

# Species response curves of oak species along climatic gradients in Turkey

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**Abstract** The genus *Quercus* is one of the most important tree species in Turkey. However, little is known on the ecological preferences of Turkish oak species regarding climate. We analyzed species response curves using a HOF-model approach to describe the general pattern of oak distributions along climatic gradients and to identify the driving climatic factors for eight oak species in Turkey. While climate data were extracted from the free available worldclim dataset, occurrence data on oak species were assembled from the literature into a vegetation database ( $n=1,104$ ). From the analyzed species response curves, only few (16%) showed unimodal responses, while most were linear (31%) or exhibited a threshold response (31%). The driving factors were seasonality of temperature and seasonality of precipitation, indicating that Turkish oak species can be characterized best by the preference of climatic stability. These findings have important implications for conservation and climate change research, which usually focuses on trends of the mean values of temperature or precipitation but less often on the seasonality. In this study, we further tested whether niche optima derived from raw mean values of occurrences could replace missing model optima due to non-responsiveness of HOF models of type I. However, we

did not find this to be a satisfactory solution. Finally, we discuss the need for the construction of a national database based on phytosociological relevés for Turkey.

**Keywords** *Quercus* · HOF model · Stability · Seasonality · *Mediterranean*

## Introduction

The genus *Quercus* is one of the most abundant and economically important genera of woody plants within the family *Fagaceae* in the northern hemisphere. *Quercus* comprises approximately 500 species of trees and shrubs that occupy a diverse array of habitat and climate types (Manos et al. 1999). In Turkey, the total forest area is around 211,000 km<sup>2</sup>, of which one-third belongs to oak forest (Çolak and Rotherham 2006; Mayer 1986).

As an economically important genus in Turkey, *Quercus* is used for coppice, timber, secondary products from acorns, for erosion control and for fodder (Borelli and Varela 2000). However, it is also one of the very problematic genera within the flora of Turkey. First, many Turkish species are heavily grazed, cut for fuel or otherwise represented by deformed specimens. In some areas, no fruiting specimen can be found. Furthermore, widespread hybridization and introgression have complicated the conservation of oaks in Turkey. In order to preserve oak species, several in situ conservation projects for Turkish oak species have been started, i.e. by creating national parks, seed stands or gene conservation forests (Bozzano and Turok 2002).

Much work has been done on the taxonomy of oak species in Europe and the Middle East (Camus 1934–1954; Kotschy 1858–1862; Menitsky 1984; Schwarz 1936, 1937; Zohary 1966). These studies diversified the genus *Quercus*

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and divided it into several subspecies and varieties. After a taxonomical revision of the Turkish oaks, their number decreased from 35 to 18 (Yaltirik 1984). Recent studies identified new subspecies, increasing the number of Oak taxa in Turkey again (Zielioski et al. 2006). Although the taxonomical situation of Turkish oak species has been mostly clarified over recent decades (Uğurlu and Senol 2005), few insights were gained regarding the ecological preferences of Turkish oaks (Özel 2002).

Presently, ecological studies on oak species in Turkey have mostly concerned general characterizations and syntaxonomical descriptions of oak forest types based on the Braun Blanquet approach (Adıgüzel and Vural 1995; Akman et al. 1978; Akman and İlarıslan 1983; Ketenoglu et al. 2010; Özen 2010). Only a few studies have analyzed the ecological niche of oak species in Turkey based on bioclimatic characterization, but see Dufour-Dror and Ertaş (2004) and Kargioğlu et al. (2009), or in growth experiments with *Quercus* seedlings (Fotelli et al. 2000). However, understanding the ecological requirements of a species is crucial for conservation efforts. Considering climate change effects, it is important to identify the relative importance of climatic parameters that determine the occurrence of a species on a regional scale (Kalusová et al. 2009), and to quantify the niche properties of a species which describe the physiological range and optimum along climatic gradients. This knowledge will allow conservationist to identify species-specific optimal conditions for conservation areas or seed storage in Turkey.

The responsiveness of a species to an ecological parameter can be described by statistical models that fit a regression model based on the occurrence of a species along an environmental gradient, leading to species-specific species response curves (Austin 1980, 1987). The Huisman–Olf–Fresco (HOF) model approach (Huisman et al. 1993), comprises a set of five hierarchically nested regression models with increasing complexity. The best-fitting model is identified as the most probable species response curve. Species response curves are often used to interpret species distributions along gradients (Chytrý et al. 2008) and are important tools in bioindication (Pepler-Lisbach 2008; Wamelink et al. 2005). Furthermore, these models allow for the quantification of niche parameters, such as the modeled species optimum (Jansen 2008a; Lawesson and Oksanen 2002; Oksanen and Minchin 2002).

In contrast to the modeled optimum, the raw optimum of a species along a gradient is simply the mean of all gradient values where the species occurred (Wamelink et al. 2005). Hence, it is always possible to identify an optimum. In contrast, HOF models of type I do not have a specific shape and thus also do not provide an optimum. Here, replacing the missing HOF model optima with raw optima could be a possibility to fill gaps for later analysis. However, to our knowledge, no study has yet tested the effectiveness of this approach.

We compiled a database on occurrences of Turkish oak species from existing literature. Here, we aim to analyze species response curves for Turkish oak species on major climatic gradients for the whole Turkey. In particular, we want to identify the response type of eight common oak species along six climatic gradients in Turkey using HOF models. Secondly, we want to quantify species optima along each gradient using two approaches: first, the raw optima of the species ranges, and second, the model optima derived from species response curves. Furthermore, we will use the raw optima to impute values for missing model optima and compare the effect when species are ranked according to the gradient positions of the optima, indicating if raw optima are suitable proxy measures for species optima. Finally, we aim at identifying the most important climatic gradient for each species in order to discuss potential threats due to climate change.

## Materials and methods

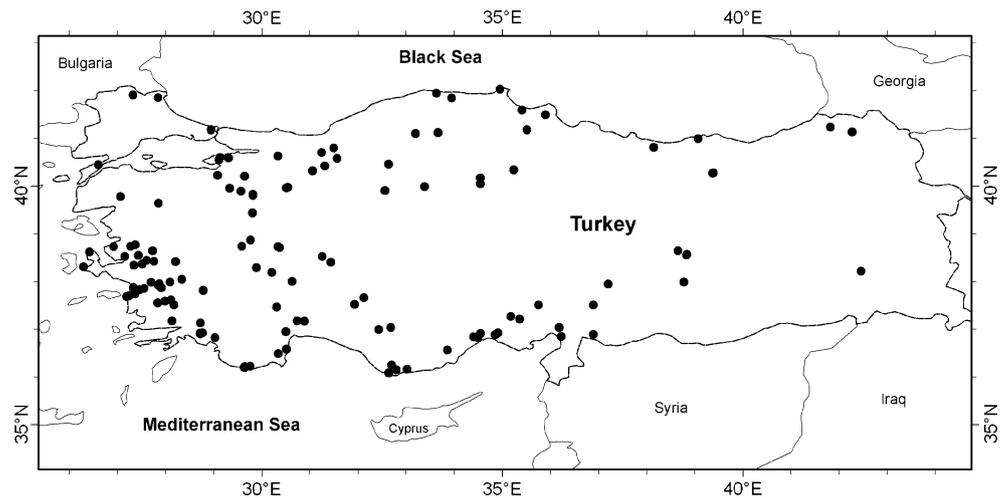
### Vegetation database and oak species distribution

We have compiled a database on the occurrences of Turkish oak species from existing literature (Appendix 1). Known coordinates and composition of the oak communities were entered directly into TURBOVEG software (Hennekens and Schaminée 2001). When coordinates were unknown for a sample, they were extracted from Google Map by using locality explanations found in the literature. In total, 1,182 occurrences localities of 18 oak species were mapped and stored in the database. However, we grouped occurrences of the same species within one raster cell of the worldclim dataset (Hijmans et al. 2005), i.e. three arc seconds, in order to avoid errors in the analysis. Furthermore, we limited the analysis to species with more than 30 occurrences in the final dataset leaving 1,104 oak community localities for analysis. The following oak species were considered for analysis: *Q. petraea* ssp. *iberica*, *Q. frainetto*, *Q. infectoria*, ssp. *boissieri*, *Q. infectoria*, ssp. *infectoria*, *Q. pubescens*, *Q. cerris*, *Q. ithaburensis* ssp. *macrolepis*, and *Q. coccifera* (Fig. 1).

### Climatic data

We extracted climatic information at the locations of all 1,104 oak community localities from the freely available bioclimatic variable dataset provided by the worldclim project (Hijmans et al. 2005). We selected five climatic variables that had either been previously used in studies with oaks or which we felt were the most suitable. These variables were annual precipitation ( $P_{\text{ann}}$ ), seasonality of precipitation ( $P_{\text{season}}$ ), annual mean temperature ( $T_{\text{mean}}$ ), annual minimum temperature ( $T_{\text{min}}$ ), and seasonality of

**Fig. 1** Distribution of the 1,104 vegetation relevés for oak communities that were used in this study. All localities were gathered from the literature (see Appendix 1)



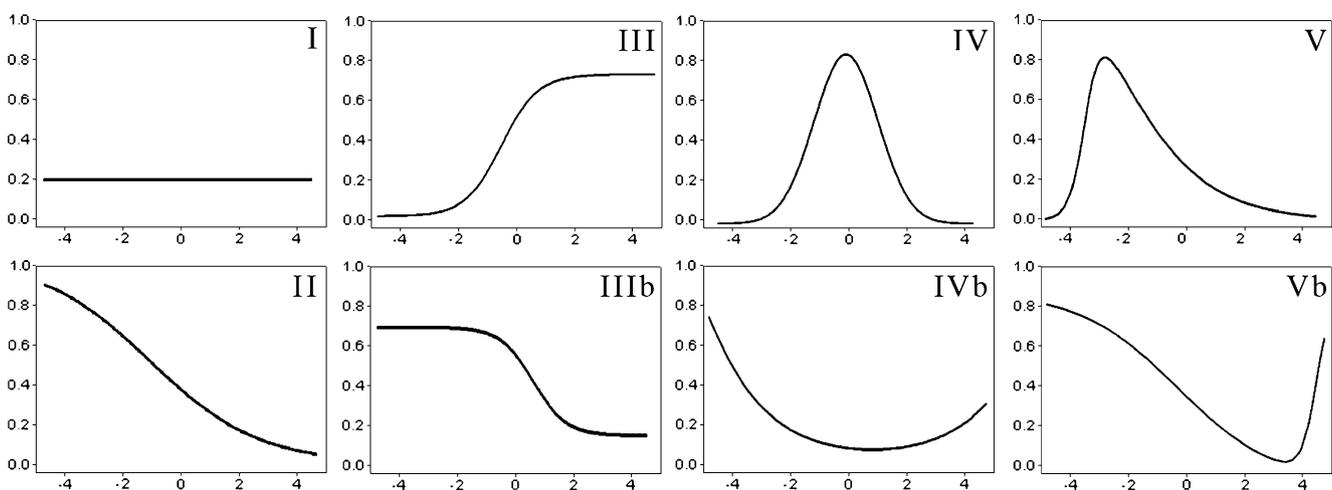
temperature ( $T_{\text{season}}$ ). A sixth climatic variable, dry season water deficit (DSWD), was calculated based on monthly worldclim data. We chose this parameter due to the observations of Dufour-Dror and Ertaş (2004), who found this to be an important descriptor for the severity of water limitation in the context of oak distribution. DSWD is expressed as water deficit in millimetres calculated as the amount of monthly rainfall (mm) minus the monthly potential evapotranspiration (mm). We calculated monthly potential evapotranspiration according to Turc's method which is the most suitable for the Mediterranean climate (Dufour-Dror and Ertaş 2004).

#### Deriving species responses with HOF models

In order to identify the ecological response of oak species to the climatic gradients, we modeled species response curves using the HOF approach (Huisman et al. 1993). Of a set of

hierarchical generalized linear models, the simplest best-fitting model was selected by comparing the models' information content using the Akaike Information Criterion (AIC). AIC is a combined measure of the goodness-of-fit and model complexity. The model with the lowest AIC is said to describe the best model (Burnham and Anderson 2002). HOF models not only allow for unimodal-symmetric responses similar to a normal distribution (Gauch and Whittaker 1972) but also for skewed and monotonous shapes of response curves. The latter types of response are particular frequent along gradients associated with environmental stress, or with species having optima close to gradient ends (Austin and Smith 1989; Rydgren et al. 2003; Normand et al. 2009).

Huisman et al. (1993) originally suggested five models of ascending complexity. Recently, Jansen (2008a) proposed additional types to reflect typical responses found in natural systems, here referred to as models IIIb, IVb and Vb (Fig. 2). The complexity of the eight models ranges from



**Fig. 2** Theoretical species response curves as proposed by Jansen (2008a). Roman numerals refer to the model types as used in the text

one to four fitted parameters. Model I (one parameter) describes no response along the studied gradient. Model II is monotone increasing or decreasing (two parameters). Model III is a threshold model showing an increase in occurrence probability after a certain value in form of a plateau (three parameters), whereas IIIb is simply a reversed model III. Model IV (three parameters) is symmetric-unimodal (normal distribution). Model IVb is a horizontally mirrored variant of model IV (three parameters). Model V describes an asymmetric unimodal response (four parameters), while model Vb is the skewed bimodal model (four parameters). HOF modeling was carried out using the package *vegdata.dev* (version 0.1, <http://geobot.botanik.uni-greifswald.de/download>) within the free statistical programming environment R (R Development Core Team 2010).

### Identifying important climatic drivers

We define the most important climatic driver as the one that best explains the distribution of a species along a gradient. Using an information theoretic approach for model selection, we compared all best species response models for a certain species along all climatic gradients based on Akaike weights ( $w_i$ ) (Burnham and Anderson 2002). Akaike weights allow the calculation of the probability that model  $i$  is the best among all alternative models considered with the data at hand.

With  $\Delta_i = \text{AIC} - \text{AIC}_{\min}$  where  $\text{AIC}_{\min}$  is the smallest AIC value in the set of competing models, Akaike weights are then calculated as:

$$w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^M \exp(-\Delta_r/2)}$$

where  $M$  is the number of models and the denominator represents the sum of all considered model AICs. The relative likelihoods are normalized to sum to 1, allowing us to denote the percentage that each model explains compared to all other models. A model with a high Akaike

weight, i.e. close to 1, has the biggest support and thus identifies the most important gradient.

### Deriving and comparing raw and model optima

The raw optima and the model optima of the species response curves along each gradient were extracted for each species using internal functions from the package *vegdata.dev* (Jansen 2008b). Model optima for model II and III refer only to a data-driven optima value since these models only allow for an “open-ended” response (Huisman et al. 1993) and hence are problematic to interpret with regard to an ecological optimum. All calculated optima refer to a realized ecological optima instead of optima based on fundamental niche theory (Austin et al. 1994).

In order to identify whether raw optima could be used for imputing missing gradient positions, we replaced the missing optima value with the raw optima for species with a model I response. Then, the species were ranked according to their gradient position and the number of matches between raw and optimum ranking values was counted. A high number of matches indicated a good performance of raw optima, while small values indicated a poor applicability of raw optima for imputation.

## Results

### Species response curves

Species response curves based on the HOF approach were modeled for eight oak species along six different climatic gradients. Linear increasing or decreasing models (model II) and the threshold model III, IIIb) were the most common models representing 63% of all response model (Table 1). Model I occurred in 21% of all models, representing no response. Unimodal models (IV, IVb, V) were only found in 17% of all models, and only on the seasonality of temperature gradient. The threshold model III and the reversed threshold model IIIb were the only

**Table 1** Optimal species response model based on AIC values

Species	T <sub>mean</sub>	T <sub>season</sub>	T <sub>min</sub>	P <sub>ann</sub>	P <sub>season</sub>	DSWD
<i>Q. cerris</i>	III	IV	III	II	II	II
<i>Q. coccifera</i>	II	II	IIIb	II	II	II
<i>Q. frainetto</i>	II	IV	I	II	II	III
<i>Q. infectoria</i> ssp. <i>boissieri</i>	I	II	I	I	III	I
<i>Q. infectoria</i> ssp. <i>infectoria</i>	I	I	I	III	III	III
<i>Q. ithaburensis</i> ssp. <i>macrolepis</i>	I	IV	III	III	V	III
<i>Q. petraea</i> ssp. <i>iberica</i>	III	IV	III	I	II	III
<i>Q. pubescens</i>	II	IV	III	II	V	IVb

Percentage of occurrence:  
model II=31%, III=29%,  
I=21%, IV=10%, V=4%,  
IIIb=2%, IVb=2%, V=0%

responses found on the minimum temperature gradient, except for model I. All other gradients had at least two different response models.

Most species showed different response curves along the climatic gradients (Fig. 3). Species that showed responses along all gradients were *Q. cerris*, *Q. coccifera* and *Q. pubescens*. The species with the fewest responses was *Q. infectoria* ssp. *boissieri*. The closely related *Q. infectoria* ssp. *infectoria* was the only species that showed responses only along the precipitation-related gradients, i.e.  $P_{ann}$ ,  $P_{season}$  and DSWD. *Q. coccifera* constantly showed a model II response except for the minimum temperature gradient. *Q. pubescens* was the species with the highest diversity in response types.

Major climatic drivers

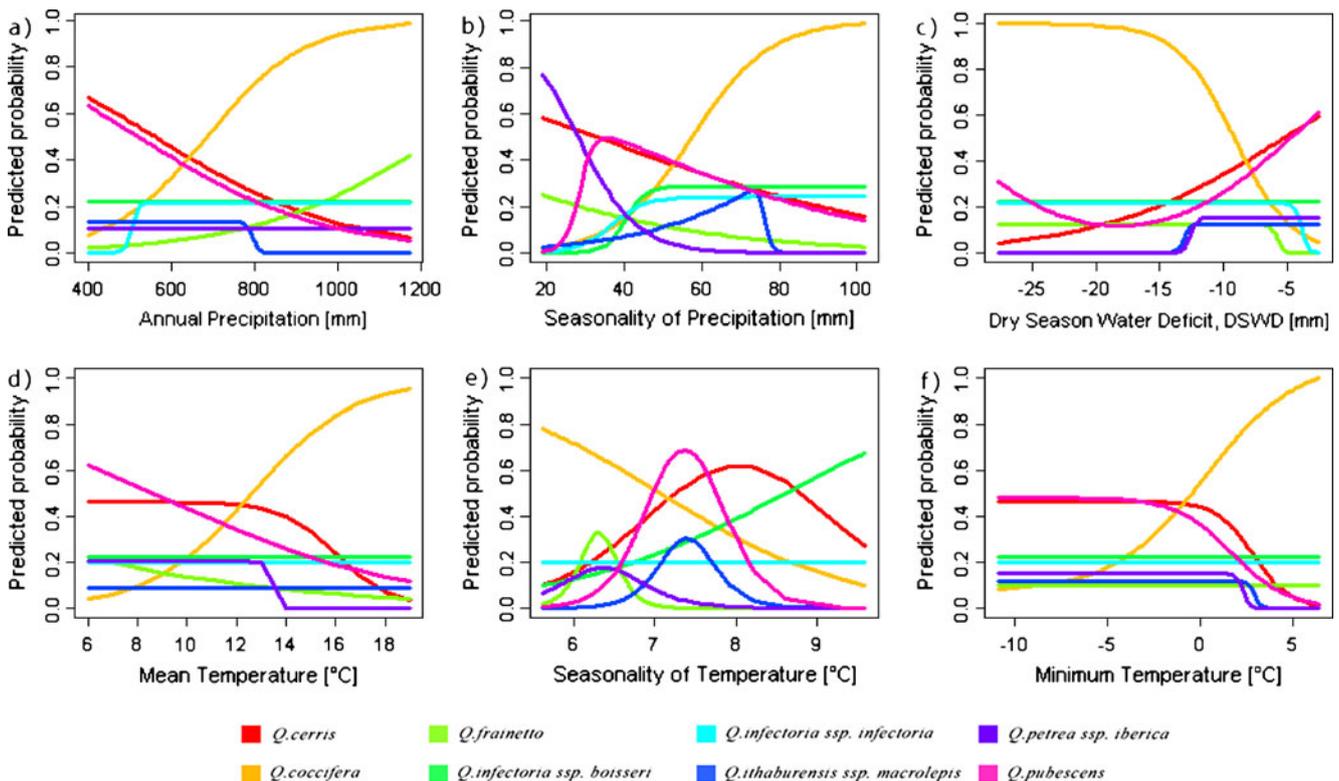
We identified the major climatic drivers for each species by calculating the weighted AIC values for each response model (Table 2). The seasonality gradients  $T_{season}$  and  $P_{season}$  were identified as the most important gradients for more than half of the species. For *Q. coccifera*, *Q. infectoria* ssp. *boissieri* and *Q. petraea* ssp. *iberica*, the seasonality of precipitation was the most important climatic gradient. For *Q. frainetto*, *Q. thaburensis* ssp. *macrolepis*, and *Q.*

*pubescens*, the seasonality of temperature did best explain the distribution of the species. Mean annual temperature explained around 56% of the occurrences of *Q. infectoria* ssp. *infectoria* and seasonality of temperature contributed an additional 20% of importance. The distribution of *Q. cerris* was instead best explained by  $T_{min}$  (57%) and DSWD (24%).  $P_{ann}$  was never the best explaining gradient.

Raw and model-derived optima

For each climatic gradient, we extracted raw optima and model-derived optima for each species (Table 3). The raw optima always lay in the range of the model-derived optima values. Largest differences between raw and model-derived optima were found for *Q. coccifera*, *Q. frainetto* and *Q. petraea* ssp. *iberica* which differed heavily in  $P_{ann}$ ,  $P_{season}$ , and DSWD. While the raw optima show rather similar values for all gradients, the standard deviation for model-derived optima are much higher. For example, the standard deviation for  $P_{ann}$  is 59 for the raw model values and 302 for the model-derived optima (data not shown).

The comparison of the ranking orders revealed that  $P_{season}$  had six identical rankings of eight species pairs,  $P_{ann}$ ,  $T_{min}$  and  $T_{mean}$  each had five identical rankings,  $T_{season}$  two, and DSWD only one. The species that differed



**Fig. 3** Species response curves for eight oak species along major climatic gradients: **a** mean annual precipitation, **b** seasonality of precipitation, **c** dry season water deficit, **d** mean annual temperature, **e** seasonality of temperature, **f** mean minimum temperature

**Table 2** Importance of climatic variables according to Akaike weights

Parameters representing climatic seasonality best explained the distribution of six species. Temperature-related parameters were important for two species, while water-related parameters were only of minor importance. Best-fitting models are marked in bold

Species	T <sub>mean</sub>	T <sub>season</sub>	T <sub>min</sub>	P <sub>ann</sub>	P <sub>season</sub>	DSWD
<i>Q. cerris</i>	0.12	0.01	<b>0.57</b>	0.03	0.02	0.24
<i>Q. coccifera</i>	0.00	0.00	0.00	0.00	<b>1.00</b>	0.00
<i>Q. frainetto</i>	0.00	<b>0.98</b>	0.00	0.00	0.01	0.00
<i>Q. infectoria</i> ssp. <i>boissieri</i>	0.06	0.13	0.03	0.07	<b>0.71</b>	0.01
<i>Q. infectoria</i> ssp. <i>infectoria</i>	<b>0.56</b>	0.20	0.04	0.07	0.08	0.05
<i>Q. ithaburensis</i> ssp. <i>macrolepis</i>	0.03	<b>0.82</b>	0.01	0.03	0.08	0.02
<i>Q. petraea</i> ssp. <i>iberica</i>	0.00	0.00	0.00	0.00	<b>1.00</b>	0.00
<i>Q. pubescens</i>	0.00	<b>1.00</b>	0.00	0.00	0.00	0.00

most often were *Q. pubescens*, *Q. petraea* ssp. *iberica*, *Q. cerris*, and *Q. frainetto*.

## Discussion

### Species responses along climatic gradients

In theory, the ecological niche of a species is optimally described by a bell-shaped symmetric unimodal curve, where the optimum along the observed gradient occurs where the maximum abundance of a species is found (Austin 2002). However, in real world datasets analyzed with HOF models, unimodal models, corresponding to model types IV or V, are rarely representative for all species responses (Lawesson and Oksanen 2002), sometimes even less than half of them (Oksanen and Minchin 2002). In our study, linear or threshold response models, i.e. models type II, III, or IIIb, were present in almost two-thirds of all models. Linear responses can be caused either by an incomplete sampling along an ecological gradient, due to a truncated gradient, i.e. such as the upper bound of a mountain range (Huisman et al. 1993), or due to near-end gradient optima of species (Normand et al. 2009). In our study, the spatial resolution was rather coarse for such an

ecological context, potentially hindering the identification of an optimum and thus favoring linear responses. This could have finally led to a higher percentage of linear or threshold responses than for unimodal models.

While linear and threshold models made up 63% of all models, we found symmetric unimodal responses in only 17%, five on the gradient of seasonality in temperature, two skewed unimodal responses on the gradient of seasonality in precipitation and one on the DSWD gradient. Seasonality is a proxy measure for climatic stability, i.e. low values of seasonality describe small seasonal differences in climate while high values refer to regions where climate shows higher variation between seasons. *Q. frainetto* is a thermophilous species mainly found in the northwest Mediterranean part of Turkey (Bartha 1998; Mayer 1986). Our analysis supports these findings but can explain it by the climatic stable environments found around the Marmara region. The two species *Q. pubescens* and *Q. ithaburensis* ssp. *macrolepis*, which partly overlap in their distributions in the higher altitudes of southwest Turkey (Mayer 1986), mainly show similar responses along the gradients, especially in their preference for medium stable climates.

Concerning *Q. ithaburensis* ssp. *macrolepis*, our findings support those of Dufour-Dror and Ertaş (2004), who reported *Q. ithaburensis* to be less drought resistant in

**Table 3** Raw and modeled optimum of species responses along climatic gradients

Species	T <sub>mean</sub>		T <sub>season</sub>		T <sub>min</sub>		P <sub>ann</sub>		P <sub>season</sub>		DSWD	
	Raw	Model	Raw	Model	Raw	Model	Raw	Model	Raw	Model	Raw	Model
<i>Q. cerris</i>	12.0	9.8	7.0	8.0	-1.8	-5.1	666.9	401.0	54.2	19.0	-8.4	-2.5
<i>Q. coccifera</i>	15.1	19.0	6.6	5.6	1.8	5.2	781.8	1,172.0	75.6	102.0	-13.7	-27.7
<i>Q. frainetto</i>	11.7	6.0	6.4	6.3	-0.7	NA	803.6	1,172.0	49.0	19.0	-11.0	-17.0
<i>Q. infectoria</i> ssp. <i>boissieri</i>	13.1	NA	7.1	9.6	-0.9	NA	719.0	NA	68.4	74.0	-10.8	NA
<i>Q. infectoria</i> ssp. <i>infectoria</i>	13.2	NA	6.7	NA	-0.3	NA	755.2	847.6	66.9	74.3	-11.7	-16.1
<i>Q. ithaburensis</i> ssp. <i>macrolepis</i>	12.7	NA	7.1	7.4	-1.5	-4.2	641.8	589.8	60.8	73.1	-8.0	-7.5
<i>Q. petraea</i> ssp. <i>iberica</i>	10.6	9.6	6.6	6.4	-2.3	-4.5	698.4	NA	32.6	19.0	-7.5	-7.3
<i>Q. pubescens</i>	11.7	6.0	7.0	7.4	-2.2	-6.2	662.5	401.0	56.9	35.6	-8.6	-15.1

Models of type I resulted in NA. For comparing ranking orders, NAs were replaced with modeled raw optima

Turkey than in Israel. Although our absolute values for DSWD differ from their study due to the application of a different evotranspiration equation, the species response curve for this species along the gradient (Fig. 3c) shows that it occurs only when DSWD is between  $-15$  and  $0$  mm, where water stress is less severe.

Opposing trends were always found between *Q. coccifera* and the two species *Q. cerris* and *Q. pubescens*. *Q. coccifera* has its main distribution in the lower altitudes of the Aegean regions of southern Turkey (Kaya and Raynal 2001) but still occurs in lower altitudes in the northwest of Turkey. Here, the distribution overlaps with the other two species. *Q. cerris* and *Q. pubescens* are widespread in the western and northern parts of Anatolia, *Q. cerris* also forms large areas of Mediterranean sclerophyllous forests in the south (Mayer 1986). In former times, *Q. cerris*–*Q. pubescens* steppic forests were often found in Inner Anatolia (Mayer 1986), indicating a closely related ecological niche. Thus, *Q. coccifera* prefers regions that are highly variable in annual precipitation and have a rather low seasonality in temperature. Furthermore, it is able to cope with high water deficits as indicated by the DSWD (Fig. 3c). The other two species always show different behavior. The linear responses often found for those species can be explained by truncated ecological gradients near the potential optimum. For example, the occurrence of *Q. cerris* below 400 mm annual precipitation is truncated by the coastline. However, a sampling based within national boundaries can also lead to linear and hence truncated gradients, as was the case with our dataset.

The subspecies of *Q. infectoria* are also known to differ in their distribution ranges (Mayer 1986). While *Q. infectoria* ssp. *boissieri* occurs mainly in southern Mediterranean montane regions of Turkey, *Q. infectoria* ssp. *infectoria* is found in the high Mediterranean mountain ranges of northwest Anatolia and at the Marmara Sea. However, in our study, response models for both subspecies did not show contrasting trends. In most cases, one of the species only showed a model I response. This could mean that either the gradient was not sampled at full length or that the species do not differ along the gradients considered due to their high ecological amplitude. In fact, both subspecies occur in the northwestern Aegean region (Mayer 1986; Uğurlu and Senol 2005). In cases of model I responses, it is most likely that gradients representing edaphical properties, such as pH or soil texture, could better explain species distributions allowing for a proper response shape. We recommend including gradients of soil properties in future studies on niche characteristics of Turkish oak species whenever possible.

#### Importance of climatic drivers

Climatic parameters are known to be most important in explaining regional scale distribution of oak species

worldwide (Nakao et al. 2010). In order to identify the best explaining and hence potentially important, climatic factor, we compared all species-specific response models using the Akaike weights. The seasonality gradients were clearly the best explaining models for six of the eight species. Hence, variability in precipitation or temperature is better at characterizing the distribution of oak species in Turkey than mean annual parameters such as  $P_{\text{ann}}$ ,  $T_{\text{mean}}$ , or  $T_{\text{min}}$ . This could be due to the spatial variability of precipitation and temperature regimes in Turkey caused by the complicated topography and the dependence on the Atlantic climatic regimes, such as the North Atlantic Oscillation (Sariş et al. 2010), making  $P_{\text{ann}}$  a rather uncertain predictor.

Climate change studies report increasing minimum temperatures throughout the country, but show high potential increases in western and southwestern parts of Turkey (Tayanç et al. 2009), while precipitation is likely to be decreasing throughout the country. This would lead to an increase in water stress due to increasing aridity. Studies on water stress responses of four oak species identified *Q. frainetto* not to be resistant against increasing water stress (Fotelli et al. 2000). However, recent studies showed that regeneration of *Quercus* species depend not only on climatic factors but to a great extent on the degree of human impact (Nakao et al. 2010; Navarro et al. 2006; Tsiourlis et al. 2010), which was not taken into consideration in this study.

A strong shift of climatic parameters could be especially challenging for endemic oak species in Turkey such as *Q. vulcanica* or *Q. aucheri* which have only a very limited distribution. Although recent studies found that both species showed remarkably high ranges in bioclimatic tolerance (Kargioğlu et al. 2009; Serteser et al. 2009), the optimal climatic conditions for those species remain unclear. In our dataset, there were too few observations for each species to analyze them with a gradient-based approach. We feel that future studies should focus especially on the ecological niche of endemic oaks, since sound conservation strategies are needed for those species in particular.

#### Raw and model derived optima

We were interested in exploring the possibility of imputing empty model optima values caused by a model I response with the raw optimum, estimated from the mean values of occurrences. Our findings show that the ranking of Turkish oak species by modeled optima and raw optima differed strongly in most cases. The only parameter that did not exhibit a model I response was  $P_{\text{season}}$ . Here, only two cases were differently ranked. However,  $T_{\text{season}}$ , which only had one model I response, ranked seven species differently. Furthermore, we found that *Q. coccifera*, *Q. frainetto* and *Q. petraea* ssp. *Iberica*, species with a linear response, were

not correctly ranked. We interpret this to be caused either through a bias introduced by the coarse spatial resolution used in this study or due to the presence of truncated gradients. In this case, the modeled optimum is equal to the maximum value of the response and thus deviates strongly from the raw mean values which are based on all positive occurrences along the whole gradient.

Wamelink et al. (2005) used a subdataset consisting of 5,428 relevés with 556 species to calculate responses based on raw mean values along a pH gradient. Compared to this, our dataset was extremely small, obviously affecting our outcome. Hence, we conclude that optima derived from the raw mean values of the species occurrences are probably not suitable for imputing model I optima, especially when the dataset is relatively small or when linear responses prevail.

#### Vegetation databases

Analysis of the ecological niche of a species based on species response curves are clearly data driven. Hence, a sound representation of the occurrence patterns of a species is absolutely necessary. Several databases on plant occurrences do exist in Turkey but they are not suitable for ecological analysis since they are either based on herbarium species (TÜRKHERB) or on occurrence notes in the Turkish Flora, referencing plant species to a very coarse grid cell system (Babaç 2004). In particular, geographically sound locations of occurrence data for oak species in Turkey are still scattered and only available through the literature. For this study, a first attempt was made to gather information on the distribution on oak species in Turkey in a vegetation plot-based database with known locations. In total, 1,104 phytosociological relevés of Turkish oak forest communities from the final database base could be used for this analysis. Vegetation plot-based databases have been identified as an important source allowing for macro-ecological analysis (Schaminée et al. 2009; Dengler and Steiner 2010). However, to our knowledge, there exists no national vegetation database based on phytosociological relevés for Turkey. Developing a sound national plot-based vegetation database for Turkey would be first step to tackle large-scale ecological phenomena such as global change.

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