017 Schmiedel, I., **Goedecke, F.** & Bergmeier, E.: Ergebnisse der Vegetationsaufnahmen im Wald und Offenland. – In: Nationalparkverwaltung Eifel (ed), Permanente Stichprobeninventur im Nationalpark Eifel. Schriftenreihe zum Nationalpark Eifel 7: 30-66, Schleiden-Gemünd
- Bergmeier, E.; **Goedecke, F.**: *Platanus orientalis* woodlands of Crete - diversity, distribution and conservation status. In: Achille, G. (ed) Scritti in onore di Franco Pedrotti. Collana Natura e aree protette 31: 29-45, TEMI, Trento.

Conference contributions

- 2017 **Goedecke, F.**; Marcenò, C., Guarino, R.; Jahn, R.; Bergmeier E.: Reciprocal extrapolation: woody species distribution on Crete and Sicily. 26th Congress of the European Vegetation Survey - Abstracts, Bilbao, Spain, p. 50
- 2016 **Goedecke, F.**; Goral, F.: Threatened habitats on Crete – conflicts and perspectives. 1st Mediterranean Plant Conservation Week – Book of Abstracts, p. 32, Ulcinj, Montenegro
- Goedecke, F.**; Jahn, R.; Bergmeier, E.: Mediterranean woody species: Ecology, potential distributions and vegetation patterns; 25th EVS-Workshop Book of Abstracts- Lectures, p. 40, Rome, Italy
- Goedecke, F.**; Goral, F.; Mahdavi, P.; Bergmeier, E.: Vegetation and Conservation Status assessment in *Platanus orientalis* woodlands of Crete, Greece; 25th EVS-Workshop Book of Abstracts- Posters, p. 49, Rome, Italy
- 2015 Goral, F.; **Goedecke, F.**; Mahdavi, P.; Bergmeier, E.: Coastal cliffs and salt marshes in Natura 2000 sites of Crete (Greece) – Distribution, Conservation status and threats; 24th EVS-Workshop Book of Abstracts, p. 119, Rennes, France

- 2015 **Goedecke, F.;** Goral, F.; Mahdavi, P.; Bergmeier, E.: Evaluation and threat of coastal sand dune habitats in the Natura 2000 sites of Crete, Greece; 24th EVS-Workshop Book of Abstracts, p. 108, Rennes, France
- 2014 **Goedecke, F.;** Bergmeier, E.: Modelling potential species distribution for Crete, Verhandlungen der Gesellschaft für Ökologie 44, p. 126, Hildesheim, Germany
- 2013 Bergmeier E.; Dimopoulos, P.; **Goedecke, F.;** Tsiripidis I.: Annual vegetation of coastal habitats in the South Aegean. 22nd EVS – Workshop Book of Abstracts, p. 6., Rome, Italy
- Dimopoulos, P.; Tsiripidis, I.; Bergmeier, E.; **Goedecke, F.;** Kallimanis, A. S.; Mucina L., Panitsa, M., Xystrakis, F., Strid, A.: Assessing the conservation status of habitat types in Greece: methodological issues and links to the Red List evaluation of ecological communities. 22nd EVS- Workshop Book of Abstracts, p. 12, Rome, Italy
- 2012 **Goedecke, F.;** Goral, F.; Bergmeier, E.: Characterization and diversity of annual dry grasslands in the South Aegean (Greece). Verhandlungen der Gesellschaft für Ökologie 42, p. 238, Lüneburg, Germany

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Files on included CD:

<i>thesis:</i>	GoedeckeF_2018_Thesis.pdf
<i>publications:</i>	Bergmeier_Goedecke_2017_PlatanusOrientalisForestCrete.pdf
	Goedecke_Bergmeier_2017_Letter_of_Acceptance.pdf
	Goedecke_et_al_2018_QuantifiedEcologyAndCooccurrenceCrete.pdf

Table A 2.1 Number of records of Mediterranean woody species from Crete for geological units.

	phylite-quartzite	neogene	quaternary	plattenkalk	tripali	tripolitza	pindos	pindos-f.	tripolitza-f.	asteroussias-f.	ophiolites	Asteroussias crystalline rocks	sum of records
	acidic	sediments		hard limestones				flyschs			various		
<i>Acer sempervirens</i>	16	7	28	213	163	110	14	1	8	1	1	2	564
<i>Arbutus andrachne</i>	23	1	1	6	.	2	33
<i>Arbutus unedo</i>	142	18	17	16	11	4	.	1	209
<i>Berberis cretica</i>	4	1	25	229	136	37	12	.	5	.	.	2	451
<i>Castanea sativa</i>	21	.	1	1	23
<i>Ceratonia siliqua</i>	52	122	58	25	34	74	17	3	8	1	4	2	400
<i>Crataegus monogyna</i>	12	13	12	22	4	17	.	.	2	.	7	.	89
<i>Cupressus sempervirens</i>	10	10	17	135	131	29	3	2	4	1	1	1	344
<i>Erica arborea</i>	99	8	12	11	3	2	1	.	.	.	2	.	138
<i>Euphorbia dendroides</i>	11	29	16	36	23	50	5	.	7	.	3	2	182
<i>Ficus carica</i>	21	63	40	38	12	31	10	5	5	1	4	7	237
<i>Juniperus macrocarpa</i>	.	41	18	.	.	3	14	2	.	6	.	.	84
<i>Juniperus oxycedrus</i>	.	2	1	37	14	2	56
<i>Juniperus turbinata</i>	15	103	31	20	.	17	39	4	3	13	6	1	252
<i>Laurus nobilis</i>	16	20	10	4	1	2	1	.	54
<i>Myrtus communis</i> subsp. <i>communis</i>	24	37	29	.	3	3	3	.	1	.	5	.	105
<i>Nerium oleander</i>	60	69	70	13	14	42	12	5	8	2	8	4	307
<i>Olea europaea</i> subsp. <i>sylvestris</i>	84	131	47	47	33	109	21	16	18	2	15	11	534
<i>Phillyrea latifolia</i>	78	48	17	31	32	133	10	1	5	.	10	1	366
<i>Phoenix theophrasti</i>	7	19	22	2	.	5	3	1	.	.	1	.	60
<i>Pinus brutia</i>	37	92	39	63	29	33	32	4	6	3	1	3	342
<i>Pistacia lentiscus</i>	113	380	123	57	73	164	52	17	17	15	8	6	1025
<i>Pistacia terebinthus</i>	42	42	17	32	18	28	6	3	4	1	4	.	197
<i>Platanus orientalis</i>	113	77	84	16	16	27	6	4	3	2	9	.	357
<i>Prunus prostrata</i>	.	1	.	136	99	18	5	.	1	.	.	.	260
<i>Prunus webbii</i>	8	31	10	16	11	22	5	6	5	1	1	1	117
<i>Pyrus spinosa</i>	80	73	45	55	31	58	15	26	17	1	13	9	423
<i>Quercus coccifera</i>	98	90	46	175	151	234	20	5	21	3	17	8	868
<i>Quercus ilex</i>	71	17	9	20	10	45	1	1	2	.	1	.	177
<i>Quercus ithaburensis</i> subsp. <i>macrolepis</i>	2	23	17	3	.	1	.	2	48
<i>Quercus pubescens</i>	85	96	43	25	5	32	4	8	11	.	35	.	344
<i>Rhamnus lycioides</i> subsp. <i>oleoides</i>	35	57	21	30	52	117	6	2	6	.	17	4	347
<i>Rhamnus saxatilis</i> subsp. <i>prunifolia</i>	.	.	1	87	72	14	3	2	179
<i>Salix alba</i>	4	10	29	1	.	1	.	.	.	1	.	.	46
<i>Styrax officinalis</i>	31	55	29	16	2	14	2	1	4	.	3	.	157
<i>Vitex agnus-castus</i>	8	22	46	7	1	18	3	6	7	.	2	4	124
<i>Zelkova abelicea</i>	3	.	20	82	53	15	20	193
Sum of records	1425	1808	1051	1707	1237	1513	344	126	178	54	179	70	9692

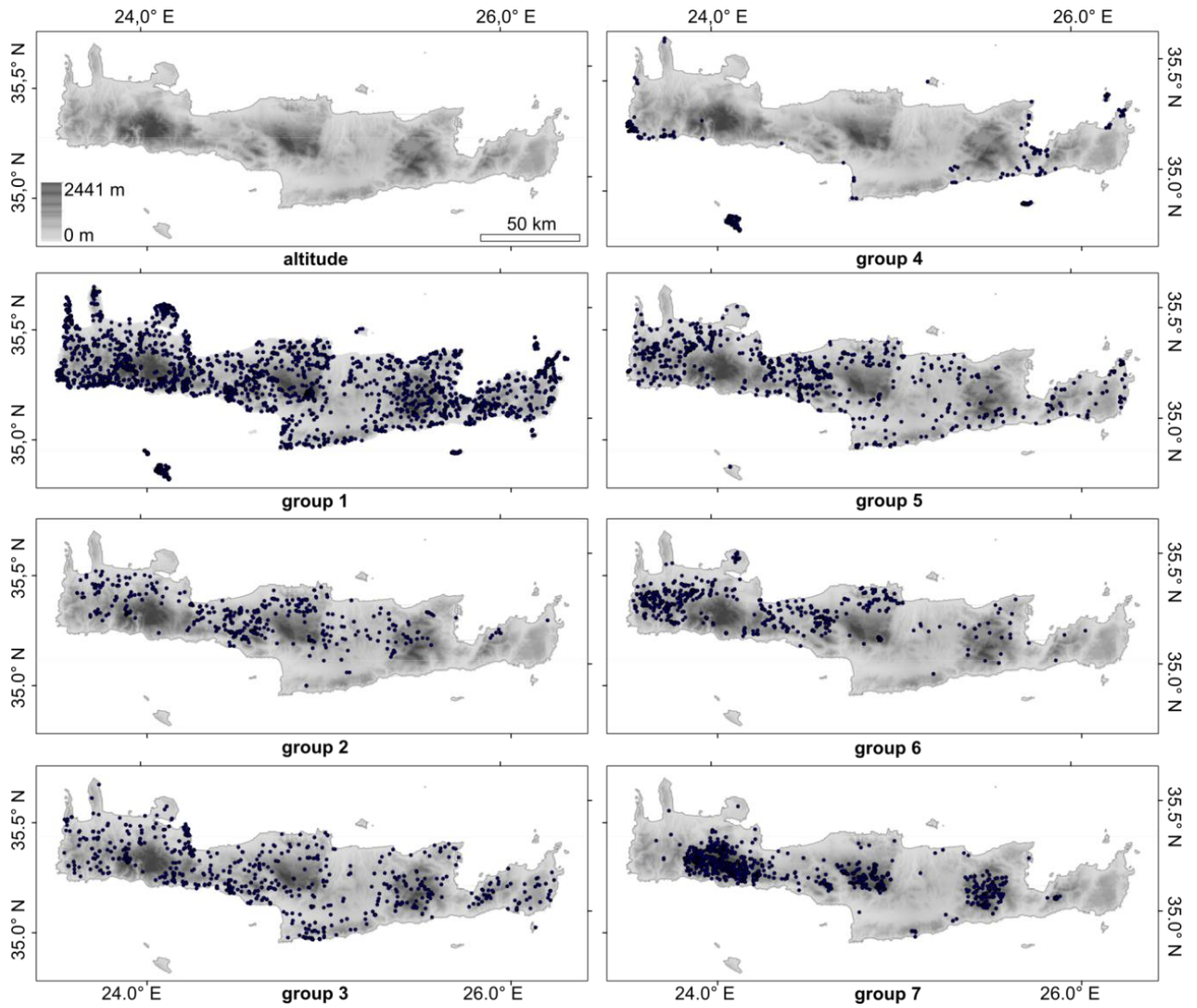


Figure A 2.1 Woody species records on Crete; clustered to groups 1-7 based on ecological spectra of geology, topography, and macroclimate; shading shows altitudinal gradients [m a.s.l.].

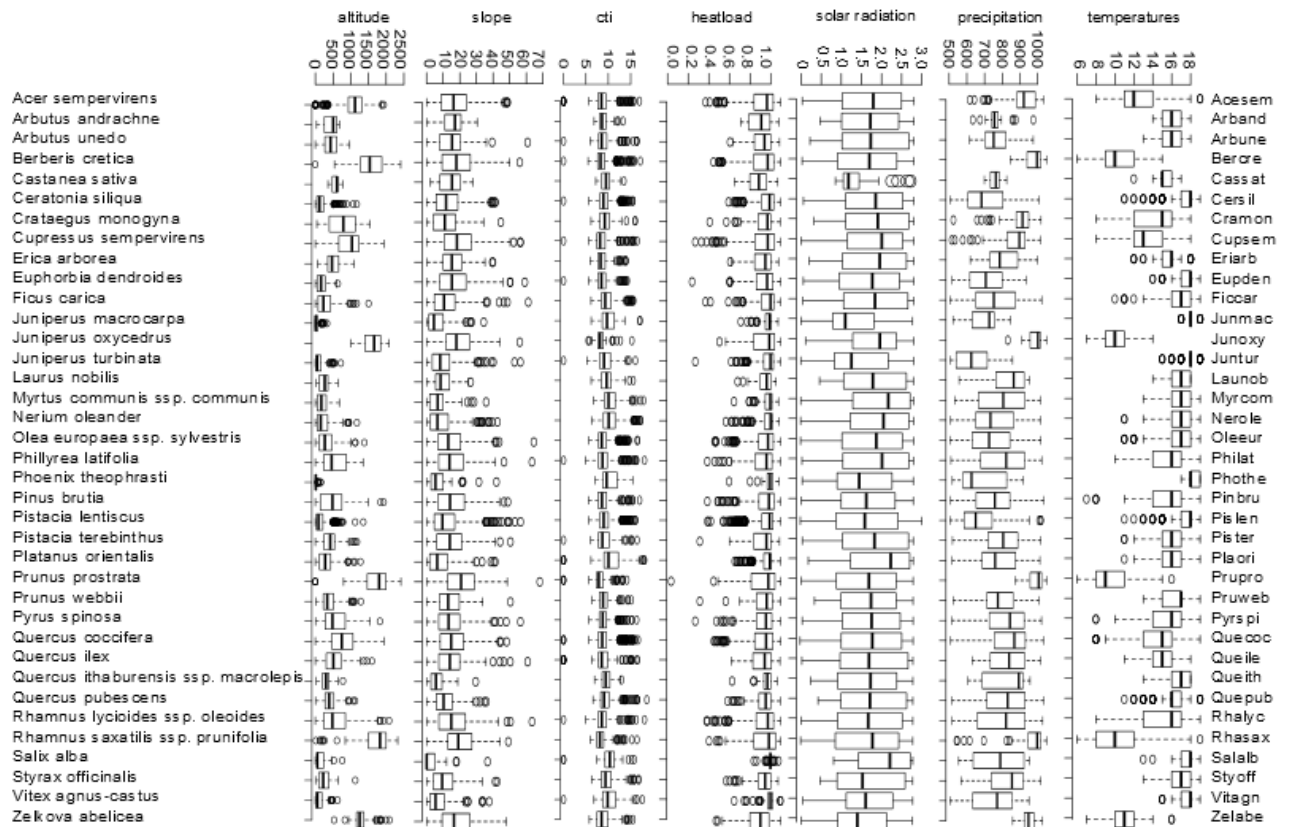


Figure A 2.2 Abiotic preferences of woody Mediterranean species from Crete; as boxplot diagrams; parameters derived from digital elevation model (DEM): altitude [m a.s.l.], slope [°], *cti* [no unit] (compound topographic index) being high in topographically wet areas as valleys and depressions, *heatload* [no unit] (topographic heatload index), solar radiation [MW/m²/year] as annual energy sum, reduced by relief-based shade; sum of annual precipitation [mm], annual mean temperatures [°C].

Figure A 3.1 Field protocol sheet for the conservation assessment of habitat 92C0 on Crete.

Habitat Type		92C0 <i>Platanus orientalis</i> and <i>Liquidambar orientalis</i> woods									
Region: Crete		(<i>Plantanion orientalis</i>)									
		Regional description: Forests and woods, for the most part riparian, dominated by <i>Platanus orientalis</i> (oriental plane) or <i>Liquidambar orientalis</i> (sweet gum), belonging to the <i>Plantanion orientalis</i> alliance									
Header data for plot assessment						Plot size: 200 m ²					
Evaluator:						Plot code:					
Date:			Old code:			Altitude (m):					
Locality:											
LAT _{centre} :			LAT _{bottomright} :			Exposition:					
LON _{centre} :			LON _{bottomright} :			Inclination (°):					
Relief						Geological substrate					
<input type="checkbox"/> Plain/Plateau <input type="checkbox"/> Slope <input type="checkbox"/> Summit/Crest <input type="checkbox"/> Bottom (valley) <input type="checkbox"/> Depression <input type="checkbox"/> Sea shore						<input type="checkbox"/> Calcareous <input type="checkbox"/> Mixed <input type="checkbox"/> Non-calcareous					
	Tree	Shrub	Herb	Stone	Rock	Photos	ID	Dir.	Coord. of Panorama		
Cover (%)						Plot			LAT:		
Maximum height						Pano			LON:		
Decide whether main habitat (dominating formation in polygon, if applicable fill table)											
OR co-habitat (not separated as own polygon, if applicable write only main habitat code)											
<input type="checkbox"/> Main habitat		Co-habitat	Co-habitat	Co-habitat	Co-habitat	Co-habitat	Co-habitat	Co-habitat			
Habitat code											
Proportion in polygon (%)											
<input type="checkbox"/> Co-habitat, main habitat code:											
Typical species (6 including the bold species necessary for habitat type in polygon)											
	BB ¹	AFOR ²		BB	AFOR		BB	AFOR			
<i>Adiantum capillus-veneris</i>			<i>Myrtus communis</i>								
<i>Aristolochia sempervirens</i>			<i>Nerium oleander</i>								
<i>Athyrium filix-femina</i>			<i>Osmunda regalis</i>								
<i>Berula erecta</i>			<i>Platanus orientalis</i>								
			(dominant)								
<i>Brachypodium sylvaticum</i>			<i>Primula acaulis</i>								
<i>Campanula cretica</i>			<i>Rosa sempervirens</i>								
<i>Carex cretica</i>			<i>Rumex conglomeratus</i>								
<i>Carex divulsa</i>			<i>Salix alba</i>								
<i>Carex idaea</i>			<i>Samolus valerandi</i>								
<i>Carex pendula</i>			<i>Styrax officinalis</i>								
<i>Cyclamen creticum</i>			<i>Vitis vinifera ssp. sylvestris</i>								
<i>Dorycnium rectum</i>											
<i>Equisetum telmateia</i>											

¹ **BB:** Baun-Blanquet scale for assessment of plot (individuals & percentage cover):
r (rare and <5%), **+** (several and <5%), **1** (frequent and <5%), **2** (5–25%), **3** (25–50%), **4** (50–75%), **5** (>75%)

² **AFOR:** Scale for assessment of the whole polygon area (outside the plot): **A** = Abundant, **F** = Frequent, **O** = Occasional, **R** = Rare

<i>Hedera helix</i>								
<i>Hypericum hircinum</i> ssp. <i>albimontanum</i>								
<i>Melissa officinalis</i>								

Specific Structures and Functions (to be assessed for the <u>whole polygon</u> , tick only if true in large polygon areas)	
Positive	Negative
<input type="checkbox"/> Rejuvenation of the dominant tree/shrub species (<i>Platanus</i>)	<input type="checkbox"/> Unsustainable tree-cutting
<input type="checkbox"/> Soil undisturbed (no significant trampling or erosion) and relief natural	<input type="checkbox"/> Significant presence of ruderal species and/or invasive neophytes
<input type="checkbox"/> Stand stratified (tree, shrub, herb layer present)	<input type="checkbox"/> Significant hydrological impact (e.g. water extraction as indicated by pipes, dams, earthworks)
<input type="checkbox"/> ≥8 species of the list present	<input type="checkbox"/>
<input type="checkbox"/> Closed canopy of trees ≥50%	<input type="checkbox"/>
<input type="checkbox"/> Considerable number of species of permanent streams present (3250, 3260)	<input type="checkbox"/> <small>If necessary specify additional significant aspects</small>

Conservation Degree assessment of Structure and Functions (ACTUAL STATUS)			
<input type="checkbox"/> FV	<input type="checkbox"/> U1	<input type="checkbox"/> U2	<input type="checkbox"/> XX
≥4 positive and no negative	≥2 positive and/or ≤2 negative	<2 positive and/or >2 negative	Not possible to assess

Prospects of Structure and Functions (FUTURE TREND and STATUS)			
Pressures (P) and Threats (T) (use codes given in instructions)		P, T or PT	Importance
Positive impacts (management actions, policy changes, etc. ; Describe impacts and give their importance)			Importance
Future Trend (positive impacts might balance higher number or importance of P or T)			
<input type="checkbox"/> FV No P or T of high importance and ≤1 of medium importance	<input type="checkbox"/> U1 ≤3 P or T of medium importance	<input type="checkbox"/> U2 ≤1 T or P of high importance and/or ≥3 P or T of medium importance	<input type="checkbox"/> XX Not able to assess P or T
Future Status			
<input type="checkbox"/> FV Structure and functions are expected to be in FV status in more than 75% of the studied locality.	<input type="checkbox"/> U1 Structure and functions are expected to be in FV status in less than 75% and U2 status in less than 25% of the area.	<input type="checkbox"/> U2 Structure and functions are expected to be in U2 status in more than 25% of the area.	<input type="checkbox"/> XX: Not able to assess future conservation status in more than 50% of the studied locality

Overall Assessment of Prospects for Structure and Functions			
<input type="checkbox"/> Good (G):	<input type="checkbox"/> Poor (P):	<input type="checkbox"/> Bad (B):	<input type="checkbox"/> Unknown (X)
The overall assessment of prospects of Structure and Functions is calculated automatically according to the matrix given in the instructions based on <u>Actual Status</u> , <u>Future Trend</u> and <u>Future Status</u> and must not necessarily be filled here.			
Notes:			

Table A 4.1 Spearman correlations of environmental parameters, pairs with values ≥ 0.6 are reduced to one; selected variables in bold font (see Table 4.3 for abbreviations), all further refer to macroclimate (Karger et al. 2016), prec= precipitation, temp= temperature, intanvar= inter-annual variation.

	slope	heatload	cti	altitude	temp annual mean	temp intanvar	temp July	temp January	annual mean prec	prec intanvar	bio9	bio8	bio7	bio6	bio5	bio4	bio3	bio2	bio19	bio17	bio16	bio15	bio14	bio13	bio12	bio11	bio10	bio1	prec July	prec January
slope	1.00																													
heatload	-0.02	1.00																												
cti	-0.39	-0.02	1.00																											
altitude	0.36	-0.03	-0.16	1.00																										
temp annual mean	-0.24	0.02	0.10	-0.73	1.00																									
temp intanvar	-0.25	-0.17	0.16	-0.14	0.31	1.00																								
temp July	-0.28	0.01	0.11	-0.71	0.98	0.40	1.00																							
temp January	-0.24	0.04	0.09	-0.75	1.00	0.28	0.97	1.00																						
annual mean prec	0.27	-0.27	-0.02	0.14	-0.31	-0.18	-0.36	-0.28	1.00																					
prec intanvar	0.25	-0.18	-0.06	0.17	-0.33	-0.31	-0.41	-0.31	0.89	1.00																				
bio9	-0.25	-0.01	0.07	-0.70	0.95	0.47	0.97	0.94	-0.36	-0.44	1.00																			
bio8	-0.31	0.01	0.10	-0.72	0.91	0.42	0.91	0.91	-0.37	-0.42	0.93	1.00																		
bio7	-0.27	-0.10	0.20	-0.22	0.43	0.73	0.52	0.40	-0.34	-0.51	0.56	0.52	1.00																	
bio6	-0.24	0.03	0.05	-0.75	0.97	0.38	0.97	0.97	-0.32	-0.37	0.98	0.94	0.47	1.00																
bio5	-0.24	-0.01	0.08	-0.70	0.95	0.46	0.98	0.94	-0.36	-0.43	1.00	0.93	0.56	0.98	1.00															
bio4	-0.30	0.01	0.11	-0.37	0.63	0.54	0.70	0.60	-0.50	-0.59	0.72	0.64	0.87	0.66	0.72	1.00														
bio3	0.19	0.00	-0.11	0.22	-0.41	-0.22	-0.47	-0.37	0.58	0.72	-0.49	-0.35	-0.59	-0.41	-0.48	-0.73	1.00													
bio2	-0.09	0.06	-0.03	-0.22	0.19	0.23	0.16	0.23	0.34	0.20	0.18	0.29	0.19	0.22	0.18	0.02	0.39	1.00												
bio19	0.30	-0.23	-0.06	0.19	-0.32	-0.21	-0.38	-0.30	0.99	0.89	-0.38	-0.40	-0.36	-0.33	-0.37	-0.51	0.59	0.34	1.00											
bio17	0.03	-0.06	0.05	-0.22	0.07	-0.23	-0.02	0.11	0.68	0.79	-0.07	-0.05	-0.37	0.02	-0.07	-0.29	0.46	0.22	0.64	1.00										
bio16	0.32	-0.22	-0.05	0.22	-0.36	-0.20	-0.41	-0.33	0.98	0.88	-0.40	-0.43	-0.36	-0.36	-0.40	-0.53	0.59	0.32	0.99	0.60	1.00									
bio15	0.18	-0.09	0.04	0.63	-0.61	0.17	-0.52	-0.65	-0.03	-0.11	-0.46	-0.55	0.08	-0.56	-0.46	-0.15	0.03	-0.31	0.02	-0.52	0.08	1.00								
bio14	0.04	-0.05	0.03	-0.25	0.08	-0.30	-0.03	0.11	0.59	0.71	-0.07	-0.04	-0.45	0.03	-0.07	-0.31	0.40	0.11	0.56	0.95	0.52	-0.54	1.00							
bio13	0.29	-0.25	-0.05	0.18	-0.34	-0.22	-0.40	-0.31	0.99	0.89	-0.40	-0.42	-0.36	-0.35	-0.39	-0.51	0.56	0.29	0.99	0.64	0.99	0.02	0.56	1.00						
bio12	0.25	-0.27	-0.02	0.11	-0.27	-0.18	-0.33	-0.24	1.00	0.90	-0.33	-0.34	-0.32	-0.28	-0.33	-0.47	0.57	0.34	0.98	0.70	0.97	-0.07	0.61	0.99	1.00					
bio11	-0.24	0.02	0.05	-0.75	0.97	0.38	0.97	0.97	-0.32	-0.37	0.98	0.94	0.47	1.00	0.98	0.66	-0.42	0.22	-0.33	0.02	-0.36	-0.56	0.03	-0.35	-0.28	1.00				
bio10	-0.25	-0.01	0.07	-0.70	0.95	0.47	0.97	0.94	-0.36	-0.44	1.00	0.93	0.56	0.98	1.00	0.72	-0.49	0.18	-0.38	-0.07	-0.40	-0.46	-0.07	-0.40	-0.33	0.98	1.00			
bio1	-0.25	0.01	0.06	-0.72	0.96	0.43	0.98	0.95	-0.36	-0.43	1.00	0.93	0.52	0.99	1.00	0.70	-0.47	0.19	-0.38	-0.05	-0.40	-0.50	-0.03	-0.40	-0.33	0.99	1.00	1.00		
prec July	0.06	-0.05	0.05	-0.21	0.03	-0.36	-0.07	0.07	0.61	0.73	-0.11	-0.08	-0.48	-0.01	-0.11	-0.34	0.37	0.06	0.57	0.95	0.53	-0.53	0.98	0.57	0.63	-0.01	-0.11	-0.07	1.00	
prec January	0.35	-0.21	-0.07	0.25	-0.40	-0.22	-0.45	-0.37	0.95	0.86	-0.43	-0.46	-0.38	-0.39	-0.42	-0.56	0.62	0.31	0.96	0.54	0.99	0.13	0.46	0.96	0.94	-0.39	-0.43	-0.43	0.48	1.00

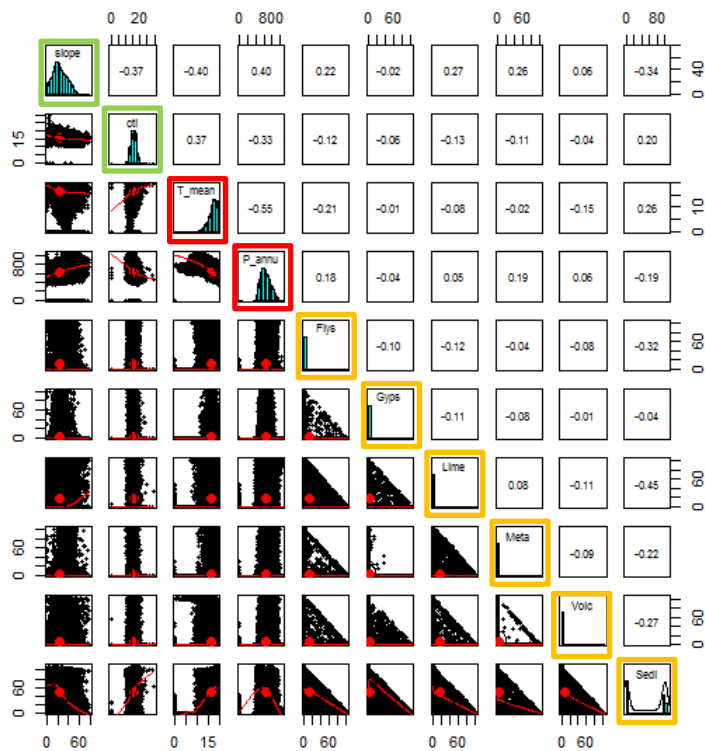


Figure A 5.1 Correlation matrix for environmental variables of $R^2 > 0.6$, mean values had priority.

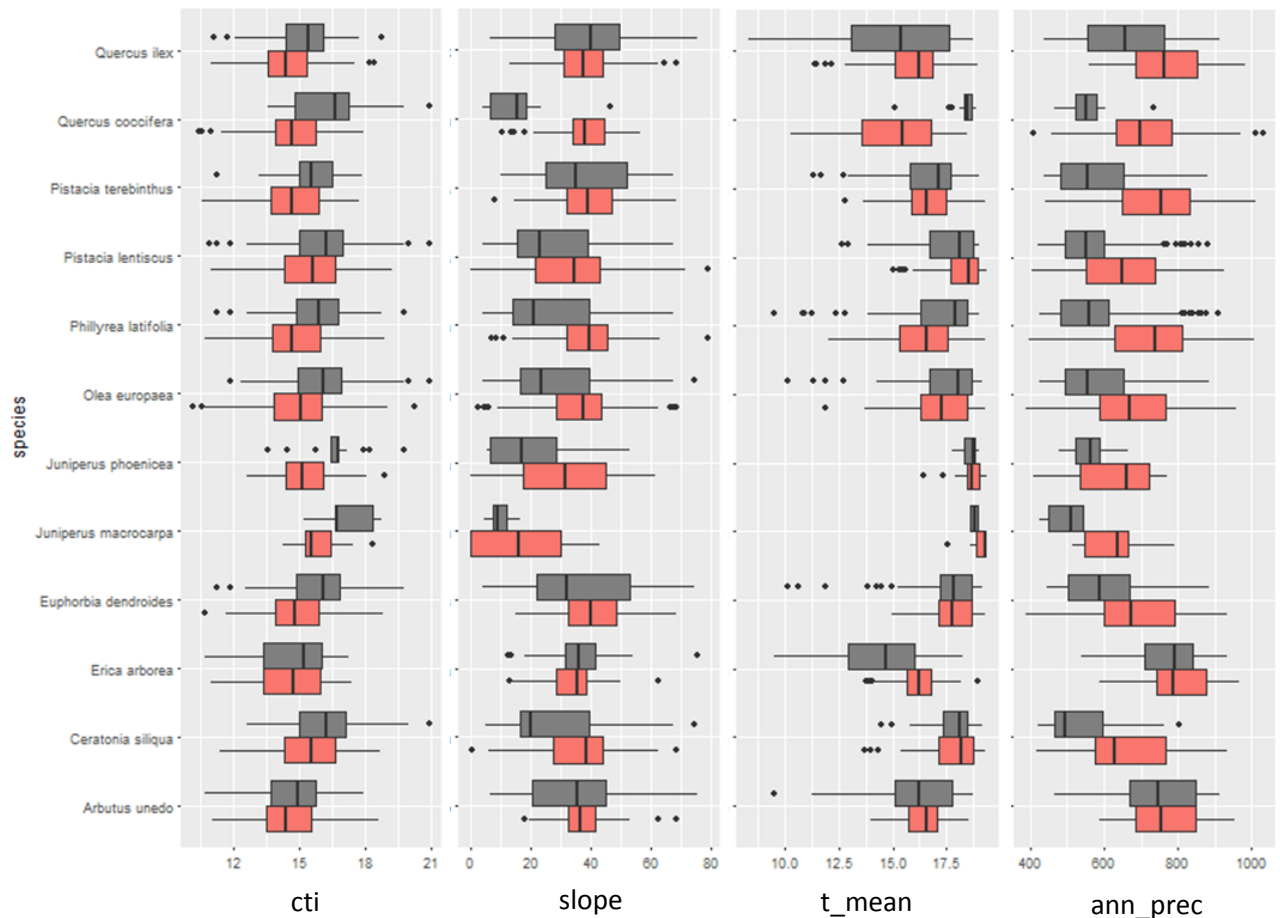


Figure A 5.2 Ecological characterisation of woody species records for (*cti* compound topographic index [no unit], *slope* angle [%], *t_mean* mean temperatures [°C] and *ann_prec* annual precipitation [mm]; lower (red) boxes refer to Crete, upper (grey) boxes refer to Sicily.

Table A 5.1 Test AUC-values (x1000) for the models trained on Crete (Cr) and on Sicily (Si), models are tested with records on the second island. The higher the AUC value the more the cell colour turns to green, while red colour represents low values. Pairs of models are displayed based on the same combination of environmental parameters; *cli* climatic variables (t_mean+ann_prec), *rel* relief variables (cti+slope), *geo* all six bedrock types.

Pairs of data combinations for models	Variable combinations in models													
	cli+rel+geo		cli+rel		cli+geo		rel+geo		cli		rel		geo	
Number of variables	10		4		8		8		2		2		6	
Training island	Cr	Si	Cr	Si	Cr	Si	Cr	Si	Cr	Si	Cr	Si	Cr	Si
Test island	Si	Cr	Si	Cr	Si	Cr	Si	Cr	Si	Cr	Si	Cr	Si	Cr
Edaphic specialists														
<i>Arbutus unedo</i>	491	840	664	827	473	848	493	811	656	818	680	772	462	812
<i>Erica arborea</i>	478	827	718	846	489	835	427	774	692	829	753	767	418	754
<i>Juniperus oxycedrus</i> subsp. <i>macrocarpa</i>	892	778	882	800	891	820	849	592	882	891	862	592	819	639
<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	845	831	878	896	853	812	627	563	879	885	481	501	626	522
Mean value	677	819	786	842	677	829	599	685	777	856	694	658	581	682
Generalists														
<i>Ceratonia siliqua</i>	636	544	667	679	615	517	544	496	626	595	518	600	532	467
<i>Euphorbia dendroides</i>	706	639	723	824	609	577	626	627	662	694	649	786	498	527
<i>Olea europaea</i> subsp. <i>europaea</i>	549	414	606	689	524	377	488	395	547	572	538	628	468	393
<i>Phillyrea latifolia</i>	452	297	485	559	446	256	432	325	399	352	494	659	441	287
<i>Pistacia lentiscus</i>	586	464	659	663	572	393	481	471	632	569	538	621	474	453
<i>Pistacia terebinthus</i> subsp. <i>terebinthus</i>	506	445	675	565	403	407	472	486	431	348	733	761	339	414
<i>Quercus coccifera</i>	426	374	186	269	494	373	477	418	183	309	239	230	607	479
<i>Quercus ilex</i>	475	399	655	573	416	366	464	410	527	413	740	784	349	354
Mean value	529	433	570	592	495	393	491	447	483	465	562	638	454	415

Table A 5.2 Relevées from Sicily integrated in the study.

Relevés from literature	<i>A. unedo</i>	<i>C. silqua</i>	<i>E. arborea</i>	<i>E. dendroides</i>	<i>J. macrocarpa</i>	<i>J. turbinata</i>	<i>O. europaea</i>	<i>P. latifolia</i>	<i>P. lentiscus</i>	<i>P. terebinthus</i>	<i>Q. coccifera</i>	<i>Q. ilex</i>	Total
Barbagallo 1983	2	2					6	7	11		3	6	37
Barbagallo et al. 1979		10		8			22	11	38	22		16	127
Bartolo et al. 1978	1	5			1	1	8	6	13		7	4	46
Bartolo et al. 1982	3	13			15	7	19	28	41		8	3	137
Bartolo et al. 1986		1					3	5	5			2	16
Bartolo et al. 1990	3	3	14				6	8	9	2	4	29	78
Bazan et al. 2006				1			8	9	7	16		14	55
Brullo 1984			14	4			4	3	4	2		22	53
Brullo and Di Martino 1974							2	4	12				18
Brullo and Marcenò 1985	12	30	32	26			49	28	46	13	9	75	320
Brullo and Ronsisvalle 1975							4	5	9		7	6	31
Brullo et al. 1997	2		2										4
Brullo et al. 2000				4				5	9				18
Brullo et al. 2001a+										4		4	8
Brullo et al. 2008	8	8	9	1	8	27	18	13	10	7	42	151	302
Furnari 1965								3	3			3	9
Gianguzzi 1999	18		27	14		1	11	13	31	14		53	182
Gianguzzi and La Mantia 2008	3			11			12	9	17	14		14	80
Guarino 1998	7	1	32	12			9	2	13			18	94
Guisso del Galdo et al. 2008				9		7		2	8				26
Marcenò, C., unpublished		2	3	15			13	2	7	5		9	56
Marcenò and Ottonello 1991			2									7	9
Marcenò et al. 2002				4			3			2		1	10
Minissale and Sciandrello 2005	4	9		6		8	22	22	28		14	12	125
Minissale et al. 2007		15		23			44	49	86	22		56	295
Molinier and Molinier 1955		3		4		2	5		4				18
Poli et al. 1979												6	6
Raimondo 1977												4	4
Raimondo 1992		9		10			14	8	8	3		20	72
Ronsisvalle and Signorello 1977												1	1
Sortino and Giaccone 1968		3		2			3		3				11
Sortino and Marcenò 1974				3									3
Traina and Marcenò 2001	1			1					5	4		3	14
Venturella et al. 1990			1				3	4	3			20	31
Unpublished relevées	1	2			3		1					2	11
Total	57	116	135	166	20	34	298	251	433	133	59	452	2154