

# Climate Niches of Tick Species in the Mediterranean Region: Modeling of Occurrence Data, Distributional Constraints, and Impact of Climate Change

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**ABSTRACT** In this study, we used ecological niche factor analysis (ENFA) and principal components analysis (PCA) of climate variables to define the climate niches and areas of potential colonization of six species of ticks in the Mediterranean region: *Dermacentor marginatus* Sulzer, *Rhipicephalus bursa* Canestrini & Fanzago, *Rhipicephalus turanicus* Pomerantsev, Matikashvili & Lototsky, *Hyalomma marginatum* Koch, *Hyalomma excavatum* Koch, and *Boophilus annulatus* (Say). ENFA generated distribution models that varied in accuracy from high to very high (area under the curve [AUC] = 0.87–0.97), with the lowest AUC obtained for *B. annulatus*. PCA provided an adequate separation of the climate niches of different species in the reduced space of the variables. Climate scenarios and factorial consensus analysis were used to evaluate the geographic impact of climate change (as turnover in habitat suitability) on the niches of the ticks and net variations in habitat availability. The scenario that was most compatible with estimates of future climate in the Mediterranean region (increase in temperature and decrease in rainfall) was predicted to produce a sharp increase in the extent of suitable habitat for *R. bursa*, *R. turanicus*, and *H. marginatum*. This scenario would result in a northward expansion of suitable habitat areas for these three species. The highest impact (highest species turnover) would be recorded at the margin of the current distribution range of the three species. A sensitivity analysis of the ecological response of the ticks to the climate change scenarios showed that the response is statistically different in different regions of the PCA-derived niche. These results outline the need to further investigate the potential of bioclimate models to obtain accurate estimations of tick species turnover under conditions of climate change over wide areas.

**KEY WORDS** Mediterranean region, ticks, climate niche, sensitivity, climate change

In recent decades, increasing use has been made of methods designed to estimate the geographic extent of the “fundamental ecological niche,” defined mostly in coarse-scale climate dimensions. Although of inherent interest in terms of the evolutionary ecology of species, estimates of the ecological niche are usually undertaken as an intermediate step in estimating the geographic distribution of a species. The extent of the ecological niche is estimated in one of two ways: 1) a “mechanistic approach” (Guissan and Zimmermann 2000) in which the responses of individuals to climate variables are determined by direct measurement or physical modeling, with fitness values of different combinations of these variables inferred from the responses; or 2) a “correlative approach” that relates data on species occurrence to data sets that summarize the environmental variables that are most closely associated with observed occurrence. Regardless of the approach used, ecological niche theory is central to understanding how environmental changes affect spe-

cies distribution patterns (Jackson and Overpeck 2000). Hutchinson (1957) conceived the niche as a multidimensional “hypervolume” with dimensions defined by those environmental factors that influence the fitness of individuals of that species. The basic idea is that the environmental space coordinates of sites where focal species are recorded are representative of suitable combinations of descriptor variables. Observed density in this space is then correlated with habitat suitability. Hutchinson’s niche envelope assumes that a steady-state equilibrium with current environmental conditions has allowed adequate time for perfect adaptation and exhaustive migration to all parts of the potential range.

Recent studies have focused on modeling the ecological requirements of species and projecting these requirements onto modeled future climate regimes to predict future geographic distributions. In this sense, there is increasing concern regarding the impact of forecast climate change on the distribution of arthropods that are involved in disease transmission. It is generally accepted that environmental change will

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modify the transmission patterns of tick-borne diseases (Patz et al. 2000), but a statistical framework in which to track the effects of such changes on niches has yet to be established.

The Mediterranean region is predicted to experience large changes in both temperature and rainfall in the near future (IPCC 2000). The effect of these changes on the geographic distribution of the major tick species in the region remains an open question. Attempts have been made to characterize the ecological niche of ticks according to vegetation (Gilot 1985), but these studies were limited to descriptions of qualitative associations. A quantitative definition of the niche of tick populations will provide the framework required to determine the sensitivity of the population to specified changes in climate variables and hence to determine the impact of projected climate change on the climate suitability of a geographic region. Multivariate statistical tools are potentially useful in estimating the dimensions of the ecological niches of species, predicting potential distributions across scenarios of change, and understanding the interactions of geographic outcomes for different species.

In the current study, we sought to develop a rigorous definition of the climate niche of several species of ticks of importance in the Mediterranean region. Particular attention was devoted to characterizing the sensitivity of the niche of each species to variations in climate variables and to assessing the impact of climate change on the geographic distribution of each tick species according to different climate scenarios.

## Materials and Methods

**Study Region and Data Sources.** This study focused on an area within the Mediterranean region (southern Europe and northern Africa) within the coordinates 11° W, 44° E and 27° N, 50° N. Our analysis was based on a set of tick records compiled from a variety of sources, including data from the literature and the collections by local experts. The tick species included in study and the number of localities where accurate records were obtained are *Rhipicephalus bursa* Canestrini & Fanzago (585 locality records), *Rhipicephalus turanicus* Pomerantsev, Matikashvili & Lototsky (430), *Boophilus annulatus* (Say) (91), *Dermacentor marginatus* Sulzer (853), *Hyalomma marginatum* Koch (773), and *Hyalomma excavatum* Koch (154). These tick species were selected with a focus on ecology, in that they all exhibit a true Mediterranean distribution (sensu Gilot 1985). *H. lusitanicum* was not included because it seems to have strong biotic requirements in its life cycle, specifically the use of Mediterranean rabbits as hosts for immatures, which restrict its spatial distribution (Pérez-Eid and Cabrita 2003). Other species, such as *Hemaphysalis punctata* Canestrini & Fanzago and *Ixodes ricinus* (L.), are found in nearby regions but are not considered to be Mediterranean (Gilot 1985); therefore, they are not included in the current study. There are additional concerns about the predictive mapping of *I. ricinus*. In previous work

(Estrada-Peña et al. 2006), it was concluded that several populations with highly different ecological preferences can be detected; modeling the distribution of *I. ricinus* in its whole distribution range produces acceptable results only if partial models are developed according to the main variables restricting the range of each population. Therefore, the use of a constrained extent (i.e., restricted to the Mediterranean region) can lead to an incorrect interpretation as only part of the environmental gradient is sampled, resulting in truncated response curves for a species (Van Horn 2002).

The original purpose was to obtain both presence and absence records and to compare the multivariate climate space of both sets of records. However, although vast stores of presence-only data exist, particularly in natural history museums, absence data are scarce, especially for poorly sampled regions. Even when absence data are available, they may be of questionable value in many situations because sampling intensity in space and time is highly clustered. Therefore, presence-only data were used in this study. Records were assembled from several sources. Some of the data came from systematic surveys at regional scale already compiled into reports or reviews. Other data were compiled at country level by several authorities. Other records were assembled from a variety of information retrieved from surveys at local scales carried out by trained staff or in the course of epidemiological studies of tick-transmitted diseases and adequately published or obtained through the courtesy of collections curators. Because of its implications in the transmission of prominent pathogens, the distribution of these ticks has been studied often in many areas of the Mediterranean region, ensuring an adequate degree of homogeneity in the records distribution. Both over- and underrecording are expected after the impact of a tick in different regions. It is assumed that habitat preferences are fully described, that all potential habitats are represented, and that habitats are well detected by the extent and resolution of the descriptor variables. It is implicit in the use of the tick distribution data set that the majority of records are derived from the realized niche of the species and that only a few of them represent captures from the periphery of the ecological space.

The database has been edited and published (ICCTD 2004) to account for accuracy and reliability and represents the largest database concerning tick distributions in the Mediterranean region. Only those captures made since 1980 and with accurate coordinates were included in the current study.

**Computation of Climate Habitat Suitability.** We used ecological niche factor analysis (ENFA) to estimate habitat suitability (HS) in the multivariate space of environmental variables, using presence-only data (Hirzel et al. 2002). This technique is based on the computation of factors that explain the major part of a species environmental distribution. An HS index is produced for each cell as a value that is inversely proportional to the weighted mean distance from the cell to the median of each ENFA factor, normalized in

such a way that the suitability index ranges from 0 to 1. Although other methods are available to compute HS in terms of a set of climate variables (for review, see Segurado and Araújo 2004), they must be applied to presence-absence data. Data for monthly rainfall and monthly minimum and maximum temperatures were obtained from <http://biogeoberkeley.edu> at a resolution of 2.5 km. Data about vegetation as the normalized derived vegetation index (NDVI) values or as qualitative information on vegetation categories were not used to train the models. Although there are many reports about the improvement of tick habitat models by using vegetation-derived features, there is a total lack of information about how vegetation would change under scenarios of climate change. Whereas the use of these features would improve the models output, one of the primary purposes of this study is the evaluation of impacts under scenarios of climate change that should be based upon the same layers of information used to build the models.

Models were developed using a random training set (50% of records) and checked against an evaluation set (remaining 50% of records). Most model performance tests are based on a confusion matrix in which the observed (actual) and predicted patterns are cross-tabulated (Fielding and Bell 1997). When absence data are unavailable or unreliable, discrimination models can be built by generating pseudo-absences (Zaniewski et al. 2002). Engler et al. (2004) proposed to delineate an envelope enclosing all occurrences in the ENFA hyperspace. Pseudo-absences are then randomly chosen outside this envelope and combined with real occurrences. The number of randomly chosen pseudo-absences is the same as the total number of real occurrences, because it is easier to find optimal threshold in this situation. From these sets, a confusion matrix is generated and hence the area under the curve (AUC) of a receiver operating characteristic (ROC) plot of sensitivity against  $1 - \text{specificity}$  (Swets 1988). Sensitivity is defined as the proportion of true positives correctly predicted, whereas specificity is the proportion of true negatives (here the pseudo-absences) correctly predicted (Fielding and Bell 1997, Pearce and Ferrier 2000). Threshold-independent measures (e.g., ROC curves) are considered to be more robust and more objective than threshold-dependent measures (e.g., Kappa statistics), because they do not rely on a single threshold to distinguish between predicted presence and predicted absence.

**Definition of Tick Climate Niches.** ENFA provides a measure of the response of each tick species to a range of monthly predictor variables; however, the climate niche of the ticks can be better realized if it is reduced to a smaller number of dimensions. Principal component analysis (PCA) was therefore performed on the original climate data set. PCA is intended to remove spurious dimensions in the data set and to produce a smaller number of variables that describe the majority of the variability, retain the ecological meaning, and are uncorrelated. Thus, there are specific portions of the PCA-derived volume associated with positive HS that are regarded as statistically sig-

nificant definitions of the climate niche of each species (Hargrove and Hoffman 2005.). We performed both a multiple regression between HS for each species and the PCA values and an analysis of variance (ANOVA) to check for significant and separate descriptors of the climate niche of each species using only PCA-reduced space.

**Climate Scenarios and Impact of Climate Change on Tick Niches.** Here, we calculate the environmental potential for each tick species under new combinations of climate variables. Global climate models remain relatively coarse in terms of spatial resolution; this compromises the desired resolution of our analysis. To address this problem, we created new climate layers with monthly increases and decreases in temperature of 1 and 2°C, and monthly variations in rainfall of 60, 80, 120, and 140% of actual values. For each combination of temperature and rainfall, the HS for each species was calculated as described above. Although climate plays an important role in tick colonization (Cumming 2000), ecological and historical factors (e.g., barriers to dispersal) limit the expansive processes of ticks. Therefore, the projected HS under the new climate scenarios should be considered only as the climate suitability for the tick in the region. This approach yielded a large number of HS maps showing every combination of temperature, rainfall, and response of tick species. To minimize uncertainty among projected scenarios, we used the consensus analysis proposed by Thuiller (2004). Briefly, a multivariate approach is used to run a consensus analysis on projections of HS turnover. The first axis captured consistent spatial patterns in turnover rate across the different projecting scenarios. Final projections were therefore made for HS turnover according to changes in temperature and rainfall. For each species, we estimated the habitat lost or gained from the number of pixels for which HS switched to negative or positive values.

Although the above-mentioned approach provided the impact of climate scenarios on the geographic distribution of the tick niche, we also wanted to determine the sensitivity of these niches, as specific portions of the niche are more sensitive to climate change than other parts. These portions would therefore display a sharper and nonlinear response to a given rate of climate change. To compute the sensitivity of these niches to changes in climate, we calculated a normalized sensitivity index (S) (Corson 2004):

$$S = \frac{(O_H - O_L) / O_M}{(I_H - I_L) / I_M}$$

where  $I_H$  is the higher value of the input parameter,  $I_L$  the lower value of the input parameter,  $I_M$  the mean of the input values,  $O_H$  the corresponding output for the higher input value,  $O_L$  the corresponding output for the lower input value, and  $O_M$  the mean of the two outputs. Input parameters were monthly climate values and output parameters were HS values. Sensitivity derived from climate scenarios was then related to the

**Table 1. Best models obtained for each tick species and related AUC values**

Species	Set of variables	AUC
<i>B. annulatus</i>	Tmax (2-11), Tmin (3-11), Rain (2-11)	0.877
<i>D. marginatus</i>	Tmax (4-11), Tmin (1-3, 6-12), Rain (4-11)	0.955
<i>R. bursa</i>	Tmax (2-8), Tmin (3-8), Rain (3-10)	0.975
<i>R. turanicus</i>	Tmax (2-7), Tmin (3-9), Rain (3-10)	0.962
<i>H. marginatum</i>	Tmax (2-8), Tmin (1-9), Rain (4-9)	0.971
<i>H. excavatum</i>	Tmax (3-9), Tmin (3-9), Rain (3-9)	0.977

Tmax, monthly maximum temperature from January (month 1) to December (month 12); Tmin, monthly minimum temperature; and Rain, monthly accumulated rainfall. The numbers after the variable name indicate the particular monthly variable included in the best model.

PCA-derived values. A multiple regression was performed to check if the highest sensitivity was associated with specific portions of the climate niche.

**Results**

The best predictive models for the six tick species involved the use of varying numbers of descriptor variables (Table 1). Winter climate features were rejected as useful variables for all species except *D. marginatus*, for which minimum winter temperatures were well represented in the best model. Most models had an AUC >0.95 (“very good” fitting); however, it should be noted that a relatively low-performance model was obtained for *B. annulatus*. The PCA procedure extracted three factors that explained ≈96% of the original variability. Axis 1 was heavily loaded with rainfall-derived features, whereas axes 2 and 3 expressed variations in maximum and minimum temperature, respectively. Therefore, rainfall is the main limiting factor in the distribution of these ticks, followed by maximum temperatures. Minimum temperatures seem to play a minor role as factor modulating the tick distribution in the studied region. Table 2 is obtained from the specific portion of the PCA-derived space to which each species is associated. High statistical differences are found concerning the first axis (derived from monthly rainfall), suggesting that these species use statistically distinct portions within this PCA-derived niche (Table 2); however, *R. bursa* and *H. marginatum* were poorly separated in this first axis signifying highly similar rainfall preferences. Both *D. marginatus* and *B. annulatus* are well separated for the rest of the species in the second axis (representing maximum monthly temperatures). Other differences can be observed in the third axis (representing the load of minimum monthly temperatures), being both *B. annulatus* and *H. excavatum* well separated in relation to the other species and poorly separated between them, indicating high affinities concerning minimum temperature requirements.

Figure 1 shows areas of predicted positive suitability and actual records for each tick species. Analysis of the climate scenarios provides an estimate of the geographic distribution of the impact of climate change (HS turnover; Fig. 2). Our analysis discriminates three

**Table 2. Separation of the climate niches of each tick species according to values in the PCA-derived multivariate space (reduced from the original set of 36 descriptor variables into three layers)**

	<i>Dmar</i>	<i>Rbur</i>	<i>Rtur</i>	<i>Hmar</i>	<i>Hexc</i>
PCA-1					
<i>Dmar</i>	0.000				
<i>Rbur</i>	0.000	0.000			
<i>Rtur</i>	0.000	0.448	0.000		
<i>Hmar</i>	0.000	0.000	0.000	0.000	
<i>Hexc</i>	0.000	0.000	0.000	0.000	0.258
<i>Bann</i>	0.000	0.000	0.000	0.000	0.258
PCA-2					
<i>Dmar</i>					
<i>Rbur</i>	0.000				
<i>Rtur</i>	0.000	0.015			
<i>Hmar</i>	0.000	0.993	0.002		
<i>Hexc</i>	0.000	0.520	0.582	0.199	
<i>Bann</i>	0.000	0.001	0.000	0.013	0.000
PCA-3					
<i>Dmar</i>					
<i>Rbur</i>	0.092				
<i>Rtur</i>	0.001	0.806			
<i>Hmar</i>	0.836	0.785	0.096		
<i>Hexc</i>	0.000	0.000	0.000	0.000	
<i>Bann</i>	0.000	0.000	0.000	0.000	1.000

Included are the *P* values of an ANOVA test by using the species as grouping variables and PCA values in the axes where each species had HS > 0. A low *P* value means for high differences in the portion of the PCA-derived climate space as used by each species. *D. marginatus* (*Dmar*), *R. bursa* (*Rbur*), *R. turanicus* (*Rtur*), *H. marginatum* (*Hmar*), *H. excavatum* (*Hexc*), and *B. annulatus* (*Bann*).

groups of species. The first group comprises *B. annulatus* and *H. excavatum*, for which an increase in temperature (Fig. 2A and E) leads to an increase in HS within regions of northern Africa and restricted parts of southern Europe. A decrease in temperature has the same effect over wide areas of northern Africa. Changes in rainfall are predicted to have little geographic impact on *B. annulatus* (Fig. 2B), but they show a clear effect on *H. excavatum* (Fig. 2F). The geographic impact of rainfall changes on the HS for *D. marginatus*, which is the sole occupant of the second of the three groups, yields a different pattern of HS turnover. A decrease in temperature results in an increase in the extent of HS in northern Africa, most of coastal Europe, and wide areas of southern Spain (Fig. 2C), whereas an increase in temperature results in a northward expansion of the suitable habitat for this species. Changes in rainfall (Fig. 2D) result in similar effects to those described for the above-mentioned changes in temperature. The impact of climate change on the colonization capacities of *H. marginatum*, *R. bursa*, and *R. turanicus*, which together constitute the third group, is similar to that of the second group. HS will increase for these species along southern Spain and northern Africa in response to a decrease in temperature and an increase in rainfall. Large areas of Europe would potentially be affected by an increase in the HS for these species after an increase in temperature and decrease in rainfall.

Table 3 shows net changes in the total area of suitable environment for each species according to the evaluated climate scenarios. Changes in rainfall result in only minor changes in total available area for *B.*



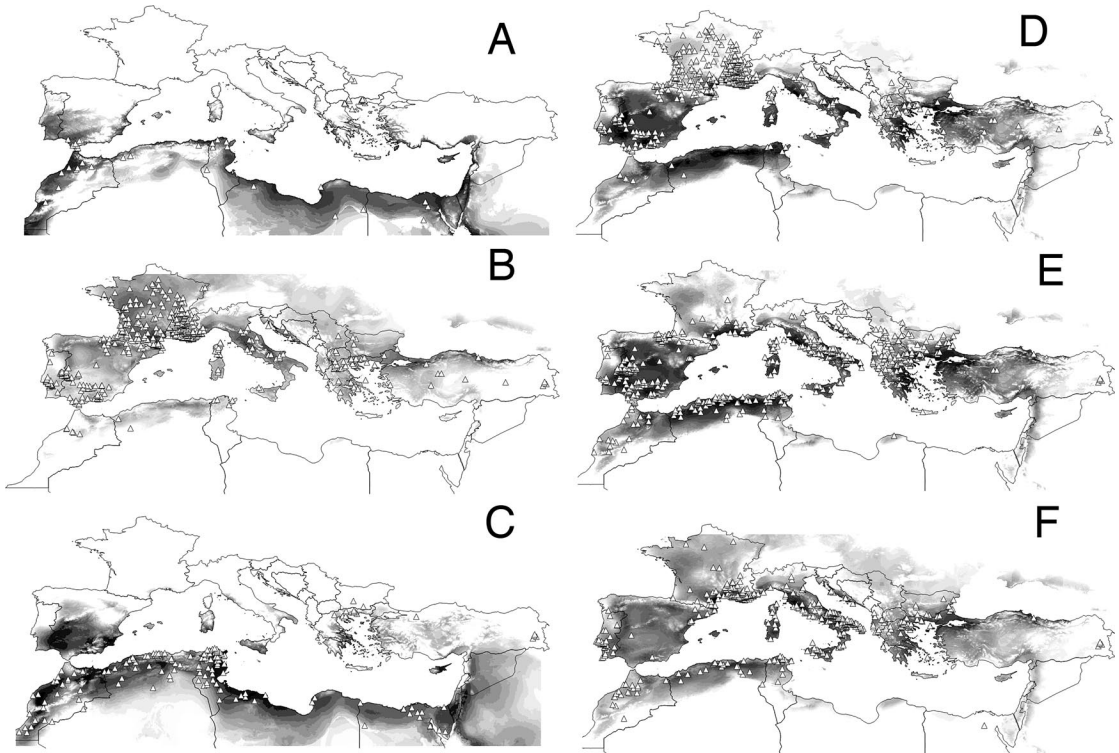


Fig. 1. Actual occurrence records (triangles) for each species, predicted zones of  $HS > 0$  (gray scale: darker areas are higher values, as obtained from ENFA analysis). (A) *B. annulatus*. (B) *D. marginatus*. (C) *H. excavatum*. (D) *H. marginatum*. (E) *R. bursa*. (F) *R. turanicus*.

*annulatus*. Both *R. bursa* and *H. marginatum* record a sharp increase in habitat availability with reduced rainfall, whereas an increase in rainfall leads to decreased habitat availability. Interestingly, every rainfall scenario results in a net loss of habitat for *D. marginatus*. Changes in temperature have marked effects on the amount of available habitat. Decreasing temperatures are predicted to result in habitat loss for *B. annulatus*, *R. bursa*, and *H. marginatum*, whereas a sharp increase in net habitat availability is predicted to accompany increasing temperatures. The opposite is observed for *H. excavatum*, whereas *D. marginatus* is predicted to experience a net loss of total habitat under every temperature scenario.

The sensitivity of the climate niche of each tick species to changes in raw climate variables was found to be associated with specific regions of the PCA-derived ecological space, as shown by multiple regressions (Table 4).

### Discussion

Several studies have modeled the potential impacts of climate change on the distribution of species by applying climate-driven simulations across a range of scales, study areas, and species. In the current study, we estimated the geographic distribution of adequate environmental suitability for six species of ticks in the Mediterranean region, and we evaluated the sensitiv-

ity of the tick climate-derived niche to climate scenarios in terms of predicted ecological response and altered distribution. The approach explored herein has been widely applied to questions of distribution and ecology in biodiversity-related studies (Peterson and Vieglais 2001, Peterson et al. 2002). Such species-specific models should be developed in parallel with other modeling efforts that focus on the response to climate change at the ecosystem level. ENFA methodology (Hirzel et al. 2002) provides a good fit for models derived using different sets of climate variables. Low predictive values for *B. annulatus* are apparently derived from the extensive distribution of this species, which extends well into Central Asia and sub-Saharan Africa. The use of constrained extent has been demonstrated to produce wrong modeling predictions for *I. ricinus* (Estrada-Peña et al. 2006). It therefore seems that this low-performance model is the result of the analysis of a partial set of records that is not necessarily close to equilibrium.

The tick species included herein have great potential in the transmission of pathogens for animals (Colebrook and Wall 2004, Estrada-Peña et al. 2004), such as *Babesia ovis* (by *R. bursa*), *B. motasi* (by *R. turanicus*), and *B. caballi* (by *H. marginatum*), or they are prominent vectors of human diseases, such as Crimean-Congo hemorrhagic fever (mainly transmitted by *H. marginatum* in eastern Europe). There is a great concern about the potential spread of pathogens

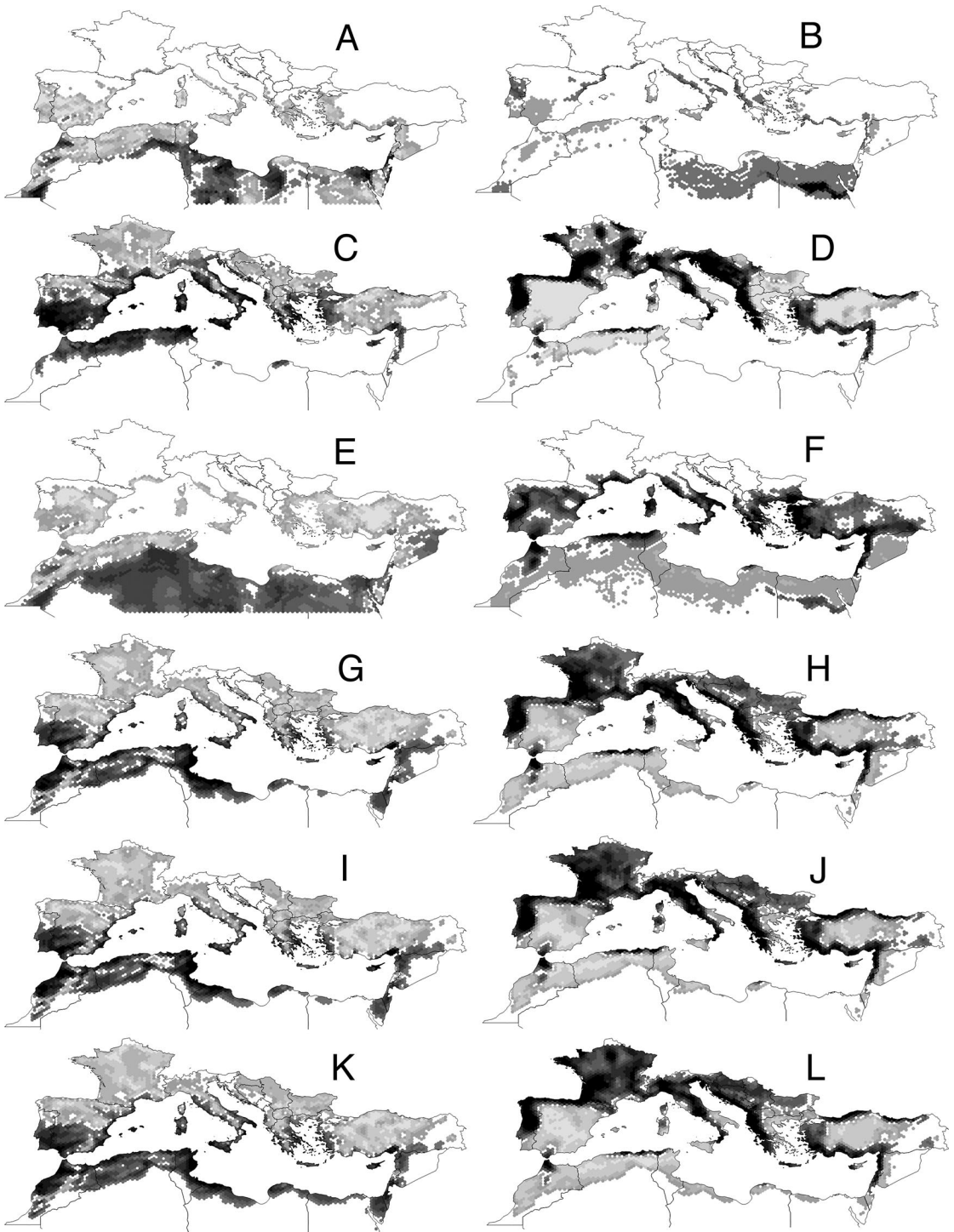


Fig. 2. Predicted geographic impact (HS turnover) of different climate change scenarios. The maps shows the forecasted changes in habitat suitability for the different tick species, with changes in temperature (left column) and rainfall (right column) analyzed by consensus analysis to show the most coherent response to a range of changes in predictor variables. Dark shades of gray indicate increased HS after a decrease in the predictor variable scenario (temperature or rainfall). Light shades of gray indicate increased HS after an increase in the predictor variable. (A and B) *B. annulatus*. (C and D) *D. marginatus*. (E and F) *H. excavatum*. (G and H) *H. marginatum*. (I and J) *R. bursa*. (K and L) *R. turanicus*.

**Table 3. Net changes in habitat (HS turnover) for the different climate scenarios evaluated using ENFA**

	<i>Bann</i>	<i>Rbur</i>	<i>Hexc</i>	<i>Hmar</i>	<i>Dmar</i>	<i>Rtur</i>
Rdec80	3.01/1.60	21.58/2.53	11.49/0.82	23.97/2.32	17.29/46.44	10.26/6.15
Rdec60	2.63/3.22	15.36/4.26	6.22/1.12	16.96/6.52	13.13/16.68	7.37/2.27
Rinc120	1.26/0.74	1.56/17.17	0.66/6.13	1.47/13.94	9.89/20.50	1.63/11.72
Rinc140	2.22/1.43	2.60/28.95	1.25/12.45	2.40/25.11	15.01/48.5	2.87/27.61
Tdec1	0.71/12.94	3.10/11.35	6.21/3.54	3.00/8.69	6.13/12.34	3.28/8.37
Tdec2	0.61/27.01	6.29/20.04	10.35/7.86	6.33/18.49	11.33/28.32	5.80/18.80
Tinc1	11.25/1.29	11.81/3.63	3.19/6.34	13.43/4.00	8.37/7.18	6.20/2.40
Tinc2	19.62/2.93	21.26/8.03	5.85/12.32	26.01/8.35	13.40/14.99	10.87/4.88

Analyzed species are *D. marginatus* (*Dmar*), *R. bursa* (*Rbur*), *R. turanicus* (*Rtur*), *H. marginatum* (*Hmar*), *H. excavatum* (*Hexc*), and *B. annulatus* (*Bann*). Scenarios are Rdec (decrease in monthly rainfall to 60 or 80% of historical values) and Rinc (increase in monthly rainfall to 120 and 140% of historical values), and Tdec and Tinc (decrease or increase of monthly temperature, respectively, of 1 or 2°C). Left and right part of every column mean for habitat gain and loss, respectively. Most prominent values are in bold type (i.e., Rinc120 represents the percentage habitat gain/loss that accompanies an increase in monthly rainfall to 120% of historical values).

along newly colonized areas by ticks as a response to changes in climate suitability. For example, it is well known that migratory birds can disperse *H. marginatum* and arboviruses into adjacent areas of southern Russia (Chumakov 1972). Although adequate studies about invasive events by ticks as a response to warmer winters have been performed in some areas (i.e., southern Canada by Ogden et al. 2006), nothing is known about the potential spread of ticks in the Mediterranean region. Because the high medical and veterinary interest of these species, surveys are necessary to account with recent changes in species distribution in parallel with long-term records of climate and vegetation trends.

Modeled niches provide stable constraints on the distribution potential of ticks. Methods based on environmental envelopes are conceptually the closest to niche theory, because they strive to delineate the envelope that best circumscribes the suitable conditions defined by environmental variables. The main assumption of such an approach is that modeled species are in equilibrium with their environment (Guisan and Zimmermann 2000) in terms of both

spatial extent and resolution. Considerable interest exists in the selection of a suitable algorithm that reflects accurately the range of a species' suitable habitat. Several studies have already highlighted the limitations of modeling algorithms (Pearson and Dawson 2003, Guisan and Thuiller 2005) and the underlying methodological uncertainties (Thuiller 2004). Although a homogeneous set of presence-absence is the ideal, the generation of pseudo-absences has been shown to significantly increase the predictive models (Zaniewski et al. 2002). In the same way, it is always preferably the use of algorithms whose results are conducive to interpretation about the variables involved in the delineation of the climate niche, than models produced by a "black box" algorithm such as GARP (Stockman et al. 2006).

In this sense, the reduction of climate space into a smaller set of reduced PCA-derived information is a better approach to understand the climate requirements by each tick species, because neither a single variable nor combination of a few variables is mostly responsible of the distribution patterns as noticed by the species. Robertson et al. (2001) previously demonstrated the suitability of PCA for describing the habitat of a target organism. Under this approach, eigenvectors derived from the covariance matrix form the orthogonal axes of an n-dimensional hyperspace in which the origin represents the theoretical core of the species niche. The current study has established that PCA provides an adequate means of reducing the dimensionality of a multivariable data set while retaining the value as a descriptor for the climate niche of ticks. Different tick species thus occupy significantly different portions of the environmental space; this is indicative of the ecological affinities between species. Central to the current study is the finding that the niche of ticks shows varying sensitivity to climate change. A given rate of climate change is therefore expected to result in different impacts in different geographic areas.

Of special concern herein is the inclusion of predictor layers derived from vegetation, as the NDVI values, or as qualitative information on vegetation categories. The use of such as information has provided sharp improvements in habitat models of other tick species (Guerra et al. 2002, Ogden et al. 2006) and

**Table 4. Multiple regression analysis between sensitivity to changes in temperature and rainfall (independent variables) and position within the climate niche and HS (dependent variables)**

	Multiple R	B-PCA1	B-PCA2	B-PCA3
BannT	0.581	0.990	0.730	0.010
BannR	0.367	0.140	0.080	0.290
DmarT	0.645	0.380	0.640	0.230
DmarR	0.843	-0.630	-0.410	-0.590
HexcT	0.846	0.890	0.640	0.270
HexcR	0.806	-0.490	-0.050	-0.370
HmarT	0.675	0.580	0.580	0.090
HmarR	0.841	-0.590	-0.280	-0.510
RburT	0.683	0.570	0.580	0.080
RburR	0.837	-0.620	-0.340	-0.510
RturT	0.708	0.550	0.550	0.060
RturR	0.824	-0.640	-0.380	-0.480

Also shown are the multiple R-values and the  $\beta$  coefficient of each principal component (the higher the absolute load of a PCA-derived axis, the greater the involvement of that axis in the response to the climate change). Analyzed species are *D. marginatus* (*Dmar*), *R. bursa* (*Rbur*), *R. turanicus* (*Rtur*), *H. marginatum* (*Hmar*), *H. excavatum* (*Hexc*), and *B. annulatus* (*Bann*). The first column contains the name of the species followed by either T (indicating sensitivity to changes in temp) or R (indicating sensitivity to changes in rainfall).



the incorporation of habitat fragmentation outputs a better insight in the prediction of abundance of *I. ricinus* in field studies (Estrada-Peña et al. 2005). Actually, NDVI has been identified as the main variable reflecting the distribution of *I. ricinus* (Estrada-Peña 2001). However, the current study evaluates the impact of climate change scenarios over the tick HS. Although the inclusion of such as information would undoubtedly improve the overall performance of base models, there is no way to build climate scenarios including vegetation features. There are currently no studies involving plausible scenarios of NDVI changes according to variations in temperature and rainfall, rendering this information useless. Furthermore, there is not a direct relationship between changes in vegetation categories and changes in climate alone, because human pressure-derived effects are the main determinants of these changes. Habitat predictive models cannot be built up using a series of information layers and then evaluated over scenarios with a different set of layers, because information about accuracy of projections on scenarios is lacking. Therefore, we preferred to avoid the use of vegetation-derived features.

One of the major weaknesses of current climate-based models for ticks is that they cannot account for migration processes as specimens track environmental change. This issue can only be adequately addressed by the inclusion of the biotic component of the tick ecosystem and landscape fragmentation (Corson 2004, Estrada-Peña et al. 2005). Recent work by Martínez-Meyer et al. (2004) has highlighted the viability of ecological niche modeling in predicting the effects of climate change on potential species distribution. A predicted northward migration of species is commonly stressed under changed climate conditions in the northern hemisphere, but little attention has been given to determining which regions would be most affected by high species turnover. Our focus on the geographic impact on the tick niche of various climate scenarios is intended to evaluate the invasive potential of these ticks and to identify the areas where major species turnover is expected (Thuiller 2004). Our analysis demonstrates that changes in HS for ticks are likely to occur under climate scenarios that are compatible with modeled climate trends for the near future. Results presented here support the hypothesis that *R. bursa*, *R. turanicus*, and *H. marginatum* would be the species with the highest rate of newly suitable habitat under scenarios of increased temperature and reduced rainfall. Under the conditions of predicted climate trends (Hulme et al. 1999), the results of the current study support a trend toward changes in tick fauna (and transmitted pathogens) over wide areas of Europe. In a biogeographic context, our results suggest that areas at the margin of the species range are generally prone to rapid changes after subtle variations in climate. The way in which this will result in actual invasions into the new potential space depends on the dispersal mech-

anisms of the ticks, introduction by means of human activities, and the role of long-distance dispersal.

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