

**Influence of vegetation types and environmental variables in structuring *Podarcis erhardii* spatial heterogeneity in Crete, Greece**

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# Influence of vegetation types and environmental variables in structuring *Podarcis erhardii* spatial heterogeneity in Crete, Greece

by

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## Abstract

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One of the main concerns in ecology has been identifying and understanding the factors that regulate variation in species distribution. The distribution of *Podarcis erhardii* (Squamata: Lacertidae) in Crete is limited to the western part of the islands and some islets in the East. The predicted potential distribution of *P. erhardii* was modelled by Herkt, who identified that the most important explanatory variable was the multi-temporal Normalized Difference Vegetation Index (NDVI) of the SPOT 4 Vegetation Instrument. The present study's aim was to identify how much of the variation in the spatial distribution of *P. erhardii* could be explained by different environmental variables, and if the spatial structure contributed to the observed patterns in highest populated NDVI classes. Seven vegetation types in the selected NDVI classes were classified with TWINSpan, and their spatial structure was assessed by partitioning the variation in four fractions: pure environmental, environmental and spatial, pure spatial and undetermined using the Borcard's method. The spatial pattern of the vegetation types assessed by environmental variables and the geographic coordinates was mostly unpredictable. Partitioning the variation of the probability of occurrence of *P. erhardii* into environmental (vegetation types) and spatial (geographic coordinates) components explained 75.2% of the overall variation. The inclusion of additional environmental variables increased the explained variation to 82.5%, and suggested that the spatial structure of *P. erhardii* and the environmental variables have a similar spatial structuring: a humidity gradient identified by actual evapotranspiration. This study identified a possible natural barrier related to a climate gradient that may be constraining *P. erhardii*'s distribution to the Western Crete. Further research should study the effect of this gradient in the locations where *P. erhardii* was observed.

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# 1. Introduction

## 1.1. Spatial heterogeneity in species distribution

One of the main concerns of ecology has been identifying and understanding nature processes (Mueller-Dombois and Ellenberg, 1974). Of special concern has been the relationship between biological dependent variables (e.g., abundance of species, structure of ecological communities) and environmental factors (e.g. soil parameters, topography) (Legendre *et al.*, 2002). Usually, this relation has been made with the use of traditional statistics, which implies many assumptions, one of which is related to the homogeneity of nature (Pickett and Cadenasso, 1995). However, from experience in the field, ecologists know that living organisms and physic processes are not distributed randomly nor uniformly, but they show spatial (and temporal) patterns (Legendre, 1993; Legendre *et al.*, 2002; Legendre and Legendre, 1998; Wagner and Fortin, 2005).

In nature, spatial patterns are found as gradients or patches. The gradients in the physical environment and the patchy structures result form energy flow of broad-scale physical processes, such as geomorphological processes, currents and wind (Legendre *et al.*, 2002; Legendre and Legendre, 1998). Additionally, the processes that control living organisms, like growth, reproduction and mortality, generate spatial autocorrelation in the data. Spatial autocorrelation is a property of random variables, that are unlikely to be independent from each other when two sampling sites are located near to each other in the geographic space (Legendre, 1993).

Considering the spatial heterogeneity (defined by Wagner *et al.* 2005 as “the spatially structured variability of a property of interest, which may be a categorical or quantitative, explanatory or dependant variable”) to understand and model ecological processes brought a new paradigm in ecology (Legendre, 1993). Moreover, decisions in biodiversity conservation and natural resources management may also have implications with this new paradigm (Dormann *et al.*, 2007; Kissling *et al.*, 2008).

In the new context, adjustments to the ecological theory and methods had to be done (Wagner and Fortin, 2005). The inclusion of the spatial structure in the ecological models include methods where the spatial structure is represented as a linear combination of the geographic coordinates of the sampling sites, or where the spatial structure is represented as a matrix of distances (Borcard *et al.*, 2004; Borcard *et al.*, 1992; Legendre, 1993). The statistical implication of the new approaches can be seen in Legendre (1993). In addition, Wagner and Fortin (2005) discuss three approaches (spatial statistics, landscape metrics and statistical modelling) used in landscape ecology that deal with spatial heterogeneity, and the new challenges that have to be achieved within this subject.

One method wildly used nowadays in ecology is the method of variation partitioning proposed by Borcard *et al.* (1992), where the ecological variation is decomposed in four fractions using partial constrained regression or ordination methods (see section 2.4.2 for details on the method) (Borcard *et al.*, 2004; Borcard *et al.*, 1992; Legendre and Legendre, 1998).

When studying the observed variations in plant or animal communities, the method of variation partitioning allows measuring the fraction of the explanatory variables that contribute to the variation in the response variable. Namely one obtains quantitatively the “pure” fraction of the biotic or abiotic environmental variables, the fraction of the spatial structure, and the fraction of the variation explained by both sets of explanatory variables (Borcard *et al.*, 1992).

Applications of this method are illustrated in Borcard *et al.* (1992). Specifically, when studying the determinants of species distribution in tropical forests, relation between environmental (including soil properties, topography, lithology, hydrologic index), historical and spatial factors have been assessed (He *et al.*, 1996; Svenning *et al.*, 2004). Also the variation in the spatial structure of shrubs and herbs was studied in China, including soil characteristics as environmental variables and the spatial factor (He *et al.*, 2007). To identify patterns in relations to the environment, amphibians, reptiles, mammals and birds of Maine were compared to geomorphology, climate, and woody plant variables (Boone and Krohn, 2000). Additionally, to study spatial patterns in amphibians and reptiles, environmental explanatory variables such as elevational gradient and environmental discontinuities caused by transition in forest type and presence of water bodies, were used (Hofer *et al.*, 2004).

In summary, the study of the spatial patterns in ecology helps to understand the processes that control species distribution (Legendre and Legendre, 1998). In this context, partitioning the variance help to recognize the spatial structure in species communities and to identify the processes which may have caused it (He *et al.*, 1996). For this purpose, the use of remote sensing techniques is essential, to obtain spatial and temporal data of the area of interest (Legendre and Legendre, 1998; Plummer, 2000).

## 1.2. The use of NDVI in species distribution

In the last years, remotely sensed indices, such as vegetation index, have become an important source of data when dealing with vegetation variables for modelling species distributions (Pettorelli *et al.*, 2005; Plummer, 2000; Shunlin, 2004). The Normalized Difference Vegetation Index (NDVI) is the earliest widely used vegetation index. It responds mainly to changes in the amount of green biomass and chlorophyll activity (Shunlin, 2004). The NDVI is calculated as the normalized ratio of the difference between the reflectance of the near-infrared radiation (NIR) and the reflectance of red radiation (R). A positive value approaching 1 indicates vegetated areas where the NIR reflectance is high and the visible reflectance is low; which is characteristic for green vegetation. Negative values correspond to clouds, water or snow where the reflection of the R band is larger than the NIR; and values near zero correspond to rocks or bare soil where the reflectance of the two bands is practically equal (Lillesand and Kiefer, 1994; Shunlin, 2004).

The correlation between the NDVI and vegetation biomass, dynamics and climatic variables, has shown good results and is well established (Leyequien *et al.*, 2007; Pettorelli *et al.*, 2005). The NDVI could then be used as a good tool to relate climate, vegetation and animal distribution in a defined time and space (Pettorelli *et al.*, 2005).

For many years the NDVI has been related to vegetation in different ways, such as the temporal and spatial distribution of vegetation communities and vegetation biomass. However, the distinction of plants to the species level using the NDVI or remote sensing is often very difficult even with data with sufficient high spectral and spatial resolution, because many groups of plants present similar NDVI values (Pettorelli *et al.*, 2005).

The NDVI has also been used as an input for animal distributions' models, mainly for mammal and birds. Even though few, studies of reptiles and amphibians also included NDVI as an explanatory variable (Leyequien *et al.*, 2007; Pettorelli *et al.*, 2005).

A range of NDVI datasets are available with different spatial and temporal resolutions that are atmospherically corrected, de-clouded and geo-referenced, and come in useful products to assess ecological problems. For example, the National Oceanic and Atmospheric Administration-Advanced Very High Resolution Radiometer (NOAA-AVHRR) has long-term NDVI data series since 1981 with a resolution varying from 8 to 16 km. An NDVI timeseries with higher spatial resolution (1 km) than the AVHRR data is generated from data from the Satellite Pour l'Observation de la Terre-Vegetation

(SPOT-VGT) which has been operational since 1998 (Pettorelli *et al.*, 2005; van Leeuwen *et al.*, 2006).

### 1.3. Reptiles and environment

Compared to other animal groups (e.g. mammals and birds), few studies have been conducted on modeling reptiles' spatial patterns (Guisan and Hofer, 2003; Qian *et al.*, 2007; Tews *et al.*, 2004). The importance in understanding the processes that affect reptiles' distribution and their relation with environmental factors is of prime importance, because their diversity is declining globally (Gibbons *et al.*, 2000).

The investigations that study reptiles' distributions and ecology include mainly the following environmental variables: structural changes in vegetation (Castellano and Valone, 2006; Hofer *et al.*, 2004), vegetation structure and ground cover (Bragg *et al.*, 2005; Jellinek *et al.*, 2004; Pianka, 1966; Pianka, 1971; Pianka, 1989), climate (Araujo *et al.*, 2007; Bragg *et al.*, 2005; Fischer *et al.*, 2005; Olalla-Tarraga *et al.*, 2006; Pianka, 1967; Pianka, 1973; Qian *et al.*, 2007; Schall and Pianka, 1978), space, shelter and food availability (Fischer *et al.*, 2005), physiography (Qian *et al.*, 2007), topography (Olalla-Tarraga *et al.*, 2006), soil properties and soil-vegetation relation (Castellano and Valone, 2006; Pianka, 1989; Pianka and Pianka, 1970).

Even though the spatial heterogeneity was found to be an important factor affecting lizards' diversity gradients in the later 60's (Pianka, 1966), it was not till the last years that spatial gradients have been considered while studying lizards (Araujo *et al.*, 2007; Boone and Krohn, 2000; Hofer *et al.*, 2004; Olalla-Tarraga *et al.*, 2006; Qian *et al.*, 2007). However, the quantification of the variance of the environmental variables and the effect of the spatial structures explaining the spatial patterns of reptiles was less considered (Boone and Krohn, 2000; Hofer *et al.*, 2004).

### 1.4. *Podarcis erhardii* (Squamanta: Lacertidae)

The target species of this research is the Erhard's wall lizard, *Podarcis erhardii* (Squamanta: Lacertidae), a reptile (about 7cm in length) endemic to the Balkans and which is widely distributed in the southern Aegean region, including western Crete and the Cyclades, Sporades and Dodekanesa islands. It is found from sea level up to 2000 m altitude and in some places in isolation rather than in a continuous range (Lymberakis *et al.*, 2005; Valakos, 1986).

*P. erhardii* has been observed in shrubby vegetation, rocky areas, in the coastline (rocky shores, sand, shingle or pebble), in rural gardens and urban centres. Populations living on islands also occur in more open spaces like sand dunes (Lymberakis *et al.*, 2005).



The diet of *P. erhardii* consists mostly of coleoptera, ants and insect larvae, depending on the season (Valakos, 1986; Valakos *et al.*, 1997).

*P. erhardii* is a threatened (Valakos *et al.*, 1997) and protected species (listed on Annex II of Bern Convention) that shows outstanding variations in morphology (28 subspecies described in Greece), habitat preference and

behaviour (Poulakakis *et al.*, 2005; Poulakakis *et al.*, 2003). Three mitochondrial lineages were identified within the island population subspecies; one of which occurs in Crete and the surrounding islets, another in the Pori islet, and the last one occurring on the Cyclades, Sporades and Dodekanesa islands (Poulakakis *et al.*, 2003).

The distribution of *P. erhardii* in Crete is limited to the western part of the island and some islets in the east (Figure 1). Poulakakis *et al.* (2003) found in their investigation that the lineage which occurs in Crete can further be subdivided into three subclades, according to the geographical site of samples. One subclade located in the Lefka Ori Mountains, another including the populations of Western Crete and the Dia islet; and the third one including the specimens from the Eastern islets.

The ecological plasticity and the variation in morphology are some aspects that make *P. erhardii* an interesting species for studies of population dynamics and biogeography (Valakos, 1986). Poulakakis *et al.* (2003) and Poulakakis *et al.* (2005) studied the relation of molecular data on the genus *Podarcis* to geological past events in the phylogeography of this species and the paleogeography of the Balkan Peninsula (Poulakakis *et al.*, 2005; Poulakakis *et al.*, 2003). Beside these studies, there is not enough evidence of which processes (historical, environmental or spatial related) may be restricting *P. erhardii*'s distribution to the western part of Crete.



**Figure 1:** *P. erhardii* distribution. Source: modified from [www.iucnredlist.org](http://www.iucnredlist.org)

## 1.5. Research problem

The distribution of *P. erhardii* in Crete has been modelled by Herkt (2007) with good results (AUC of test partition=0.86). The research showed that the most important explanatory variable assessed by a Jackknife test was a remotely sensed index, the multi-temporal Normalized Difference Vegetation Index (NDVI) of the SPOT Vegetation instrument (Herkt, 2007). This result suggests that *P. erhardii*'s distribution may be related to some characteristic of NDVI (e.g. climate, vegetation). Additionally, many studies in the ecology of lizards have shown strong relations with the vegetation types, litter content, cover structure, climate and topography (see section 1.3).

The results of the investigation of Herkt (2007) showed the importance of different environmental variables to predict the potential distribution of *P. erhardii*. However, there is a clear need to identify how much of the variation in the spatial distribution of *P. erhardii* can be explained by these environmental variables (and specifically vegetation types), and if the spatial structure contribute to the observed patterns.

## 1.6. Research objectives

The main objective of this research is to examine to what extent the spatial structure and the environmental explanatory variables (emphasizing in vegetation types) contribute to the spatial distribution of *P. erhardii* in highest populated NDVI classes.

To achieve the main objective, the following specific objectives have been proposed:

1. To identify the prevailing vegetation types in the NDVI classes with highest observations of *P. erhardii*
2. To study the spatial distribution of the prevailing vegetation types and to relate it to environmental variables
3. To assess the contribution of the prevailing vegetation types and the spatial structure to the probability of occurrence of *P. erhardii*
4. To assess the variation in the probability of occurrence of *P. erhardii* by spatial structuring and environmental explanatory variables

## 1.7. Research hypothesis

- 1 – H<sub>1</sub>: Differentiable vegetation types within the NDVI classes with highest observations of *P. erhardii* can be identified using a divisive clustering method (TWINSPAN) on the basis of species constancy.
- 1 – H<sub>0</sub>: Differentiable vegetation types within the NDVI classes with highest observations of *P. erhardii* cannot be identified using a divisive clustering method (TWINSPAN) on the basis of species constancy.
- 2 – H<sub>1</sub>: Climate, soil parameters and topography together with the geographic coordinates explain significantly ( $p < 0.05$ ) the spatial variation in the prevailing vegetation types.
- 2 – H<sub>0</sub>: Climate, soil parameters and topography together with the geographic coordinates do not explain significantly ( $p < 0.05$ ) the spatial variation in the prevailing vegetation types.
- 3 – H<sub>1</sub>: The prevailing vegetation types and the spatial structure (built from the geographic coordinates) can significantly ( $p < 0.05$ ) be attributed to the probability of occurrence of *P. erhardii*.
- 3 – H<sub>0</sub>: The prevailing vegetation types and the spatial structure (built from the geographic coordinates) do not explain significantly ( $p < 0.05$ ) the probability of occurrence of *P. erhardii*.
- 4 – H<sub>1</sub>: The inclusion of additional environmental variables (spatial structure, soil properties, climate and topography) to explain the variability in the probability of occurrence of *P. erhardii*, diminish significantly ( $p < 0.05$ ) the unexplained variation.
- 4 – H<sub>0</sub>: The inclusion of additional environmental variables (spatial structure, soil properties, climate and topography) to explain the variability in the probability of occurrence of *P. erhardii*, does not diminish significantly ( $p < 0.05$ ) the unexplained variation.

## 1.8. Research questions

The following research questions are proposed for the study:

1. Which are the prevailing vegetation types within the NDVI classes with highest observations of *P. erhardii*?
2. Can environmental variables and the spatial structure explain the variation in the prevailing vegetation types?
3. How much of the variation of the probability of occurrence of *P. erhardii* can be attributed to the prevailing vegetation types and to the spatial structure?
4. How much of the variation of the probability of occurrence of *P. erhardii* is explained by environmental variables, spatial structure and the combination of both?



## 2. Methods

### 2.1. Study area

Crete is an island of 8336 km<sup>2</sup> that is located at the South of Greece (figure 2). It is the largest island of the country and holds approximately 600000 inhabitants. The landscape consists mainly of mountains and few plains in the coastal area, where the majority of the population lives (Chartzoulakis and Psarras, 2005).

The island of Crete has a sub-humid climate with long hot and dry summers and cold and humid winters. The annual media precipitation is 927mm; however, the presence of the mountains makes rainfall patterns vary in different areas, for example in the lower lands 300mm while in the mountains 2000m. Moreover, precipitation is higher in the Northwest coasts while in the Southeast it is lower and has more hours of total sunshine. These differences in climate create various micro-climes along the island (Chartzoulakis and Psarras, 2005). While the eastern part of the island is the driest and sunniest area of Europe, other mountainous areas are covered by snow around eight months each year (Yale University, 2005).

Crete holds different ecosystems even though human presence dates for more than 8000 years. This island is one of the richest areas in the Mediterranean for plant diversity; it holds 1700 plant species from which 160 are endemic (Yale University, 2005). It is also very rich in fauna biodiversity and holds many endemic species. The main reasons for this high endemism are: the island's geographic position (between three continents: Europe, Asia, and Africa), its long isolation from land masses (around five million years) and its topography (Tzatzanis *et al.*, 2003; Yale University, 2005).



**Figure 2:** Location of the study area. Source (World2C™ Multimedia, 2007)

The main reason to choose Crete as the study area of this research is the particular distribution of *Podarcis erhardii* in the island. Nevertheless, the inter-institutional agreement between the Natural History Museum of Crete (NHMC), University of Crete and the International Institute for Geo-Information Science and Earth Observation (ITC) is also important for the data acquisition and the logistics in the fieldwork.

## 2.2. Data

### 2.2.1. Species data: *Podarcis erhardii*

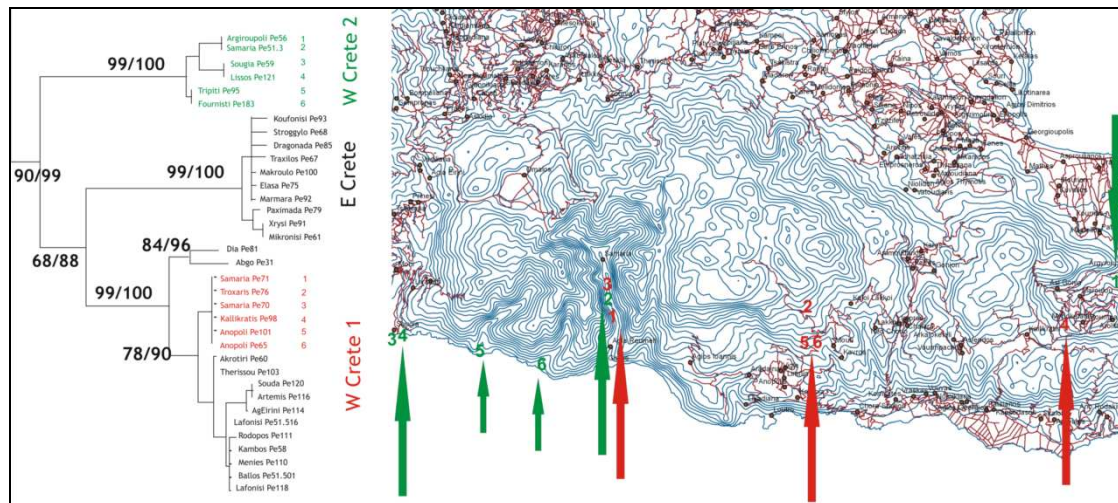
The set of presence only data was obtained from the Natural History Museum of Crete (NHMC, 2006). In Crete, this dataset is the only source available containing information of *P. erhardii* occurrences. For this study it is assumed that the data of the NHMC is correct and the investigation will be based on this information.

The information used from the NHMC dataset consisted of point observations (X, Y coordinates) dating from 1990 to 1999. Repeated observations of the same site were avoided using the information of the earliest date, and additionally only the points with accuracy of less than 1km were included.

This database consists of 69 observations (Appendix A), which includes the main island of Crete and the Eastern islets. As discussed in section 1.4 in Crete three different subclades can be differentiated by their geographical location, one present in the Eastern islets and the other two in the main island (Poulakakis *et al.*, 2003). The population of the Eastern islets was excluded from the study because of time, economic and accessibility constrains.

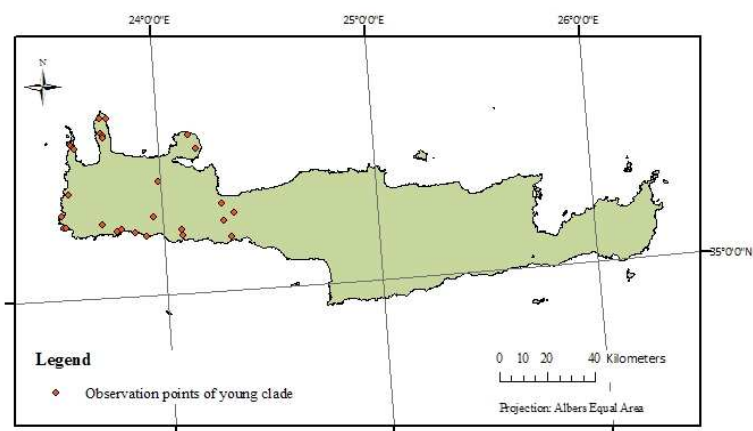
Between the two remaining subclades present in the main island, one is a relict population (5.2Mya) and the other one is a young population (2.3Mya). Though they correspond to different mitochondrial lineages and may be found sympatrically in the area of the mountains (see figure 3), it is not possible to distinguish between the two groups either morphologically or by where they were found (Lymberakis, 2007).

Because there is not enough information to differentiate firmly between the two subclades, but still time and accessibility were limiting the work, observations found above 800masl, semi mountainous (Papiomitoglou, 2006) were excluded to exclude subclade 1 of the study.



**Figure 3:** Relict (in green) and young (in red) specimens of the two subclades living in Western Crete. Source: Lymberakis, 2007 (personal communication)

The final database consisted of 28 observation points of *Podarcis erhardii* collected within 1991 and 1999 and with a spatial accuracy less than 1 km (figure 4).



**Figure 4:** Presence-only data of *P. erhardii* used in the research. Source: (NHMC, 2006)

### 2.2.2. Environmental predictors

Data of 16 environmental variables (Table 1) were collected and pre-processed to ensure spatial compatibility and accuracy by Herkt (2007), except for the multi-temporal NDVI (see below for details in its processing). These variables, for the whole island, constitute the remotely sensed predictors dataset.

**Table 1:** Environmental variables dataset. Source: modified from Herkt (2007)

Variable	Spatial resolution	Date	Source
Altitude	3 arc seconds (~90m)	2000	USGS/SRTM
Aspect	3 arc seconds (~90m)	2000	USGS/SRTM
Slope	3 arc seconds (~90m)	2000	USGS/SRTM
Geology	n/a	n/a	NHMC
Soil type WU	1:1,000,000 (1km)	1986	Wageningen University
Soil type WRB full	1:1,000,000 (1km)	2004	ESBN
Volume of stones	1:1,000,000 (1km)	2004	ESBN
NDVI	1km	2006	CNES/Spot Image
Dominant land use	1:1,000,000 (1km)	2004	ESBN
Land cover CORINE	1:100,000 (~300m)	2000	EEA
Potential evapotranspiration	0.5 degrees (~50km)	1996	USGS/NIEHS
Actual evapotranspiration	0.5 degrees (~50km)	1996	USGS/NIEHS
Annual precipitation	30 arc seconds (~1km)	2005	Wordclim/Hijmans et al.
Mean annual temperature	30 arc seconds (~1km)	2005	Wordclim/Hijmans et al.
Min temperature of the coldest month	30 arc seconds (~1km)	2005	Wordclim/Hijmans et al.
Isothermality	30 arc seconds (~1km)	2005	Wordclim/Hijmans et al.

The dataset of environmental predictors in addition with the soil variables (see section 2.3.2) was used to describe the sampling sites in relation with the plant communities. Moreover, it was used as one component of the Bocard's method (Borcard *et al.*, 1992) for the partition of the ecological variation in the vegetation data and in *Podarcis erhardii*'s probability of occurrence.

### Multi-temporal NDVI data

The research used NDVI data derived from the VEGETATION sensor on board the SPOT-4 platform. The 10-day composite NDVI (S10 product) images are de-clouded and geo-referenced and were obtained via ITC from the Vlaamse Instelling voor Technologisch Onderzoek (VITO) Image

Processing centre (Mol, Belgium) [www.VGT.vito.be](http://www.VGT.vito.be). With 1 km<sup>2</sup> resolution 300 NDVI images are available from eight years (from April 1998 to July 2006).

The temporal series of NDVI images were combined to produce one singular NDVI map for the eight years in ERDAS/IMAGINE (ERDAS, 2006). The ISODATA clustering was used to perform an unsupervised classification with convergence threshold set to 1.0, and the number maximum number of iterations set to 50 (Skidmore *et al.*, 2006). The optimum number of classes for the NDVI map was found to be 27, which was robust and detailed enough (see Appendix B for details the number of classes' selection).

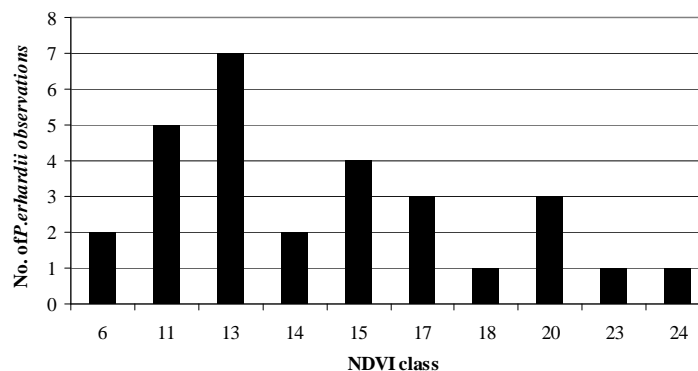
The unsupervised classification method was used in this case because there was not enough information about the characteristics of the specific classes in Crete. Besides, (Wang and Tenhunen, 2004) found that the differences of unsupervised and supervised classification of multitemporal NDVI were minimal, and achieved similar accuracy for their study area. In addition, this variable obtained with the same procedure (for 6 years) is the most important predictor variable explaining *P. erhardii* particular distribution in Crete (Herkt, 2007).

## 2.3. Data collection

### 2.3.1. NDVI classes' selection

The NDVI classes with the highest number of observations of *P. erhardii*, based on the data provided by the NHMC (see 2.2.1), were selected for the study. These classes were also selected if they were distributed along the island and if they were representative for different altitudes (from 0masl to 1000masl). These criteria were used to make the Eastern-Central and Western part of the island comparable, where *P. erhardii* is apparently absent and present respectively. The result of this stage was a stratification of the study area.

The 28 observations of *Podarcis erhardii* were crossed with the 27 classes of the multi-temporal NDVI map in ArcMap 9.2 (ESRI, 2006). The classes with highest presence of the target species were class 11, 13 and 15 (figure 5).

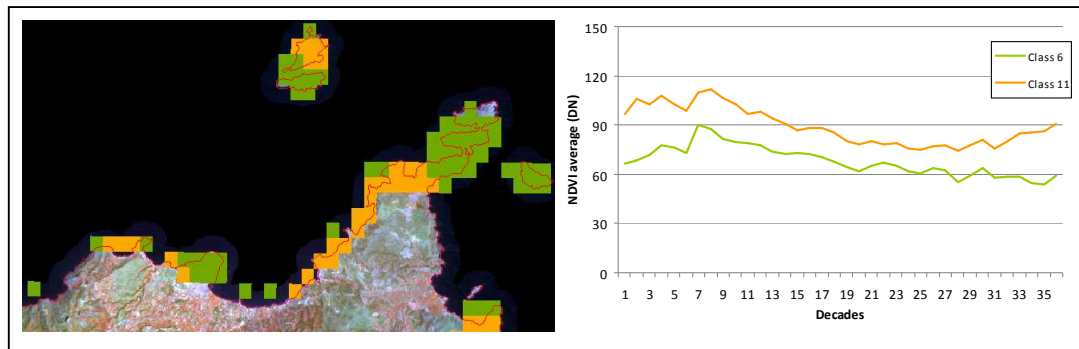


**Figure 5:** Number of *P. erhardii*'s observations per NDVI class

In addition, class 6 was joined with class 11 because these classes occur together along the island, as it can be seen in figure 6a (e.g. in the northeast peninsula of Crete). Moreover, the annual behavior of both classes is similar for the eight years' information (figure 6b).

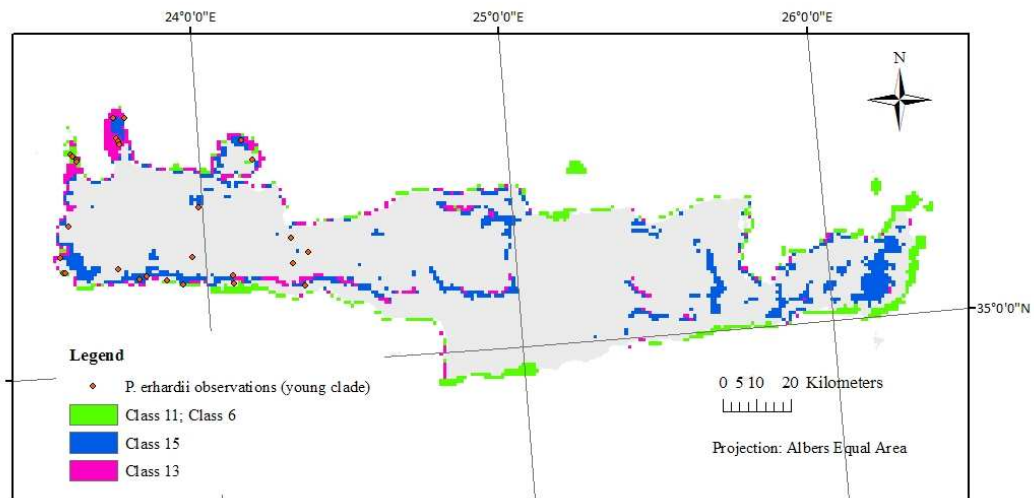
The variation in behavior between the profiles of both NDVI classes may be related to the presence of water in pixels of class 6, which makes the NDVI values of this class be lower. Even though the islets

were not considered in the study, *P. erhardii*'s observations in those islets occurred mainly in both classes (6 and 11).



**Figure 6:** NDVI classes 6 and 11; (a) spatial distribution of both classes in the northeast peninsula; (b) annual averaged profiles

Class 15 shows a homogeneous distribution along the island, from approximately 20m to 900m of altitude. Class 13 also is distributed along the island (from 20m to 1000m of altitude) however, in the western part is less frequent. Finally, classes 6 and 11 are closer to the sea (from 20m to 500m of altitude) (figure 7). As classes 11, 13 and 15 met the criteria of selection, they were used as a way of stratification of the study area.



**Figure 7:** Spatial distribution of selected NDVI classes

### 2.3.2. Field measurements

The stratification of the study area provided by the selected NDVI classes was used to allocate 107 sampling points (number of sites that could be visited in the period of the fieldwork, taking into consideration time spend in the relevé, distances between sampling points, and a minimum of 30 sampling units per NDVI class, in order to be representative for that unit).

Simple random sampling was used because every unit has an equal chance of selection (Doherty, 1994); and moreover there were no preliminary observations or analysis that correlated vegetation with specific environmental variables, that could have guide another sampling design.

Not all the pixels of the classes in the NDVI map were connected. So, they were removed using ArcMap 9.2 (ESRI, 2006) considering the area, which also removed isolated pixels, if present. The sampling points were allocated (using the Generate Random Points from the HawthTools of

ArcMap) not further than 250m from any existing road (NHMC, 1998), as a reasonable distance to walk, and to some distance away from the roads to eliminate the disturbance of the vehicles.

The main objective of the fieldwork was to collect information about the plants species present in each relevé, and the cover percentage of plants, rocks, stones and soil. At each site (15m radius plot size) a complete list of species was recorded and an abundance value was given using the following criteria:

**Table 2:** Abundance scale used for plant species

Abundance	Criteria
0 Absent	Not present in the plot
1 Rare	Just one specie
2 Frequent	Few species
3 Abundant	Species present everywhere

Additionally, for each relevé the vegetation cover was visually estimated, separately trees from shrubs (>0,5m high), mini shrubs (<0,5m high), herbs and litter. Also, the cover percentage of soil, stones and rock outcrops was recorded. An example of the relevé sheet is presented in Appendix C. The survey was carried out from the 18th of September to the 3rd of October. One of each plant species was collected for its further identification in the herbarium of the NHMC.

A second objective of the fieldwork was to collect soil samples to further obtain by laboratory analysis information about their chemical properties. Therefore, for each sampled stand one soil sample was collected at 5cm below the surface.

In the laboratory, the dried soil samples were mixed and passed through a 2mm sieve to remove gravel and debris. Soil-water extracts (1:25) were prepared for estimation of electrical conductivity (EC) and pH, using electric conductivity-meter and electric pH-meter respectively (Van Reeuwijk, 2002). Soil nutrients (Ca, K, Na and Mg) were determined using an atomic absorption spectrophotometer (Perkin–Elmer 2380) and evaluated as part per million (ppm) of soil water extracts. These soil parameters were used together with the environmental variables listed in table 1 to examine their relationships with the plant communities obtained from TWINSpan and afterwards with *P. erhardii*'s distribution.

In the field some random points had to be moved. The only two reasons for moving a point were:

- Dangerous or restricted access (e.g. military area)
- The point felt in an olive tree plantation, agricultural field or human-made construction

In the first case the new point was positioned at the shortest distance (reachable without danger) from the point, in the same NDVI class (representing no problem because the areas were homogeneous). In the second case because lizards are found mainly in rocky and shrubby vegetation (Lymberakis *et al.*, 2005; Valakos, 1986; Valakos *et al.*, 1997), and the main objective was to relate the findings where *P. erhardii* apparently lives, tree plantations or agricultural fields were avoided. In this case, the new point was moved to the nearest suitable area (area with semi-natural vegetation) in the same NDVI class.

## 2.4. Data analysis methods

### 2.4.1. Vegetation classification

To identify the prevailing vegetation types in the sampling sites, the vegetation data was analyzed using the two-way indicator species analysis (TWINSpan) in the computer program WinTWINS 2.3

(Hill and Šmilauer, 2005), which was used to classify 49 species in 107 sampling sites. All species whose importance value was less than 1% were eliminated to avoid irrelevant influence in the results (Vogiatzakis *et al.*, 2006).

TWINSPAN, one of the most used methods in community ecology (Jongman *et al.*, 1995; Legendre and Legendre, 1998), is a numerical method for classification of vegetation that belong to similar groups. The sampling sites are ordered first by a divisive hierarchical clustering, and then using this classification the species are classified according to their ecological preferences (Hill, 1994; Hill and Šmilauer, 2005).

All the default settings were used for WinTWINS. The output of TWINSPAN is an ordered two-way table, which shows in a concise way the species' synecological relations (Hill, 1994). To construct the final table some groups of the hierarchy were moved to make neighboring groups as similar as possible (Legendre and Legendre, 1998). Finally the degree of constancy was determined, calculated as the number of relevés in which the socioecological group (cluster of species with similar distributions) occurs (Mueller-Dombois and Ellenberg, 1974).

After the vegetation types (also called “plant communities”) were obtained from the TWINSPAN output, the vegetation structure and physical characteristics of the sampling sites were analyzed and used for further description of each vegetation group.

Additionally the variation in the continuous environmental variables (Table 1) in relation to the vegetation types obtained by TWINSPAN, was assessed using one-way analysis of variance (ANOVA) in R 2.6.1 (R, 2007). This analysis was performed to find out significant variations among plant communities (Abbadi and El-Sheikh, 2002; Abd El-Ghani and Amer, 2003; Jafari *et al.*, 2004).

#### **2.4.2. Partition of the ecological variation**

Many theories (e.g. environmental and the biotic control model) are used to explain the spatial heterogeneity observed in plant and animal communities (Borcard *et al.*, 1992; Dale *et al.*, 2002; He *et al.*, 1996). A good summary of them and their uses can be found in Wagner and Fortin (2005). The method of Borcard *et al.* (1992), nowadays widely applied in ecology, was used in this research for three purposes. First, it was applied to evaluate the contribution of the spatial structure and the environmental variables to the spatial patterns in the prevailing vegetation types obtained by TWINSPAN. Second, to assessment the contribution of the prevailing vegetation types in the spatial distribution of *P. erhardii*. And third it was used to quantify the variation in the probability of occurrence of *P. erhardii* by spatial structuring and environmental explanatory variables.

Borcard's method was chosen among others mainly because it gives a measure of the fraction of the variation in the species matrix explained by: the environmental variables alone, the spatial structure of the species data alone, or the combination of both sets of explanatory variables (Borcard *et al.*, 1992), while other methods don't.

In this method the ecological variability is decomposed into four fractions using constrained and partial canonical ordination techniques: canonical correspondence analysis and redundancy analysis (RDA) (Borcard *et al.*, 2004; Borcard *et al.*, 1992). The fractions resulted from the partition of the total variation of the species data are the following:

(a) *Pure environmental contribution*: fraction of the species variation that can be explained by ‘pure’ environmental variables, independently of any spatial structure.

(b) *Environmental and spatial contribution*: spatially structured variation of the dependant variable(s) that can be explained by the spatial structure of the independent environmental variables in the model. This fraction of the variation is explained by the environmental and the spatial regression models. It

can result from the relations of the species with spatially structured environmental conditions, but also from other existent processes unidentified in the regression model under study.

(c) *Pure spatial contribution*: spatial effect that cannot be attributed to the environmental variables in the model. It refers to spatially structured processes that affect the dependent variable(s) which are not adequately described by the environmental variables used as independent variables in the model.

(d) *Undetermined contribution*: fraction of the dependant variable explained neither by spatial coordinates nor by environmental variables. It may be consequence of stochastic fluctuations, sampling error, or local variability not detected due to the sampling scale.

#### **2.4.2.1. Vegetation types**

The distribution of each vegetation type obtained by TWINSpan was evaluated by the four fractions proposed by Borcard *et al.* (1992), using as input the following matrices:

- Dependant variable: each vegetation type
- Spatial matrix: spatial coordinates (x, y) of the 107 sampling sites
- Environmental variables: climate, soil parameters and topography

Different factors that determine vegetation composition and plant species distribution have been studied for many years; including climate, soil properties and topography (He *et al.*, 2007). In the Mediterranean plants spatial distribution has been attributed mainly to climate, soil properties, altitude, surface cover type and human activities (Vogiatzakis *et al.*, Rundel *et al.*, 1998). Ordination results suggest the following factors to be of major effect on the variance in vegetation: rock type, soil type, altitude, geographical situation, degree of substrate fixation, and inclination (Bergmeier, 2002).

In this research the spatial distribution of the vegetation types attributed to the environment (fraction 'a' in Borcard's method) was tested as a function of climate, soil parameters and topography factors. To avoid the interference of intercorrelated variables in the analysis, they were tested with the Pearson correlation coefficient. If a high correlation was found ( $r > 0.7$ ) between two variables, only one of them was retained for the analysis (Vogiatzakis *et al.*, 2006).

#### **2.4.2.2. Spatial heterogeneity of *Podarcis erhardii***

To examine the contribution of the environmental variables and the spatial structure in the spatial heterogeneity of *P. erhardii* two approaches were followed. The first one uses as explanatory variables the prevailing vegetation types obtained with TWINSpan. In the other hand, the second approach includes other environmental factors in the set of explanatory variables. The selection of the environmental variables for the second approach was made based on previous investigations: vegetation types, spatial structure, climate and topography (Araujo and Williams, 2000; Bragg *et al.*, 2005; Castellano and Valone, 2006; Fischer *et al.*, 2005; Guisan and Hofer, 2003; Jellinek *et al.*, 2004; Olalla-Tarraga *et al.*, 2006; Pianka, 1966). As in the previous section, only the environmental variables not intercorrelated were used in the analysis (see 2.4.2.1).

The spatial coordinates (x, y) of the 107 sampling sites were used to construct the spatial database for both approaches. Additionally, the predicted probability of occurrence of each sampling site was used as dependant variable. The probability of occurrence was obtained with Maxent 3.0.4-beta (Phillips *et al.*, 2007) for the "young" clade.

The maximum entropy approach (Maxent) is a general-purpose method for making predictions or inferences from presence-only data. Maxent estimates the target species probability distribution by



finding the probability distribution (statistical model) of maximum entropy (closest to uniform) subject to constraints (what we know about the features, which are environmental variables or functions thereof, at the sample points) (Phillips *et al.*, 2004). The method computes in an iterative process many probability distributions in the grid. It starts assuming a uniform probability distribution in the entire area and as each feature and its relative weight gets sequentially updates, the gain increases exponentially at suitable areas (Phillips *et al.*, 2006).

Maxent was preferred in this research (instead of well established modeling methods, such as GAM, GARP and BIOCLIM) because it has gives effective predictions of species spatial distribution from occurrence data, and seem to give better results than traditional modeling methods (Elith *et al.*, 2006).

Suitable areas predicted with the model known to be not inhabited were removed from the prediction (Anderson *et al.*, 2003; Phillips *et al.*, 2006).

The significance of the model obtained by the partition of the variation was determined using redundancy analysis. The explanatory variables were selected sequentially by the residual variance explained, and were included to the model if  $p \geq 0.05$  using 200 permutations. Additionally, to obtain the relative importance of each individual explanatory variable contributing to the total variation of the dependant variable, a hierarchical partitioning analysis was performed (Chevan and Sutherland, 1991).

All the analysis of partition of the variation were made in vegan: Community Ecology Package: R package version 1.8-8 (Oksanen *et al.*, 2007). The hierarchical partitioning analysis was carried out using hier.part: Hierarchical Partitioning: R package version 1.0-3 (Walsh and Mac-Nally, 2008).



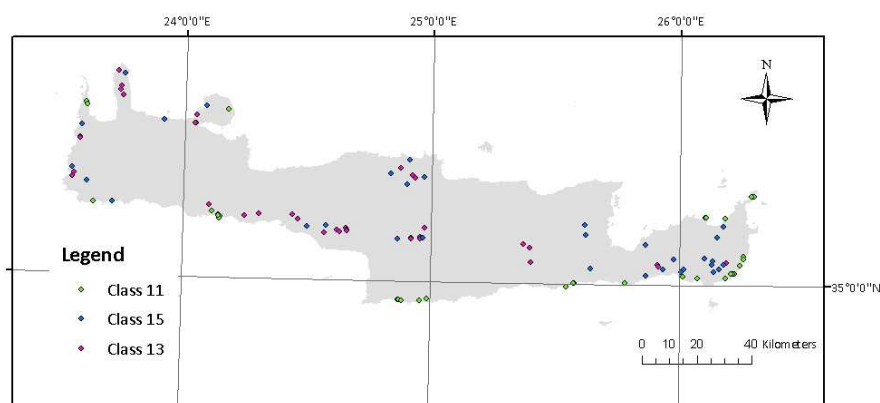
## 3. Results

### 3.1. Vegetation of the study area

In the 107 visited sampling points (table 6, figure 8) a total of 49 species were identified, representing 25 families. Herbs constituted about 7% of the recorded species, while the woody perennials (shrubs and mini-shrubs) dominated (80%) (Appendix D shows some pictures of the identified plants).

The largest families included Labiatae (n=11), Liliaceae (n=5), Leguminosae (n=3), Cistaceae (n=3) and Euphorbiaceae (n=3), representing the 22.4%, 10.2 %, 6.1%, 6.1% and 6.1% of the total plants, respectively. *Urginea maritima* was present in 84% and *Coridothymus capitatus* in 78% of the total relevés; however, no species occurred at all the 107 sites sampled.

Some species had a wide range of distribution, e.g. *Calicotome vilosa* and *Genista acanthoclada*. In the other hand, *Anthyllis hermanniae* and *Stachys spinosa* were found just in the western part of the island.



**Figure 8:** Spatial distribution of the 107 sampling points in the three selected NDVI classes

### 3.2. Vegetation classification

The TWINSPLAN classification of the 107 sampling sites resulted in seven site groups (Table 3), which will be referred here as plant communities or vegetation types (Mueller-Dombois and Ellenberg, 1974). Due to the limited amount of vegetation relevés, the vegetation types are dealt in a general way. The vegetation types were named making use of the dominant species (one or more) or the one(s) that were distinctly important in a certain group of sites. Appendix E includes the complete list of the plant species used in table 3.

**Table 3:** Synoptic table resulted from the vegetation classification

Plant community	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7
<b>Number of relevés</b>	21	18	19	22	13	8	3
1. <i>Erica manipuliflora</i>		-----	-----				
2. <i>Phlomis lanata</i>	=====	-----	-----	=====			
3. <i>Quercus coccifera</i>				=====	=====	=====	=====
4. <i>Pistacia lentiscus</i>	=====	=====				=====	=====
5. <i>Sarcopoterium spinosum</i>	=====				-----		
6. <i>Eurphobia dendroides</i>				-----	-----		
7. <i>Rhamnus saxatilis</i>			=====	=====	=====	=====	
8. <i>Phlomis cretica</i>			=====		=====	=====	
9. <i>Ballota pseudodictamnus</i>					=====	=====	
10. <i>Anthyllis hermanniae</i>							=====
11. <i>Calicotome vilosa</i>	-----	-----	-----	-----	-----	-----	-----

----- Presence less than 20%  
 ===== Presence between 20 - 50%  
 ===== Presence between 50 – 80%  
 ===== Presence above 80%

The seven vegetation groups could not easily be linked to a specific NDVI class (Fig. 7). Table 4 shows that 61% of the relevés of the vegetation groups 1 and 2 are present in class 11; the 54% of the sampling sites of vegetation group 5 is present in class 13; the relevés of vegetation group 3 occur mainly in class 13 (58%) and 15 (37%); and 50% of the relevés of vegetation group 4 is present in class 15. Vegetation groups 6 and 7 have too few relevés; however, they are mainly present in classes 13 and 15.

**Table 4:** Relation between the selected NDVI classes and the vegetation groups

Vegetation group	NDVI class		
	11	13	15
1	14	3	4
2	10	3	5
5	3	7	3
3	1	11	7
4	6	5	11
6	1	4	3
7	0	2	1

To examine if the three selected NDVI classes were significantly different, the environmental variables of the sampling sites were summarized (table 5). Significant differences can be seen in many of the environmental parameters of NDVI classes 11, 13 and 15.

The reason why the vegetation types could not be easily linked to a specific NDVI type, even though between NDVI classes significant environmental differences were found, could be that vegetation formations in the island are often intermixed (e.g. maquis and phrygana). This formations naturally are found in different altitudes for example; however due mainly to overgrazing in the region, now they can exist in other areas (Chatzaki *et al.*, 2005).

**Table 5:** Mean, standard deviation ( $\pm$ ) and ANOVA F values of the environmental variables of the sampling sites associated with the three NDVI classes

Environmental variables	Class 11	Class 13	Class 15	F-ratio	P
Altitude (m)	119.3 $\pm$ 108.1	575.3 $\pm$ 309.8	407.2 $\pm$ 264.1	32.38	<b>0.000</b>
Slope (deg)	12.7 $\pm$ 7.5	17.3 $\pm$ 9.5	11.8 $\pm$ 6.8	4.80	<b>0.010</b>
Mean annual temperature ( $^{\circ}$ C)	18.3 $\pm$ 0.8	15.8 $\pm$ 1.7	16.7 $\pm$ 1.4	31.48	<b>0.000</b>
Isothermality ( $\text{dy}^{-1}$ )	305.2 $\pm$ 12.7	313.5 $\pm$ 8.6	305.1 $\pm$ 8.9	7.76	<b>0.001</b>
Min temp.coldest month ( $^{\circ}$ C)	9.0 $\pm$ 1.0	6.2 $\pm$ 1.8	7.3 $\pm$ 1.4	34.29	<b>0.000</b>
Precipitation (mm)	631.3 $\pm$ 103.6	833.9 $\pm$ 153.1	717.3 $\pm$ 120.6	22.24	<b>0.000</b>
Actual evapotranspiration (mm)	538.2 $\pm$ 26.8	509.5 $\pm$ 22.9	529.5 $\pm$ 32.8	9.88	<b>0.000</b>
Potential evapotranspiration (mm)	1255.7 $\pm$ 45.0	1207.9 $\pm$ 29.0	1242.6 $\pm$ 44.8	13.20	<b>0.000</b>
Tree cover (%)	0.2 $\pm$ 0.5	1.0 $\pm$ 1.6	5.0 $\pm$ 10.5	6.23	<b>0.003</b>
Shrub cover (%)	4.6 $\pm$ 7.4	7.3 $\pm$ 9.9	15.8 $\pm$ 13.6	10.57	<b>0.000</b>
Mini shrub cover (%)	39.0 $\pm$ 18.0	38.6 $\pm$ 18.1	38.4 $\pm$ 18.6	0.01	0.990
Herbs cover (%)	3.5 $\pm$ 2.5	3.0 $\pm$ 2.8	4.5 $\pm$ 4.2	1.87	0.160
Litter cover (%)	2.8 $\pm$ 1.9	3.6 $\pm$ 2.3	4.1 $\pm$ 5.3	1.29	0.279
Bare soil cover (%)	8.2 $\pm$ 4.8	10.4 $\pm$ 7.7	8.1 $\pm$ 7.7	1.30	0.278
Stones cover (%)	22.1 $\pm$ 17.2	9.9 $\pm$ 7.1	10.9 $\pm$ 11.4	10.19	<b>0.000</b>
Rock outcrops cover (%)	21.3 $\pm$ 14.8	28.3 $\pm$ 17.1	19.3 $\pm$ 15.8	3.12	<b>0.048</b>
pH	7.1 $\pm$ 0.3	7.0 $\pm$ 0.3	7.0 $\pm$ 0.3	2.07	0.132
EC (ms/cm)	0.3 $\pm$ 0.2	0.2 $\pm$ 0.1	0.3 $\pm$ 0.1	5.77	<b>0.004</b>
Ca (ppm)	34388.0 $\pm$ 39999.7	8425.1 $\pm$ 17200.8	11891.2 $\pm$ 18734.3	9.21	<b>0.000</b>
Mg (ppm)	3329.1 $\pm$ 3345.5	2203.4 $\pm$ 3833.2	1740.0 $\pm$ 2226.7	2.24	0.112
Na (ppm)	260.3 $\pm$ 193.8	102.0 $\pm$ 67.3	121.1 $\pm$ 82.3	15.91	<b>0.000</b>
K (ppm)	715.1 $\pm$ 445.2	593.7 $\pm$ 284.1	630.4 $\pm$ 370.7	0.98	0.380

### 3.2.1. Vegetation groups

*Group 1: Phlomis lanata* vegetation type. The 21 sampling sites belonging to this community were found in places where mini shrubs, rock outcrops and stones covered in average the 82%. The altitude varied from 23masl to 842masl and the mean precipitation was 656mm. Compared to the other sites the average of calcium, potassium, sodium and magnesium in the soil was high.

*Group 2: Pistacia lentiscus* vegetation type. This community included 18 sampling sites which were present between 27masl and 997masl. As the previous community type they were found in places where mini shrubs, stones and rock outcrops were abundant. The mean precipitation of the sampling sites was 660mm. This group was found in the places with the highest content of calcium, magnesium and sodium in the soil.

*Group 3: Rhamnus saxatilis - Phlomis cretica* vegetation type. This community was represented in 19 sampling sites. They were found between 50 and 990masl. The terrain was covered in 70% by mini shrubs and rock outcrops. The mean precipitation of this community is the highest of all the groups (873mm), and the mean temperature the lowest (15.3  $^{\circ}$ C).

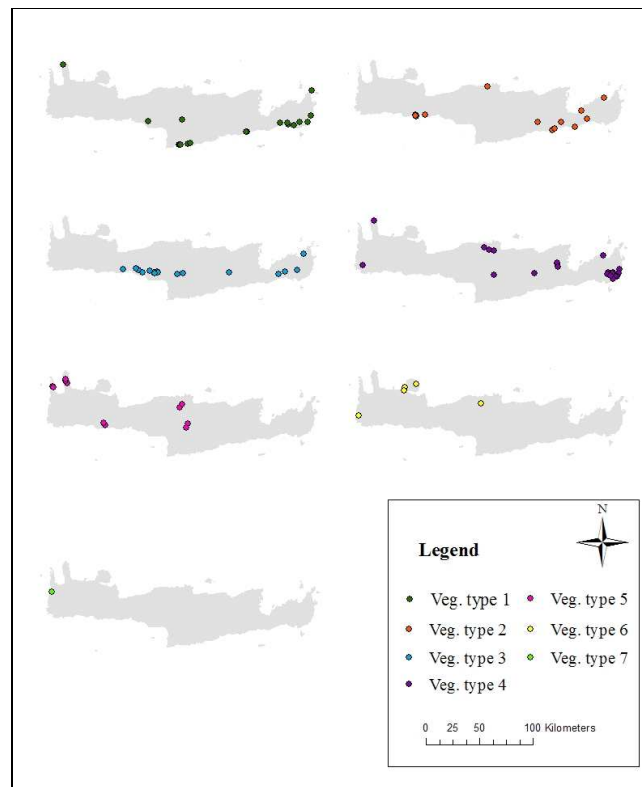
*Group 4: Sarcopoterium spinosum* vegetation type. The 22 sampling sites were found between 26 and 870masl. As the previous group the group was found in places where mini shrubs and rock outcrops were abundant. The mean precipitation was 711mm and the content of calcium, magnesium, potassium and sodium in the soil was moderate.

*Group 5: Ballota pseudodictamnus* vegetation type. This community represented by 13 sampling sites, present between 33 and 900masl. This group was found in places where mini shrubs, rock outcrops and bare soil covered in average the 74%. The mean precipitation of the sampling sites was 808mm. The content of calcium, magnesium and sodium in the soil was the lowest, but the content of potassium was the highest.

*Group 6: Quercus coccifera* vegetation type. This group of eight sampling sites was found places covered mainly by shrubs, mini shrubs and rock outcrops. They were found in low places (23 to 380masl), where the mean precipitation was 660mm and the mean temperature 18.2°C. The soil had moderate content of calcium, magnesium, potassium and sodium.

*Group 7: Anthyllis hermanniae* vegetation type. All of the three sampling sites of this group were found in the Western Crete, between 43 and 250masl. The places were covered by mini shrubs in more than 50%. The mean precipitation was 660mm and the mean temperature 17.6 °C. The content of potassium in the soil was the lowest compared with the other communities, but the content of calcium was the highest of all.

The summary of the environmental variables for each sampling site (continuous and obtained in the field), for the seven vegetation groups is presented in Table 6. Of the remotely sensed predictors, altitude, mean annual temperature, isothermality, minimum temperature of coldest month, precipitation, annual and potential evapotranspiration show highly significant differences between the seven vegetation types. Of the measured soil parameters, calcium, magnesium and sodium show also show significant differences between groups.



**Figure 9:** Spatial distribution of the seven vegetation types

**Table 6:** Mean values, standard deviation ( $\pm$ ) and ANOVA F values of the environmental variables in the sampling sites representing the seven vegetation groups obtained by TWINSpan

Environmental variables	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	F <sub>v</sub> -ratio	P
Altitude (m)	221.6 $\pm$ 282.2	212.6 $\pm$ 242.2	660.3 $\pm$ 260.7	454.8 $\pm$ 277.3	506.9 $\pm$ 250.2	134.4 $\pm$ 132.7	163.0 $\pm$ 106.9	8.93	<b>0.000</b>
Slope (deg)	14.6 $\pm$ 8.5	12.6 $\pm$ 8.7	18.2 $\pm$ 8.9	13.0 $\pm$ 6.4	13.0 $\pm$ 10.0	8.4 $\pm$ 4.1	18.0 $\pm$ 5.2	1.78	0.112
Mean annual temperature (°C)	17.9 $\pm$ 1.4	17.8 $\pm$ 1.4	15.3 $\pm$ 1.5	16.7 $\pm$ 1.4	15.9 $\pm$ 1.1	18.2 $\pm$ 0.8	17.6 $\pm$ 0.5	10.67	<b>0.000</b>
Isothermality (dy <sup>-1</sup> )	303.0 $\pm$ 9.2	307.4 $\pm$ 15.3	315.0 $\pm$ 10.9	302.1 $\pm$ 6.4	313.1 $\pm$ 8.1	310.6 $\pm$ 8.7	313.0 $\pm$ 0.6	4.54	<b>0.000</b>
Min temperature of coldest month (°C)	8.7 $\pm$ 1.6	8.5 $\pm$ 1.5	5.7 $\pm$ 1.7	7.4 $\pm$ 1.5	6.3 $\pm$ 1.2	8.6 $\pm$ 0.8	8.1 $\pm$ 0.5	10.52	<b>0.000</b>
Precipitation (mm)	662.0 $\pm$ 142.7	654.4 $\pm$ 125.4	872.9 $\pm$ 139.1	711.2 $\pm$ 121.0	808.5 $\pm$ 148.6	660.8 $\pm$ 78.0	657.3 $\pm$ 19.6	7.23	<b>0.000</b>
Actual evapotranspiration (mm)	538.8 $\pm$ 27.3	535.5 $\pm$ 23.5	527.9 $\pm$ 21.3	539.8 $\pm$ 31.4	492.8 $\pm$ 16.3	493.0 $\pm$ 4.1	488.0 $\pm$ 10.4	10.48	<b>0.000</b>
Potential evapotranspiration (mm)	1258.6 $\pm$ 41.3	1241.1 $\pm$ 41.0	1220.6 $\pm$ 43.8	1263.4 $\pm$ 43.9	1201.0 $\pm$ 7.4	1189.6 $\pm$ 6.9	1203.0 $\pm$ 3.5	7.94	<b>0.000</b>
Tree cover (%)	1.7 $\pm$ 4.6	2.7 $\pm$ 7.9	1.2 $\pm$ 2.7	1.1 $\pm$ 2.5	0.9 $\pm$ 1.4	8.0 $\pm$ 17.1	1.0 $\pm$ 1.7	1.44	0.207
Shrub cover (%)	5.9 $\pm$ 9.1	9.1 $\pm$ 12.0	5.4 $\pm$ 10.8	9.9 $\pm$ 9.1	13.6 $\pm$ 14.9	18.1 $\pm$ 13.6	6.7 $\pm$ 11.5	1.87	0.093
Mini shrub cover (%)	33.3 $\pm$ 17.3	42.6 $\pm$ 18.7	46.1 $\pm$ 19.5	37.7 $\pm$ 15.9	31.9 $\pm$ 13.6	32.5 $\pm$ 8.5	55.0 $\pm$ 39.1	1.96	0.079
Herbs cover (%)	3.7 $\pm$ 3.1	3.1 $\pm$ 3.2	3.5 $\pm$ 3.1	3.8 $\pm$ 2.2	3.0 $\pm$ 3.8	6.8 $\pm$ 5.1	1.3 $\pm$ 1.2	1.70	0.129
Litter cover (%)	2.4 $\pm$ 1.1	3.9 $\pm$ 5.6	3.5 $\pm$ 2.9	3.0 $\pm$ 2.2	3.3 $\pm$ 1.8	7.3 $\pm$ 5.5	2.3 $\pm$ 1.2	2.24	<b>0.046</b>
Bare soil cover (%)	8.0 $\pm$ 5.8	7.2 $\pm$ 5.6	9.9 $\pm$ 8.7	7.5 $\pm$ 4.9	14.2 $\pm$ 9.0	8.8 $\pm$ 6.8	6.7 $\pm$ 2.9	1.89	0.090
Stones cover (%)	24.9 $\pm$ 14.4	21.2 $\pm$ 19.7	9.8 $\pm$ 7.6	9.8 $\pm$ 8.3	8.2 $\pm$ 5.0	6.5 $\pm$ 9.0	10.0 $\pm$ 5.0	5.61	<b>0.000</b>
Rock outcrops cover (%)	23.1 $\pm$ 16.2	13.7 $\pm$ 13.0	23.1 $\pm$ 18.1	29.3 $\pm$ 15.1	27.7 $\pm$ 16.9	21.3 $\pm$ 9.2	19.0 $\pm$ 26.9	1.92	0.086
pH	7.1 $\pm$ 0.4	7.1 $\pm$ 0.2	6.9 $\pm$ 0.5	7.1 $\pm$ 0.3	7.0 $\pm$ 0.2	7.1 $\pm$ 0.3	7.0 $\pm$ 0.2	1.27	0.278
EC (ms/cm)	0.3 $\pm$ 0.1	0.3 $\pm$ 0.2	0.2 $\pm$ 0.2	0.3 $\pm$ 0.1	0.2 $\pm$ 0.1	0.3 $\pm$ 0.2	0.3 $\pm$ 0.1	0.90	0.496
Ca (ppm)	21631.0 $\pm$ 33014.8	44414.7 $\pm$ 38212.5	9552.6 $\pm$ 18869.0	11610.9 $\pm$ 25127.9	3350.8 $\pm$ 6236.6	6920.0 $\pm$ 9253.1	30133.3 $\pm$ 33184.9	4.62	<b>0.000</b>
Mg (ppm)	2831.0 $\pm$ 3509.7	4672.6 $\pm$ 3836.6	2576.8 $\pm$ 4278.0	1438.2 $\pm$ 1699.0	869.2 $\pm$ 1155.5	1212.5 $\pm$ 1488.6	1933.3 $\pm$ 1476.4	2.89	<b>0.012</b>
Na (ppm)	200.9 $\pm$ 109.4	238.2 $\pm$ 236.3	104.5 $\pm$ 80.8	160.4 $\pm$ 147.1	91.2 $\pm$ 34.0	130.3 $\pm$ 77.5	171.3 $\pm$ 138.0	2.36	<b>0.036</b>
K (ppm)	746.0 $\pm$ 391.7	541.1 $\pm$ 410.8	514.3 $\pm$ 239.5	684.2 $\pm$ 431.2	795.0 $\pm$ 269.3	700.6 $\pm$ 405.6	426.7 $\pm$ 273.9	1.52	0.180

Table 7 show the results of the Pearson moment correlation where it can be seen that some variables are highly correlated. Significant correlations ( $p < 0.001$ ) occurred between altitude, precipitation, mean annual temperature and minimum temperature of the coldest month in one hand, and between potential evapotranspiration, actual evapotranspiration and isothermality in the other hand. To avoid unreliable results only one variable was used of highly correlated variables ( $r > 0.7$ ) (Vogiatzakis *et al.*, 2006). As a result, the variables considered for further analysis were: altitude, annual average of actual evapotranspiration, slope and isothermality [calculated as (mean monthly maximum - mean monthly minimum) / (maximum temperature of warmest month - minimum temperature of coldest month)\*100 (Hijmans *et al.*, 2005)].

**Table 7:** Pearson moment correlation ( $r$ ) between remotely sensed predictors

1	Altitude	1.00							
2	Actual evapotranspiration	-0.07	1.00						
3	Potential evapotranspiration	-0.19	<b>0.89</b>	1.00					
4	Precipitation	<b>0.73</b>	-0.37	-0.61	1.00				
5	Slope	0.33	-0.03	-0.15	0.38	1.00			
6	Isothermality	0.32	-0.56	<b>-0.79</b>	<b>0.71</b>	0.23	1.00		
7	Mean annual temperature	<b>-0.94</b>	0.18	0.28	<b>-0.75</b>	-0.40	-0.40	1.00	
8	Min temperature of coldest month	<b>-0.93</b>	0.24	0.36	<b>-0.78</b>	-0.40	-0.48	<b>0.99</b>	1.00
		1	2	3	4	5	6	7	8

On the contrary, results from table 8 show that soil parameters are mainly uncorrelated, with exception between calcium, magnesium and sodium. Therefore, all soil parameters were kept for further analysis.

**Table 8:** Pearson moment correlation ( $r$ ) between soil parameters

1	Ca	1.00					
2	EC	0.24	1.00				
3	K	-0.38	0.25	1.00			
4	Mg	0.61	0.08	-0.24	1.00		
5	Na	0.59	0.53	0.01	0.33	1.00	
6	pH	0.23	0.17	0.14	0.27	0.40	1.00
		1	2	3	4	5	6

### 3.3. Partition of the ecological variation

The approach proposed by Borcard *et al.* (1992) was used for two purposes. First, it was applied to evaluate the contribution of the spatial structure and the environmental factors in the spatial patterns of the seven vegetation types. And second, to examine the spatial patterns of the distribution of *P. erhardii* explained by environmental and spatial factors.

As the method proposes, the whole variation of each vegetation type can be partitioned in (a) pure environmental variation, (b) environmental and spatial variation, (c) pure spatial variation and (d) unexplained variation (Borcard *et al.*, 1992). The partitioning was based on linear regression because the dependant factor was a single variable (presence or absence of the vegetation type in one case, and probability of occurrence of *P. erhardii* in the other one). The partitions explained by the predictors (a, b and c) were assessed with an unbiased method, adjusted R squares. The testable fractions were then assessed using RDA (Peres-Neto *et al.*, 2006).

#### 3.3.1. Vegetation types

For the presence or absence of each vegetation type (dependant variable) the spatial matrix was composed by the coordinates (x, y) of the 107 sampling sites. The environmental matrix was composed by climate variables (actual evapotranspiration and isothermality), topography variables



(altitude and slope), and the soil parameters (pH, EC, Ca, Mg, Na and K). However, only the environmental variables which were significant ( $p < 0.05$ ) were included in the RDA model. Figure 10 shows the results of the partitioning of the variation.

Figure 10 shows that different processes control the variation of the seven vegetation types along Crete. In the case of vegetation type 1: *Phlomis lanata* the overall amount of explained variation was 15.1%. Soil parameters, climatic and topographic variables explained 7.1% (a+b in figure 10) of the variation of this vegetation type, where 0.6% (b in figure 10) was predicted by the geographical coordinates of the sampling sites. The contribution of each significant environmental variable to the pure environmental variation is summarized in table 9. In *P. lanata* vegetation type, altitude, which has a very wide range in the 21 sampling sites belonging to this group, and actual evapotranspiration, one of the highest compared with the other vegetation types, explain almost the 60% of the environmental variation. The unexplained variation was high (84.9%) for this vegetation type.

The overall amount of explained variation in vegetation type 2: *Pistacia lentiscus* was 14.4%. Soil parameters, climatic and topographic variables explained 13.6% (a+b in figure 10) of the variation, where 2.4% (b in figure 10) was predicted by the geographical coordinates of the sampling sites. The content of magnesium and sodium in the soil, the highest compared within vegetation types, contributed with 55% to the pure environmental variation (table 9). In *P. lentiscus* vegetation group the unexplained variation was also high (85.6%).

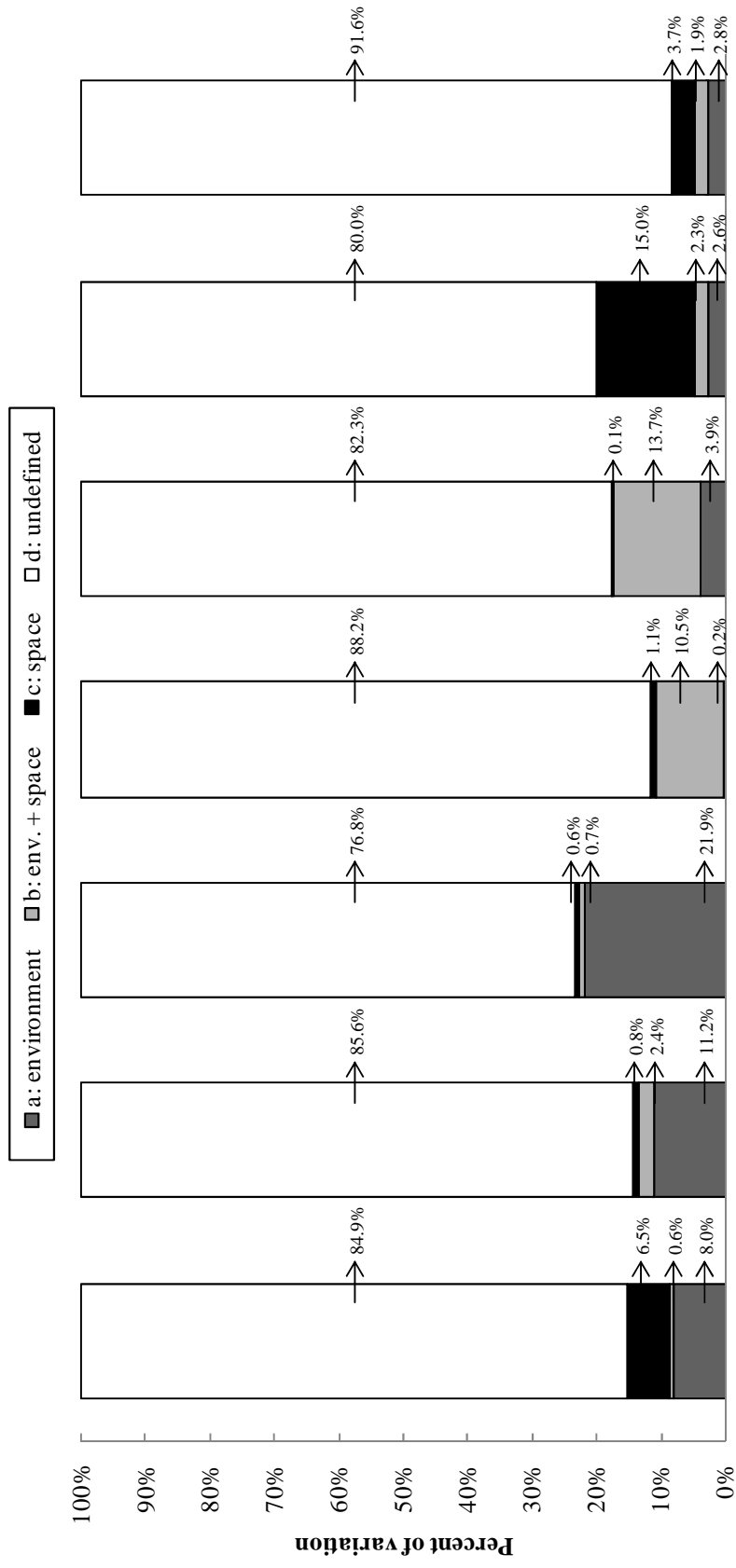
Soil parameters, climatic and topographic variables explained the 22.6% (a+b in figure 10) of the overall variation in *Rhamnus saxatilis* - *Phlomis cretica* community (vegetation type 3), where 0.7% can be attributed to the geographical coordinates of the plots (b in figure 8). This group is present in average in higher altitude areas, where also the precipitation is higher than the other vegetation types. This distinction is also reflected in the individual contribution of altitude and isothermality to the pure environmental variation, which sum up to 66% (table 9). The unexplained variation in *R. saxatilis* – *P. cretica* community is the lowest of the vegetation types, but remains high 76.8%.

In vegetation type 4: *Sarcopoterium spinosum* the overall amount of explained variation was 11.8%. The pure environmental variation explained by the climatic and topographic variables accounts for 10.8% (a+b in figure 10), where 10.5% (b in figure 10) was predicted by the geographical coordinates of the sampling sites. The soil parameters were not included in the model because they were not significant, whereas the climatic variables and altitude explained 97% of the pure environmental variation (table 9). The unexplained variation was high (88.2%) in this group.

The overall amount of explained variation in vegetation type 5: *Ballota pseudodictamnus* was 17.7%. Topographic and climatic variables explained 17.6% (a+b in figure 10) of the variation, where 13.7% (b in figure 10) was predicted by the geographical coordinates of the sampling sites. The most important individual contribution to the environmental variation was from the actual evapotranspiration (table 9). In *B. pseudodictamnus* vegetation group the unexplained variation was also high (82.3%).

In vegetation type 6: *Quercus coccifera* the overall amount of explained variation was 20.0%. Topographic variables explained the 4.9% of the variation (a+b in figure 10), where 2.3% can be attributed to the geographical coordinates of the sampling sites (part b). The pure spatial variation (part c) for this community is high (15%). The unexplained variation for *Q. coccifera* vegetation type is 80%.

The overall amount of explained variation in vegetation type 7: *Anthyllis hermanniae* was 8.4%. Climatic and topographic variables explained 4.7% (a+b in figure 10) of the variation, where 1.9% (b in figure 10) was predicted by the geographical coordinates of the sampling sites. More than the half of the pure environmental variation was explained by the actual evapotranspiration variable (table 9). In *A. hermanniae* vegetation group the unexplained variation was the highest (91.6%).



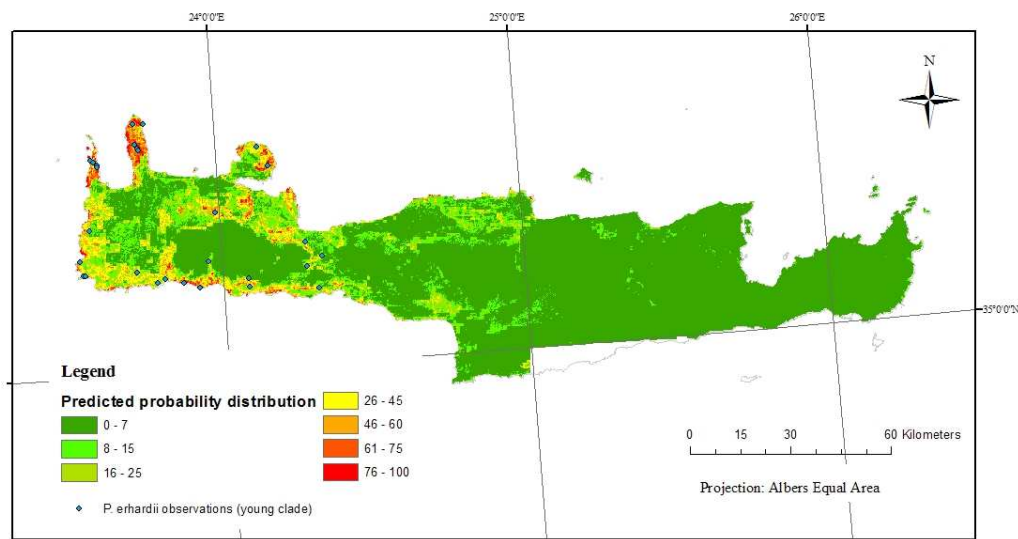
**Figure 10:** Variation partitioning of the seven vegetation types

**Table 9:** Independent effects of environmental variables for the seven vegetation types

Environmental variable	Independent effects (%)						
	Vegetation type						
	1	2	3	4	5	6	7
Altitude	38.9	19.7	41.4	26.5	12.7	60.4	26.3
Slope	8.0	5.3	7.7	3.1	3.2	39.6	14.1
Isothermality	14.9	6.6	24.6	45.9	---	---	6.0
Actual evapotranspiration	19.0	8.7	8.3	24.4	84.1	---	53.6
pH	1.3	---	9.3	---	---	---	---
EC	10.9	---	1.2	---	---	---	---
Ca	---	---	3.8	---	---	---	---
Mg	2.0	39.6	3.6	---	---	---	---
Na	4.9	14.5	---	---	---	---	---
K	---	5.8	---	---	---	---	---

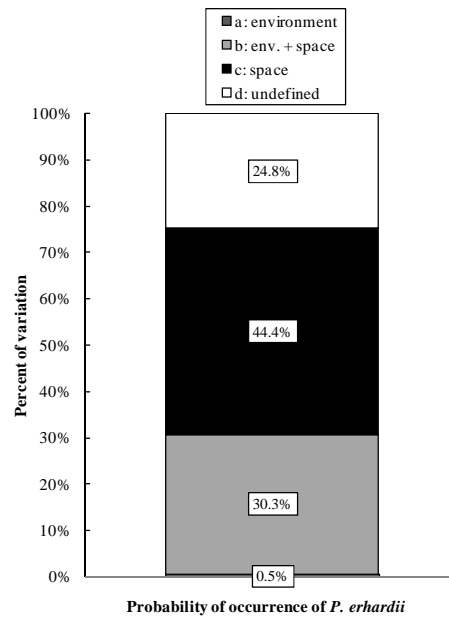
### 3.3.2. Spatial heterogeneity of *Podarcis erhardii*

Two approaches were followed to examine the contribution of the environmental variables and the spatial structure in *P. erhardii*'s spatial heterogeneity, using Borcard's method. Both of them used the predicted probability of occurrence of each sampling site as the dependant variable obtained with Maxent (figure 11). The spatial matrix was build with the location (x and y coordinates) of the 107 sampling sites (part 'c' in Borcard's method).



**Figure 11:** Predicted probability of occurrence of *P. erhardii* (young clade). AUC: 0.971. Regularized training gain = 1.762

In the first approach the spatial patterns of the probability of occurrence of *P. erhardii* are explained by the prevailing vegetation types obtained with TWINSpan. The resulting partition of the variation is shown in figure 12. The overall explained amount of variation was 75.2% of *P. erhardii*'s probability of occurrence. The vegetation types explained 30.8% (parts a+b in figure 12) of the variation, where the spatially structured environmental contribution (b in figure 12) was 30.3%, while the pure environmental contribution was low (0.5%), though significant.



**Figure 12:** Variation partitioning of the predicted probability of occurrence of *P. erhardii* evaluated with the seven vegetation types

The contribution of each vegetation type to the probability of occurrence of *P. erhardii* is shown in table 10. It can be seen for example, *B. pseudodictamnus* (vegetation type 5) is the group which explains the most (27.2%) of the environmental variation.

**Table 10:** Independent effects of the seven vegetation communities in the probability of occurrence of *P. erhardii*

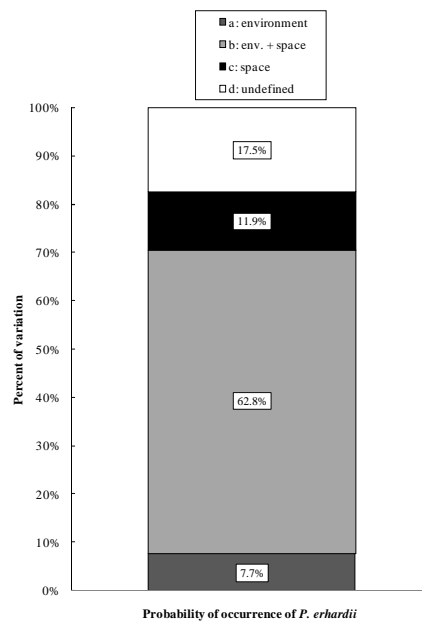
Vegetation type	Independent effects (%)
1	15.3
2	5.2
3	16.2
4	10.4
5	27.2
6	16.2
7	9.5

From figure 12 it can also be seen that the contribution of the pure spatial component (part c) was fairly large (44.4%) and significant ( $p < 0.005$ ). High (c) may be caused by environmental factors that were not included in the analysis, or by historical processes, or by environment-independent processes (like biotic factors such as reproduction or predation) (Borcard *et al.*, 1992). The proportion of fraction (c) in the model can be reduced by including other environmental variables that affect the subject of study, followed by recomputing the model (Borcard and Legendre, 1994).

Therefore, in the second approach the probability of occurrence of *P. erhardii* was examined including other environmental factors in the set of explanatory variables besides the vegetation types. The resulting environmental variables (based on previous investigations in lizards) included the seven vegetation communities, structure (in terms of cover percentage) of the sampling sites, soil parameters, actual evapotranspiration, isothermality, altitude and slope.

The results of the variance partitioning showed that local variations in the environment (part a) and the spatially structured environmental contribution (part b) explained 70.5% of the total variation in the predicted probability of *P. erhardii*'s occurrence (figure 13). From this fraction the 62.8% was predicted by the geographical coordinates of the sampling sites (part b), which is the spatial structuring in the probability of occurrence of *P. erhardii* shared by the environmental variables.

The contribution of the pure spatial component (part c) was lower than in the first approach (11.9%), which means that adding new environmental variables helped understanding better the processes in the probability distribution of *P. erhardii*. The unexplained variation was relative low (17.5%).



**Figure 13:** Variation partitioning of the predicted probability of occurrence of *P. erhardii*

From the hierarchical partitioning analysis of the relative importance of individual explanatory variables, actual evapotranspiration was the best explanatory variable of the pure environmental contribution. Other variables as pH and *B. pseudodictamnus* community were also good explanatory predictors (table 11).

**Table 11:** Independent effects of the environmental variables in the probability of occurrence of *P. erhardii*

Environmental variable	Independent effects (%)
pH	7.2
EC	3.7
Ca	2.1
Mg	6.0
Na	5.6
K	0.5
Vegetation type 1	3.8
Vegetation type 2	1.3
Vegetation type 3	4.1
Vegetation type 4	2.6
Vegetation type 5	6.8
Vegetation type 6	4.1
Vegetation type 7	2.4
Tree cover (%)	2.9
Shrub cover (%)	2.3
Minishrub cover (%)	1.7
Herbs cover (%)	3.1
Litter cover (%)	4.4
Bare soil cover (%)	5.8
Stones cover (%)	1.4
Rock cover (%)	3.5
Actual evapotranspiration	14.7
Isothermality	5.0
Altitude	3.5
Slope	2.0

## 4. Discussions

### 4.1. Vegetation types within the NDVI classes

In the 107 sampling sites of the three NDVI classes, a total of 49 species were identified, representing 25 families. Woody perennials (shrubs and mini-shrubs) dominated in the area (80%), while herbs only constituted about 7% of the recorded species. The exclusion of the not significant species resulted in a considerable decrease of the species used for the next analysis, which summed only 55% of the initial 49 species. Compared with the high presence of plants reported in Crete (Yale University, 2005), this study only gathers 3% of it in the selected study area.

On the basis of species constancy and characteristic species seven vegetation types were classified with TWINSpan (table 3). Vegetation types *Phlomis lanata* and *Pistacia lentiscus* were found mainly in NDVI class 11 (67% and 56% respectively). This class is characterized mainly by low altitude sampling sites, with the highest rates of evapotranspiration and the lowest precipitation (see table 5); in the other hand, Ca, Mg, Na and K values in the soil samples were the highest. The high values can be attributed to the proximity to the sea, as it can be seen in figure 8.

Vegetation type *Phlomis lanata* is mainly present in the eastern and central Crete (see figure 9) except for one point which is placed in class 13 and thus could be considered an outlier. The spatial distribution of vegetation type *Pistacia lentiscus* coincides with the description of Papiomitoglou (2006) for the most abundant species.

In general, in vegetation types 2 and 3 in one hand, and vegetation types 4 and 5 in the other hand maquis (evergreen sclerophyllous species like *Q. coccifera*, and *E. manipuliflora*) and phrygana (seasonal dimorphic plants like *S. spinosum*) occur together which is consistent with previous studies (Monokrousos *et al.*, 2004).

Vegetation type *Sarcopoterium spinosum* could be an indicator of post-fire activities, abandoned fields or overgrazed areas (Hill *et al.*, 1998). As it can be seen in figure 9, it is mostly absent in western Crete, however, this phrygana could be found all over the island (Papiomitoglou, 2006). This vegetation type was found mainly in the NDVI class 15. In this class tree cover and shrubs (>0,5m high) cover was the highest, which may explain the higher value in the vegetation index.

Vegetation type *B. pseudodictamnus* was found mainly in the central and western part of the island, where species like *Q. coccifera*, *R. saxatilis* and *S. spinosum* were also present. It can be found more than 50% of the times in the NDVI class 13, which is present in the highest altitudes, thus highest annual precipitation and coldest temperatures compared to the other classes. In the contrary, this NDVI class was characterized by the lowest values in the soil parameters. This vegetation type was also found for the western part in a previous study (Boteva *et al.*, 2004).

The main species that integrated *C. vilosa* socioecological group were besides *C. vilosa*, *G. acanthoclada* and *A. aphyllus*. This species were present in the seven vegetation types and distributed along the island, which also corresponds with Hill *et al.* (1998).

*Q. coccifera* vegetation type was mainly found in the central and western Crete, however as in the case of vegetation type *A. hermanniae* (found mainly in the West) few sampling sites were classified in these vegetation types, 8% and 3% respectively. As discussed in the limitations of the study (see 4.4) additional information for the western part of the island may complement these findings.

## 4.2. Partition of the variation in the prevailing vegetation types

Plant species living in separate places, but under similar environmental conditions or sharing similar historic conditions, show common structures. Additionally, the abundance of one species reflects that certain biological and physical conditions are met, so that it can be present (Johnson, 1973). To evaluate the contribution of the selected environmental factors and the spatial structure which affect the variability of the seven vegetation types identified by TWINSpan, the Borcard's method was applied.

The first three vegetation types, namely *Phlomis lanata*, *Pistacia lentiscus* and *Rhamnus saxatilis* – *P. phlomis cretica* showed the higher portion of the variation explained by the environmental variables considered in this study, though small (8%, 11% and 22% respectively).

In *P. lanata* vegetation type the spatial contribution (fraction 'c') is relative high in the explained variation, which shows that some fundamental processes (e.g. biotic factors) or local effects were not included (Borcard *et al.*, 1992).

In *P. lentiscus* vegetation type the explanatory variable which explains almost the 40% of the variation in the pure environmental fraction is the content of magnesium (see table 9). This is congruent with the results found in the field (table 6), where the highest amount of magnesium was found in this group. This vegetation type was the only one correlated to the content of potassium even though the content of potassium in the places where this vegetation type was found was one of the lowest. This result coincides with a study held in one Mediterranean coast of Turkey where the species *P. lentiscus* showed preferences for low potassium contents in the soil. That study found also that *P. lentiscus* was correlated with different content of calcium (Dogan *et al.*, 2003). From table 8 it can be seen that the content of calcium and magnesium was positive and moderately correlated, so it can be also inferred that this group shows preferences for this type of soil.

The pure environmental fraction in *Rhamnus saxatilis* - *Phlomis cretica* vegetation type explained almost 22% of its variation. In this fraction, altitude and isothermality accounted for more than the 65% of the variation. The variation in the altitude can be explained in terms of the species that composed this vegetation type; while *P. cretica* is found mainly in lowland and middle altitudes, *R. saxatilis* is found in higher altitudes (Chatzaki *et al.*, 2005). Comparing this vegetation type with the others, it can be seen that the increase in altitude is strongly correlated to the increase of precipitation and low temperatures (table 8), characteristic also found in the Mediterranean region (Aschmann, 1973).

The highest fraction of the explained variation in *Sarcopoterium spinosum* and *Ballota pseudodictamnus* vegetation types was the spatial structuring shared with the environmental variables (part b). This common variation between the spatial components and the environmental variables may result of the relation of the vegetation types with some "external space-structuring processes". In this case, the vegetation types share a similar spatial structuring with the environmental variables, which can be explained by some common underlying causes (Borcard *et al.*, 1992). For instance the actual evapotranspiration in vegetation type *B. pseudodictamnus* which shows a gradient along the island.

The spatial pattern of the vegetation type *Quercus coccifera* was only significant with topographic variables. Surprisingly the soil variables did not explain the variability of this group whereas they found to be correlated for example in the South of France (Lossaint, 1973). The high value of fraction 'c' could be attributed to certain environmental factors that were not included in the study which may have increased the explain variation of this vegetation type (Borcard *et al.*, 1992).

The variation in the vegetation type *Anthyllis hermanniae* was explained by the climatic and topographic variables only in 4.7%. The actual evapotranspiration accounted for more than the 50% in



the contribution to the pure environmental variability (table 6), which is the lowest value compared to the other vegetation types, and also related to the western part of the island.

Even though, many studies have found positive and significant correlations between vegetation types and soil properties, in this research only three of the plant communities were explained partly by these parameters (Abbadi and El-Sheikh, 2002; Abd El-Ghani and Amer, 2003; Dogan *et al.*, 2003; Jafari *et al.*, 2004; Monokrousos *et al.*, 2004; Vogiatzakis *et al.*, 2006). This suggests that other environmental variables may structure the vegetation types found in the selected NDVI classes or that processes like disturbance prevail in the vegetation distribution (Abd El-Ghani and Marei, 2007).

In general, the unexplained variation (fraction d) was very high in all the vegetation types. This can be attributed to other local environmental variables besides the ones included in this study, that explain better the spatial structure of the vegetation. Additionally, some other spatial structures that have been missed could also play an important role in the distribution of these vegetation types (Borcard *et al.*, 1992). However, a high fraction 'd' can also be attributed to sampling error (He *et al.*, 1996), which could have affected significantly the results (see section 4.4)

In the present study the spatial matrix which explained the spatial patterns was built only with the location of the sampling points (their geographic coordinates). A way of improving the results could be adding to this two-dimensional matrix all the terms of a cubic trend surface regression, to capture not only the effect of linear gradient patterns, but also the quadratic and cubic terms of the coordinates which may describe more precisely features like patches or gaps (Borcard *et al.*, 1992; Legendre, 1993).

### **4.3. Variation of the probability of occurrence of *P. erhardii***

#### **4.3.1. Vegetation types and spatial structure**

In most habitats vegetation types influence on the distribution of animal species (Johnson, 1973). Studies on reptiles' distributions showed high correlation with soil properties and soil-vegetation relation (Castellano and Valone, 2006; Pianka, 1967; Pianka, 1989; Pianka and Pianka, 1970). Therefore, the first approach to explain the spatial distribution of *P. erhardii* was to correlate its probability of occurrence with the vegetation types found in the selected NDVI classes.

The results show that both the environmental variables (in this case the seven vegetation types) and the spatial structure (the geographic coordinates) explained significantly ( $p < 0.05$ ) the variation in the probability of occurrence of *P. erhardii*. However, the pure contribution of the vegetation types was very low (0.5%), while the spatially structured environmental contribution (fraction b) was 30.3%.

The contribution of the vegetation type *B. pseudodictamnus* to the pure environmental fraction was the highest (27.2%). As seen previously (table 3), this vegetation type was composed by the following socioecological groups: *Q. coccifera*, *S. spinosum*, *E. dendroides*, *R. saxatilis*, *P. cretica*, *B. pseudodictamnus* and *C. vilosa*. Some studies done in the feeding ecology of *P. erhardii* also found that *P. erhardii* was present in vegetation which was mainly maquis and phryganic, including species like *Q. coccifera*, *P. lentiscus*, *O. europea* var. *sylvestris*, and *Thymus sp.*, *Genista sp.* and *S. spinosum* respectively (Valakos, 1986; Valakos *et al.*, 1997).

The environmental conditions that describe *B. pseudodictamnus* vegetation type differentiate them significantly from the others mainly in terms of soil properties and climatic variables (see table 6). This group has the lowest concentrations of calcium, magnesium and sodium; on the contrary the highest concentration of potassium. The actual evapotranspiration and the mean annual temperature found in the sampling sites that hold this vegetation type are one of the lowest.

Figure 9 shows that *B. pseudodictamnus* vegetation type is mainly present in the central and eastern part of Crete, which coincides with the presence of *P. erhardii* in the two western peninsulas (Gramvoussa and Rodopos).

The contribution of the pure spatial component (part c) to the variation of the probability of occurrence of *P. erhardii* was quite large (44.4%). As discussed previously this fraction was mainly caused by environmental factors that were not included in the analysis (Borcard *et al.*, 1992) as it was shown in section 3.3.2. The spatial patterns of animals (or plants) can be better explained as a combination of different environmental variables which contribute to their variability (Pianka, 1989).

#### 4.3.2. Environmental variables and spatial structure

In a second stage, the probability of occurrence of *P. erhardii* was examined including as environmental parameters the seven vegetation communities, cover structure (percentage) of the sampling sites, soil parameters, actual evapotranspiration, isothermality, altitude and slope. The spatial matrix was build with the location ( $x$  and  $y$  coordinates) of the 107 sampling sites.

The environmental variables explained 70.5% of the variation in the spatial distribution of the probability of occurrence of *P. erhardii*. Almost 90% of this fraction was predicted by the geographical coordinates of the sampling sites, which means that the probability of occurrence of *P. erhardii* and the environmental variables have a similar spatial structuring. This can result in part from the same response to some underlying causes (e.g. humidity gradient), or that the probability of occurrence of *P. erhardii* may vary spatially as a function of the environmental variables in the model (Borcard *et al.*, 1992; He *et al.*, 1996). The other 10% of this fraction was explained by the environmental variables which did not show any spatial pattern.

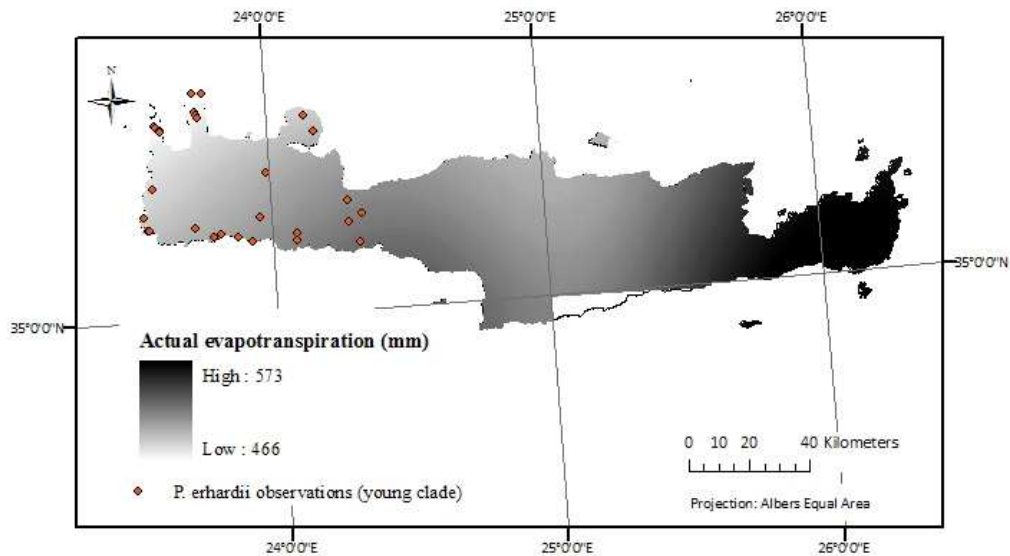
Form the hierarchical partitioning analysis of the relative importance of individual explanatory variables, actual evapotranspiration was the best explanatory variable. Figure 14 shows that the actual evapotranspiration is lower in the western part of the island and increases gradually to the east. This climatic variable is related negatively with precipitation and isothermality (table 7), which means that in regions with low values of evapotranspiration, precipitation and isothermality (ratio of the mean diurnal range and the temperature annual range) are higher.

The results of this research are similar to the findings of Olalla-Tarraga *et al.* (2006), who explored the geographical patterns of lizards due to body size and environmental gradients, and found that the potential evapotranspiration was the best predictor (Olalla-Tarraga *et al.*, 2006). In addition, Quian *et al.* (2007) found that reptiles' richness was strongly associated with environmental variables representing energy (e.g. temperature and actual evapotranspiration), productivity and water.

Vegetation type *B. pseudodictamnus* explains almost 7% of the environmental variation of the probability of occurrence of *P. erhardii* (table 7). As seen previously this vegetation variable was also influenced by the actual evapotranspiration and had a high fraction 'b' in Borcard's method. This result may be indicating that vegetation type *B. pseudodictamnus* and the probability of occurrence of *P. erhardii* result from similar response to gradients in humidity.

The pure spatial fraction 'c' was reduced from 44.4% to 11.9% by including other environmental factors beside the vegetation types. The small remain portion (11.9%) indicated that almost all the spatial-structuring process had been included. As discussed before, this result could be further improved by adding to the two-dimensional matrix (geographic coordinates) all the terms of a cubic trend surface regression (Borcard *et al.*, 1992; Legendre, 1993).

The unexplained variation (fraction d) is quite small (17.5%), which means that the variation of the probability of occurrence of *P. erhardii* was fairly explained by the environmental variables and the geographic coordinates of the sampling sites, considered in this study.



**Figure 14:** Actual evapotranspiration in Crete and *P. erhardii* observations

The probability of occurrence of *P. erhardii* obtained with Maxent (using the 28 observations of the young clade) showed that the model performed well on the training data with an AUC of 0.971. The Jackknife analysis to test the performance of the environmental variables (Appendix F) showed that for the probability of occurrence of *P. erhardii*'s young clade, the best environmental predictors were the actual evapotranspiration and the multi-temporal NDVI.

Previous studies show that NDVI is correlated to climatic variables such as rainfall (Justice *et al.*, 1986) and thus in this study evapotranspiration, which emphasizes the importance of this variable in *P. erhardii*'s distribution. Moreover, the vegetation type *B. pseudodictamnus* found in NDVI classes with the highest number of observations of *P. erhardii* was also correlated with evapotranspiration, which suggests that NDVI could be proxy of this climatic variable and this particular vegetation type in this study (Leyequien *et al.*, 2007; Pettorelli *et al.*, 2005).

The results of this study provide information of a possible natural barrier that can be constraining *P. erhardii*'s distribution to the Western part of Crete. However, some issues have to be considered before making absolute conclusions. The relict population in the main island date back from 5.2Mya when the eastern part of Crete was separated from the main island (a good explanation of this historic events related to *P. erhardii* can be found in Poulakakis *et al.*, 2005). In the other hand, the population of the eastern islets dates form 2.3Mya. So, the only possibility was the colonization of the relict clade to the whole island, including the islets in the East, and then further extinction of *P. erhardii* in the East and Central part of Crete (Poulakakis *et al.*, 2005).

This fact raises two main questions: why they were extinct? And if they were extinct in the Central and Eastern part of the main island, why the remaining population inhabiting the West didn't recolonize it? The first question can be answered by the effects of human influence which was and is evidently higher in the Central and Eastern Crete, for thousands of years by ancient and modern civilizations (Tzatzanis *et al.*, 2003). Additionally, residuals of volcanic activity could also impact on the presence of *P. erhardii* if this was stronger in the Eastern and Central part of the island, because animal species that can live in areas with similar climate and plant structures should differ on historic events upon them (Pianka, 1973). However, this subject in Crete is in constant debate (Keenan, 2003). The second question, could be answered if there are natural barriers (such as the evapotranspiration gradient) which restricts the realized niche of the species, and simply they won't pass them because they are cannot survive in those environments. Or it is related to *P. erhardii*'s dispersal abilities

(Wagner and Fortin, 2005) (e.g. locomotion) and just a matter of time till they cross the “frontier”. These questions leave open the doors of further research.

#### 4.4. Limitations of the study

##### Sampling design

The sampling design was based in two assumptions. In the first one, the relict (5.2Mya) and young (2.3Mya) *P. erhardii*'s populations of the main island were separated based on the geographical site of samples taken in the study of Poulakakis *et al.* (2003). However, as it can be seen in figure 3 there is an overlap of the young and old populations in the south-western part of the island, so an arbitrary limit at 800 m altitude was taken in the study. Thus, the results might not only correspond to the young clade, but also to the relict population that cannot be differentiated (because there is not enough information yet according to Lymberakis, 2007) in that specific area. Nevertheless, the environmental conditions in the area where the specimens were found represent the habitat requirements of *P. erhardii* and should not affect the results found in the present study.

The second assumption is that the NDVI classes that were selected based on the observations of the young clade of *P. erhardii*, reflected the most the species niche requirements (the range of environmental variables within a species can survive and reproduce) (Hirzel *et al.*, 2006). In this sense, as the classes were distributed along the island, it was assumed that they could be used to find differences between the West (where in a wide sense *P. erhardii* is present) and the rest of the island. However, as it can be seen in figure 7 (and figure 5) the species is also present in other NDVI classes, and a group of observations which occur in the frontier of *P. erhardii*'s distribution were not represented in the study. Even so, those observations fell in classes 17, 23 and 24, which are not evenly distributed along the island, and would have not been useful for the objectives of this study. Though, a further research that looks in the local conditions of this border in *P. erhardii*'s distribution might give insights of the limiting factors that affect this species.

To collect information in the field, sampling points were allocated randomly in the selected NDVI classes. By using random sampling biases on the selection of sample sites were avoided (Edwards *et al.*, 2006). However, two main drawbacks were identified in the study due to the use of this approach in the survey sampling. The first one is related to the uneven distribution of the sampling points (see figure 8), where the eastern part of the island was oversampled compared to the western part. On the other hand, making a distinction in the island between West, Center and East would have brought other biases, simply because nature processes are subject of many forces that may not behave in our conception of where to place those geographic limits (Whittaker *et al.*, 2001). In this study generality and may be also realism were sacrificed on behalf of simplicity (Edwards *et al.*, 2006).

The second drawback is related to mixed pixels in the NDVI classes, due to the coarse resolution (~1 km<sup>2</sup>) of the SPOT images. Because the pixels included many different features (Cracknell, 1998; Fisher, 1997), random selected sampling points in some cases failed in “undesirable” places, such as water bodies, roads, greenhouses, etc. In those cases, the points were replaced to the nearest suitable areas, though including some how bias because of the selection of sample sites (Edwards *et al.*, 2006). Many approaches have been proposed to work with mixed pixels, usually higher spatial resolution imagery, or ancillary data or new; see for example (Busetto *et al.*, 2008; Rocchini, 2007). In the future, to improve the sampling design one of these approaches could be used in the NDVI SPOT times-series.

Another aspect that should be reconsidered is the effect of the plot size or data resolution, which is the size of the sampling unit (Austin, 2007; Austin, 2002). In the survey some plant species may not have been fully represented due to size of the sampling unit causing bias and overestimation of the differences between sampling sites. However, the “minimal area” (minimum area where the vegetation type is adequately represented) recommended for shrubs and grass in template-zones vegetations fluctuate between 25–100m<sup>2</sup> (Mueller-Dombois and Ellenberg, 1974). Moreover, in the study of Vogiatzakis *et al.* (2006) about the vegetation composition in the Lefka Ori massif the area, the data resolution was between 100-500m<sup>2</sup>, smaller than the 700m<sup>2</sup> considered in this study, which suggests that all plants in the vegetation type should be adequately represented in the assumed data resolution.

The field survey was done from the 18th of September to the 3rd of October. This was not the best period to identify plant species, because they are beginning the dormancy period, which may have affected their correct identification. However, this variable was out of this research’s control. For further studies a better time could be between March and April, when the plants are expected to be growing (Abbadi and El-Sheikh, 2002).

### **Analysis methods**

TWINSPAN is widely used method in vegetation community (Jongman *et al.*, 1995; Legendre and Legendre, 1998). However, some critics to the method include failures identifying secondary gradients, the arbitrary selection of the cutting points and the use of detrended correspondence analysis (DCA) (Legendre and Legendre, 1998). Other methods like the Unweighted Paired Groups Using Arithmetic Averaging (UPGMA) have been commonly recommended for clustering analysis; nevertheless, in some cases TWINSPAN performs better than UPGMA (Cao *et al.*, 1997).

Partitioning the variation using redundancy analysis (RDA) or canonical correspondence analysis (CCA) as in Borcard’s method involve with similar problems as found in linear regression (Wagner and Fortin, 2005). This method is continually being improved and a further research could include these new suggestions (Borcard *et al.*, 2004; Legendre *et al.*, 2002).



## 5. Conclusions and recommendations

### Conclusions

1. Seven differentiable vegetation types were identified with TWINSpan in the selected NDVI classes, which held the highest number of *P. erhardii*'s observations.
2. The spatial structure of the seven vegetation types was assessed partitioning their variation in four fractions: pure environmental, environmental and spatial, pure spatial and undetermined. The seven vegetation types were correlated differently to the environmental variables included in the study. While some were affected by soil factors (e.g. vegetation type 2), others (vegetation types 5 and 6) were just correlated to topographic variables. The spatial pattern of the vegetation types assessed by environmental variables and the geographic coordinates was mostly unpredictable.
3. Partitioning the variation of the probability of occurrence of *P. erhardii* into environmental (seven vegetation types) and spatial (geographic coordinates) components explained 75.2% of the overall variation.
4. The inclusion of additional environmental variables increased the explained variation of the probability of occurrence of *P. erhardii* to 82.5%, and suggested that the spatial structure of *P. erhardii* and the environmental variables have a similar spatial structuring (a humidity gradient shown by the actual evapotranspiration). This result provides information of a possible natural barrier that can be constraining *P. erhardii*'s distribution to the Western Crete.
5. Understanding the processes that structure *P. erhardii*'s distribution in Crete is an essential tool for its protection and conservancy.

### Recommendations

In general terms, it is recommended to study the variation in the probability of occurrence of *P. erhardii* by spatial structuring and environmental explanatory variables of the relict population that inhabits the mountains Lefka Ori, where information on vegetation types is available (Vogiatzakis *et al.*, 2006). Additionally, study the variation of the population that inhabits the islets in the East.

A similar study could explore the variation in the presence-only observations (NHMC, 2006) by spatial structuring and environmental explanatory variables, paying special attention to the effect of the evapotranspiration gradient in the locations where *P. erhardii* was observed.

In the other hand, as discussed previously, the matrix of two-dimensional geographical coordinates,  $x$  and  $y$ , could be completed as suggested by (Legendre, 1993) by adding all terms for a cubic trend surface regression to describe better more complex features rather than linear gradient patterns.





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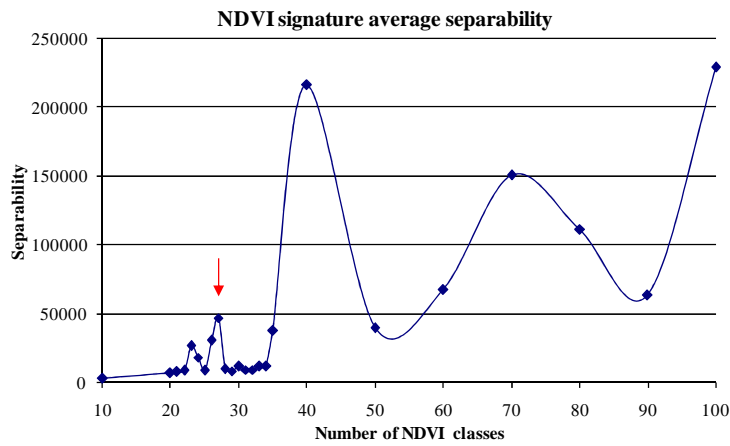
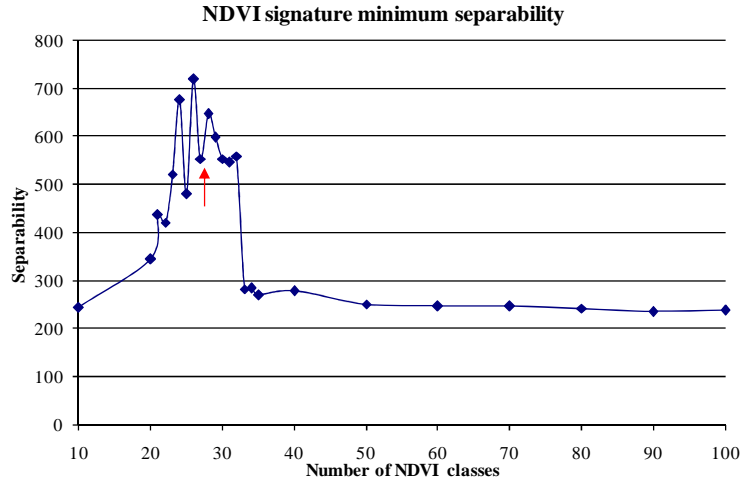
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## 7. Appendices

### Appendix A: List of observations specimens of *P. erhardii*. Source (NHMC, 2006)

No	POINT_X	POINT_Y
1	2619538	3930805
2	2619677	3926226
3	2620422	3925965
4	2620544	3926421
5	2621222	3926381
6	2623431	3939710
7	2625559	3960502
8	2626485	3959956
9	2627788	3958947
10	2627820	3958342
11	2640142	3926533
12	2641929	3970372
13	2642332	3964444
14	2643014	3963360
15	2643314	3962542
16	2645682	3970183
17	2647655	3923260
18	2650367	3924076
19	2657290	3922658
20	2662984	3921029
21	2666901	3928676
22	2670515	3942998
23	2676898	3928567
24	2677676	3927250
25	2677736	3928288
26	2677929	3928527
27	2677929	3928527
28	2678661	3928712
29	2681061	3923137
30	2681332	3920336
31	2681340	3922766
32	2681387	3926088
33	2681429	3926661
34	2682576	3924025
35	2683056	3923409
36	2683297	3925289
37	2683498	3923994
38	2685389	3923901
39	2687294	3961320
40	2688447	3950588
41	2691048	3955770
42	2699796	3924840
43	2702612	3924241
44	2702728	3932568
45	2702929	3925193
46	2706852	3918525
47	2708625	3928022
48	2804680	3945850
49	2805299	3945934
50	2805707	3946105
51	2807572	3946018
52	2807775	3945585
53	2807937	3945530
54	2807953	3945184
55	2860687	3882604
56	2865795	3882388
57	2908355	3890312
58	2908565	3890991
59	2908896	3887218
60	2909030	3891521
61	2910026	3890097
62	2913710	3938134
63	2913710	3938134
64	2914179	3934800
65	2914220	3936078
66	2914191	3934294
67	2920560	3899573
68	2931543	3926580
69	2932114	3926579

### Appendix B: Number of NDVI classes selection



**Selection:** More or less half-way the range of the high minimum separability and at the small peak of the average separability



**Appendix C:** Example of the relevé sheet used in the fieldwork

<b>Sample sheet</b>			
<b>General information</b>			
Date:		Sample N°	
Time:		NDVI class	11 / 13 / 15
X:		P. erhardii	Y / N
Y:			
Exposure:		Weather conditions:	
Overall unit:			
Remarks:	Natural	Seminatural	Agricultural
	Humanmade		
<b>On the spot</b>			
	Cover (%)		Picture num.
Tree ( m)			
Shrub (0,5- m)			
Minishrub (0-0,5m)			
Herb			
Litter			
Soil		Type:	Color:
Stones		Type:	Color:
Comments			

**Appendix D: Example of some plant species identified in the field**



*Coridothymus capitatus*



*Asparagus aphyllus*



*Calicotome vilosa*



*Sarcopoterium spinosum*



*Urginea maritima*

**Appendix E: Plant species used in the synoptic table resulted from the vegetation classification**

<b>No</b>	<b>Species</b>
1	<i>Teucrium brevifolium</i>
2	<i>Satureja thymbra</i>
3	<i>Erica manipuliflora</i>
4	<i>Pyrus spinosa</i>
5	<i>Osyris alba</i>
6	<i>Salvia pomifera</i>
7	<i>Phlomis lanata</i>
8	<i>Euphorbia acanthothamnos</i>
9	<i>Quercus coccifera</i>
10	<i>Pistacia lentiscus</i>
11	<i>Coridothymus capitatus</i>
12	<i>Urginea maritima</i>
13	<i>Asphodelus aestivus</i>
14	<i>Sarcopoterium spinosum</i>
15	<i>Euphorbia dendroides</i>
16	<i>Rhamnus saxatilis</i>
17	<i>Phlomis cretica</i>
18	<i>Smilax aspera</i>
19	<i>Ballota pseudodictamnus</i>
20	<i>Stachys spinosa</i>
21	<i>Anthyllis hermanniae</i>
22	<i>Carlina graeca</i>
23	<i>Genista acanthoclada</i>
24	<i>Calicotome vilosa</i>
25	<i>Cistus creticus</i>
26	<i>Olea europaea</i>
26	<i>Asparagus aphyllus</i>

**Appendix F: Jackknife test of regularized training gain for young clade of *P. erhardii*, run in Maxent**

