

The tick *Ixodes ricinus*: distribution and climate preferences in the western Palaearctic

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Abstract. In this study, multivariate spatial clustering on monthly normalized difference vegetation index (NDVI) maps is used to classify ecological regions over the western Palaearctic. This classification is then used to delineate the distribution and climate preferences of populations (clades) of the tick *Ixodes ricinus* L. (Acari: Ixodidae) from a geographically extensive dataset of tick records and a gridded 2.5-km resolution climate dataset. Using monthly layers of the NDVI, regions of similar ecological attributes were defined and nine populations with significant differences in critical climate parameters ($P < 0.005$) were detected. Grouping of tick records according to other categories, such as political divisions, a $4^\circ \times 4^\circ$ grid overlying the study area, or the CORINE) and USGS) vegetation classification schemes did not provide significantly separated populations ($P = 0.094\text{--}0.304$). Factor analysis and hierarchical tree clustering provided an ecological overview of these tick clades: two Mediterranean and one Scandinavian (western) clades are clearly separated from a node that includes clades of different parts of central Europe and the British Isles, with contrasting affinities between the different clades. The capture records of these ecologically separated clades produce a clear bias when bioclimate envelope modelling is applied to the mapping of habitat suitability for the tick in the western Palaearctic. The best-performing methods (Cohen's kappa = 0.834–0.912) use partial models developed with data from each ecoregion, which are then overlapped over the region of study. It is concluded that the use of ecologically derived ecoregions is an objective step in assessing the presence of ecologically different clades, and provides a guide in the development of data partitioning for habitat suitability modelling.

Key words. *Ixodes ricinus*, clades, habitat suitability modelling, normalized difference vegetation index-derived ecoregions.

Introduction

Ecological niches delineate the set of conditions under which species can maintain long-term populations. There is a wide theoretical treatment of the features of the ecological niche (Holt & Gomulkiewicz, 1996; Holt, 1996) that clarifies the relationships between ecological niche, geographical distributions and evolutionary dynamics. These studies suggest that, in general, long-term natural selection pressure maintains the ecological niche without substantial modification. This reasoning is consistent with the idea that the ecological niche of a species places long-term stable constraints on the geographical distributional potential of that species.

The bioclimate envelope modelling (BEM) approach has its foundations in ecological niche theory. Hutchinson (1957)

defined the fundamental ecological niche as comprising those environmental conditions within which a species can survive and grow: a conceptual space whose axes include all the environmental variables affecting that species (Leibold, 1995). A fundamental niche consists of the set of all conditions that allow for long-term survival, whereas its realized niche is that subset of the fundamental niche that the species actually occupies. Predictive modelling of the geographical distribution of a species based on the environmental conditions of sites it is known to occupy constitutes an important technique in analytical biology. In this context, a niche-based model represents an approximation of the ecological niche of a species in the examined environmental dimensions. In a study over a large region, spatial variation exists in the environmental conditions available to the species. It is expected that for large regions with typical spatial variations in

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environmental conditions, differentiated populations of the target species may exist, with each population occupying different steps within the fundamental niche of the species. These populations (clades) are obscured when niche-based models are applied to the entire area over which the species is distributed. Although a BEM describes suitability in ecological space, it is typically projected into geographical space, yielding a geographical area of predicted presence for the species. Given that the prediction engines are fed with every available record, geographically projected results can be dangerously biased if populations are not recognized and modelled separately (Osborne & Suárez-Seoane, 2002). There are also implicit ecological assumptions in the set of environmental variables selected for geographical modelling. Ignoring the significant set of variables that describe the distribution of a target species and delineating their populations across its range may lead to inconsistent results or lack of reproducible projections.

Previous studies have explored the relationships between abundance and remotely derived or surface interpolated surrogates for the ecological determinants of disease vector distribution and abundance. Modelling of tick distribution has already been addressed (Cumming, 2000; Estrada-Peña, 2001) for different species, sources of environmental variables and modelling algorithms. However, the impact on the model output of the distribution range of the target species, the existence of statistically different populations and the global importance of the ecological features supported by those, have not yet been adequately addressed. Although it is recognized that mechanistic models that describe the life cycle of prominent tick species are necessary to understand the intricate tick-borne pathogens cycles in nature (Randolph, 2002), there is still a lack of information regarding basic behaviour of the ecological requirements of the vectors.

Different methods have been proposed to predict species distributions based on presence data only. These methods search for an 'environmental envelope', characteristic of the points in which the species is present, to extrapolate to the remaining area under study (Guisan & Zimmerman, 2000). As larger areas are modelled, however, it is highly likely that heterogeneity in the predictor variables increases and that areas are included in which ticks respond to habitats in different ways because of differing ecological status. It is also reasonable to guess that if every record is used to feed the modelling algorithm, the final output will be a consequence of the dominance of records in a particular region. The difficulty in distribution modelling is that models assembled on one small area may not apply to other areas, whereas a single model built over a large area may have weak local predictive power.

The aim of this study was to address the statistical discrimination of the ecological niche of separate tick populations. The division in ecoregions was further used to produce an overview of the habitat in which the different populations of the tick *Ixodes ricinus* L. reside. The implications of these findings in modelling the distribution of the tick over large areas are further addressed.

Materials and methods

Ecoregions are designed to help to visualize and understand similarities across complex multivariate environmental factors

by grouping areas into categories (ecoregions). This study assumes that ecoregions can be delineated using quantitative abiotic characters, and that the shape of the multivariate Hutchinsonian niche associated with each ecoregion is statistically distinct. Thus, tick populations associated with each niche are subjected to different environmental conditions that can be further analysed. The procedure used herein involves spatial delineation of the different ecoregions of the western Palearctic according to multivariate rules, including the assigning of the tick records to environmental ecoregions and a statistical study of the climate that is experienced by every tick population to check for significant differences.

Classification and production of ecoregions

Multivariate geographic clustering uses standardized values for selected environmental conditions in a map of individual raster cells as coordinates that specify the cell position in environmental data space (Hargrove & Hoffman, 1999). This step is intended to produce a very high number of small cells (preliminary ecoregions) that will be clustered again according to similarity of environmental characteristics. The environmental feature selected to produce the unsupervised classification is monthly normalized difference vegetation index (NDVI) values. This is a parameter with biological meaning that has previously been used to delineate ecological regions (for a review, see Perry *et al.*, 2002). Monthly 1 km NDVI data were obtained between 1992 and 2002; the monthly average for this time period was computed. A multidimensional image composed of 12 monthly values was used for classification into ecoregions. The number of preliminary ecoregions to be detected by unsupervised classification was arbitrarily set to 3000.

This set of preliminary ecoregions was used to perform a hierarchical agglomerative clustering procedure. This is a tree-clustering method that uses the dissimilarities or distances between preliminary ecoregions to construct the final set of ecoregions. Mahalanobis distance was used as a measure of dissimilarity and the weighted pair-group average was used as amalgamation method. A value of 0.05 was included as the cut-off probability for assignment to a given ecoregion. The final output of this procedure is a classification of the large array of preliminary ecoregions into clusters, considered herein the final ecoregions.

Tick distribution dataset

This study is based on a set of records of *I. ricinus*, obtained from museum collections and published reports. The original purpose was to obtain both presence and absence records and to compare the multivariate ecological 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. A total of 3858 records were selected, which have an adequate reference to spatial coordinates and were collected between 1976 and 2000, to match the time period of the climate dataset.

Records were assembled from several sources. Some of them came from several systematic surveys at regional scale already compiled into reports or reviews (Spain, compiled by Estrada-Peña, 2000; France by Gilot, 1985; Greece by Papadopoulos, pers. comm.; Norway by Mehl, pers. comm.; Sweden by Talleklint & Jaenson, 1998; Czech Republic, by Daniel *et al.*, 2003; Latvia, Ministry of Health, pers. comm.). Some others were compiled at country level by several authorities (Portugal by Caeiro, 1999; Poland by Siuda, 1987, 1995; Italy by Manilla, 1998). 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 (Ireland, United Kingdom, the Netherlands, Denmark, Germany, Slovakia) and adequately published or obtained through the courtesy of collections curators. Because of its implications in the transmission of prominent pathogens, the distribution of the tick has been studied often in many areas of the western Palaearctic, therefore assuring an adequate degree of homogeneity in the records distribution. Care was thus taken to obtain a homogeneous sample of the distribution of the tick in the western Palaearctic, but both over and under-recording are expected following the impact of the tick in different regions. It is assumed that habitat preferences are fully described, all potential habitats 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. No attempts were done to include records from northern Africa, as *I. ricinus* is much restricted there (Bouattour *et al.*, 1999) and some bias is expected when using records from zones where the tick is marginal.

Climate features

A geographically extensive gridded data set that contains monthly records of temperature (mean, minimum and maximum) and precipitation (monthly total) at a resolution of 2.5 km was used. Because monthly climate values are commonly correlated (e.g. mean monthly temperature and maximum monthly temperature) and because of the lack of ecological information derived from these raw data, a set of 19 variables compiled from the raw data before was used (available at <http://biogeo.berkeley.edu>). These variables are the climate descriptors, as included in Table 1, and were involved in further statistical analysis.

Statistical analysis of climate for the discriminated ecoregions

Each record of the distribution of *I. ricinus* in western Palaearctic was assigned to one of the recognized ecoregions. It is implicitly assumed that each ecoregion has the same geographical

Table 1. The set of predictor variables used at 2.5 km of resolution over the study area

Predictor variable
1 Annual mean temperature
2 Mean diurnal range (mean of monthly maximum temperature – minimum temperature)
3 Isothermality ($2/7*100$)
4 Temperature seasonality (standard deviation *100)
5 Maximum temperature of warmest month
6 Minimum temperature of coldest month
7 Temperature annual range (5–6)
8 Mean temperature of wettest quarter
9 Mean temperature of driest quarter
10 Mean temperature of warmest quarter
11 Mean temperature of coldest quarter
12 Annual precipitation
13 Precipitation of wettest month
14 Precipitation of driest month
15 Precipitation seasonality (coefficient of variation)
16 Precipitation of wettest quarter
17 Precipitation of driest quarter
18 Precipitation of warmest quarter
19 Precipitation of coldest quarter

distribution as) the set of tick records (population or clade) assigned to it. The next step was to confirm that the proposed tick clades experience significantly different climate patterns, that the separation of records according to NDVI-derived ecoregions is accurate, and that they can be treated as being statistically different. This was done by ANOVA analysis of the descriptor variables, using clades as independent (grouping) variable. To provide additional support for the results obtained for this analysis, ANOVA was also performed on tick records grouped according to other clustering procedures. Records were grouped according to country, to the pertinence to a cell of an arbitrary grid of $4^\circ \times 4^\circ$ over the study area, and to vegetation categories derived from the CORINE and USGS schemes of classification. The CORINE and USGS schemes are systems of classification of the dominant vegetation commonly derived from satellite surrogates.

The distance that clades are separated in the multivariate space according to the descriptor variables was also computed and used to evaluate the relationships between clades. This was performed by factor analysis of the set of clades and descriptor variables. Coordinates in the factorial space of each record were used to compute the coordinates of the centroid of each population in the space of descriptor variables, and subsequently the distance between populations. Calculated distances between populations were used to construct a tree diagram of affinities between them.

Modelling of spatial suitability for the tick

The main goal was to demonstrate the different performance of spatial predictive models if based on complete or partial (clade-derived) distributional datasets. An additional aim was to find a method for producing the best modelling output by adequately

weighting the features of each clade according to its prevalence and environmental niche.

Ecological Niche Factor Analysis (ENFA) was used to estimate habitat suitability in the multivariate space of environmental variables using presence-only data (Perrin, 1984). This technique is based upon the computation of factors explaining the major part of species environmental distribution. A habitat suitability index of each cell is produced as a value that is inversely proportional to the weighted mean distance of the cell to the median of each ENFA factor, normalized in such a way that the suitability index ranges from zero to one (Hirzel *et al.*, 2000). Models were developed with a random training set and checked against an evaluation set. The total modelling approach used a training set consisting of 50% of the total tick records; this was then evaluated against the remaining 50% of the total tick records. A further modelling approach was developed, using data partitioning, with 50% of records from each of the detected clades of the tick. This model was applied in two different ways. First, models developed for each ecoregion (from records collected within that ecoregion) were applied only to the ecoregion of reference to check for local predictability. Second, habitat suitability was calculated for the entire study area as an average of values obtained from the algorithms developed for each ecoregion.

Model testing was done using the remaining 50% of records not used in the training set. Evaluating the performance of the model first required the derivation of matrices of confusion that identified true positive, true negative, false positive and false negative. From the values of the matrix of confusion we calculated Cohen's kappa; this provides a measure of the extent to which a model correctly predicts occurrence at rates that are better than chance expectations. Hence, Cohen's kappa was calculated for both separated ecoregions and for the whole territory.

Results

A total of 10 ecoregions were identified on the basis of multivariate spatial clustering classification of monthly NDVI-derived values (Fig. 1). Figure 2 shows plots of the seasonal amplitude of monthly NDVI values for ecoregions from which samples of *I. ricinus* were collected. *I. ricinus* was absent in ecoregion 1, corresponding to high altitude mountains. Three ecoregions (numbered 2–4) were recorded for the Baltic area, showing an NDVI pattern with high values during summer. Ecoregions 2, 3 and 4 contain only 1.3%, 4.3% and 6.9% of *I. ricinus* records. Ecoregions 5, 7 and 9 are defined in parts of Central Europe, the U.K. and Ireland, and are characterized by a sharp rise in NDVI profile during spring and a slow decrease over winter. In total, ecoregions 5, 7 and 9 account for almost 50% of the tick records (23.2%, 7.3% and 17.4%, respectively). Ecoregion 10 encompasses parts of France and central Italy, and accounts for 15.6% of the records. Finally, ecoregions 6 (5.8% of records) and 8 (18.2%) encompass large parts of Spain and Portugal, as well as small parts of the Mediterranean region. Although both of these ecoregions have a similar NDVI pattern, values for ecoregion 6 are always lower than for ecoregion 8.

Figure 3 provides the groupings of populations after factor analysis according to climate variables and hierarchical tree building. Figure 3 provides the separation of populations in the multivariate space (descriptor variables), whereas the geographical scope of these populations coincides with the ecoregions defined in Fig. 1. Numbering of these figures is also the same as ecoregions to improve comparative detection between figures. There exist three large clusters of populations. One of these comprises the single population 2 (P2), which is quite separated from the rest of the assemblages but closer to the main Central-European group of populations. Both P6 and P8 are also clearly separated from the main group of populations. Within the main cluster of tick records, P5 is a large assemblage, embracing P3 and P4 (well related), as well as P7, P9 and parts of P10, which appears to be less related to this large group than the other populations.

Records of *I. ricinus* grouped in clades according to these ecoregions show highly significant differences ($P < 0.005$) for the 19 descriptor variables used to test the hypothesis of homogeneity and tested by ANOVA. The P -values have less statistical significance values if records are grouped according to countries ($P = 0.304$), a $4^\circ \times 4^\circ$ grid ($P = 0.311$), the CORINE ($P = 0.191$) and the USGS ($P = 0.094$) vegetation classifications. Raw climate variables (minimum and maximum monthly temperature and monthly rainfall) experienced by each clade are included in Fig. 4. Clear differences between clades are evident. For example, there is an average difference of 7–8°C in minimum temperatures for different clades in July–August (compare P2 with P6 and P8 in Figs 4a and b). Even for clades with relatively similar climate values (e.g. P6 and P10), the difference in minimum temperatures is up to 4°C over any given period. Recorded differences in this parameter are even higher during winter: P8 and P9 record differences of up to 9°C during January. Similar results are observed for maximum temperatures. Patterns of monthly rainfall show greater differences between clades, both in terms of total rainfall and seasonal pattern, with some clades recording a marked period of drought in summer (i.e. P10 and, in particular, P6 and P8), whereas others record substantial summertime rainfall (P3, P4 and P5). Figure 4 also provides the number of days with temperatures above 6°C and the total accumulated °Celsius above 6° at days of the year 90, 180, 270 and 360. Population 8 has not been included in this part of the figure because it shows no significant differences with P6 in terms of the analysed variables. It is interesting to note that P6 and P8 are present in areas where average temperatures are above 6°C every day of the year, whereas other populations (e.g. P2 or P3) occupy areas with only 170–210 days a year above 6°C. In terms of total accumulated °Celsius above 6°C, P6 and P8 occupy areas with a high rate of accumulated degrees (up to 5400°C/day), whereas the second clade in the range (P4) bears an average of only around 4000°C/day.

The comparative performance of predictive maps is significantly different if records for the tick area used together (total approach maps) are compared with records used separately by ecoregions. Maps developed using records from the whole territory produce a Cohen's kappa of 0.642. Maps developed using records from each ecoregion and used to build partial models for each ecoregion had an overall kappa of 0.912 when

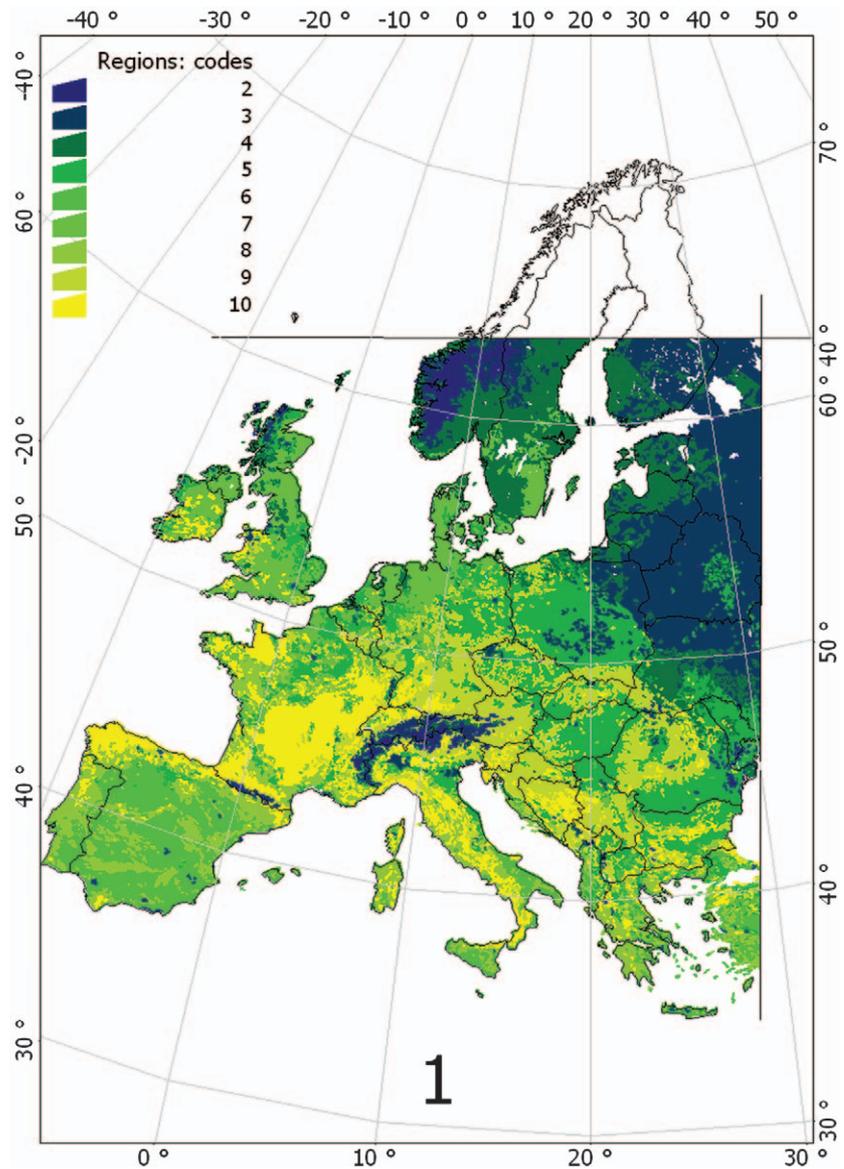


Fig. 1. The distribution of ecoregions in western Palaearctic, as detected by geographical multivariate clustering of monthly normalized difference vegetation index (NDVI) values. Each ecoregion is marked with a unique colour and number. The numbering of the ecoregion is retained for the clades of ticks as expressed in Fig. 3.

measured over the complete territory. Table 2 lists the partial (by ecoregions) and total kappa values recorded for the study region following the development of partial predictive maps from records from each ecoregion. It is interesting to note that different ecoregions vary markedly in terms of predicting adequate habitat for the tick within the single territory and for separate ecoregions. When records from a single ecoregion are used to map the entire study region, the overall agreements are always very low.

Discussion

This study focuses on the use of multivariate spatial clustering from NDVI-derived monthly layers as an objective method to recognize ecologically related clusters (clades) within a set of

records of the tick *I. ricinus* in the western Palaearctic. The rationale behind this approach is to partition distribution data for the tick over a large region into regions with ecological meaning, and to determine the environmental factors that are experienced by each tick population. The aim of the NDVI-derived stratification is to form a sufficiently detailed statistical zonation of Europe's environment with applicability to tick ecology, as well as being well correlated with climate data. ANOVA analysis shows that climate variables, as associated with these ecologically derived groups, have highly significant differences between clades; these differences are not observed when records are grouped according to pseudo-random rules (countries or grid) or even according to schemes of vegetation classification. Multivariate clustering based on fine spatial resolution has been used to produce a spectrum of quantitative ecoregions (Hargrove & Hoffman, 2004). NDVI values have been used in this study

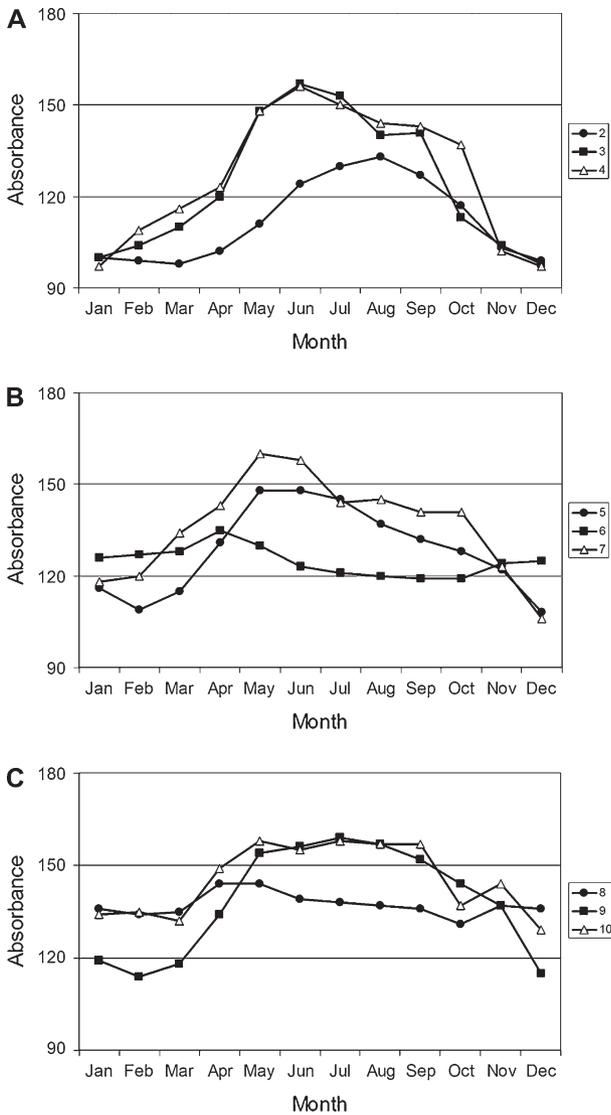


Fig. 2. Normalized difference vegetation index (NDVI) monthly patterns of the ecoregions depicted in Fig. 1. Each chart plots the monthly pattern of absorbance raw values for a given ecoregion.

because seasonal and spatial changes in this parameter are generally considered to be one of the most powerful single indicators of tick distribution (Estrada-Peña, 1999). It is argued that multivariate spatial clustering is a preliminary and objective step in the characterization of the ecological (multivariate) space within a large region, and is useful in ascertaining the degree of similarity of ecological forces that drive each population processes. The tick clades as detected herein are highly correlated with other statistically objective divisions of the habitat in Europe, such as the EnS (Environmental Stratification of Europe) (Metzger *et al.*, 2005), but show only a weak correlation with the potential natural vegetation (Olson *et al.*, 2001).

The use of climate to quantify the multivariate ecological space for populations of species or subspecies has already been

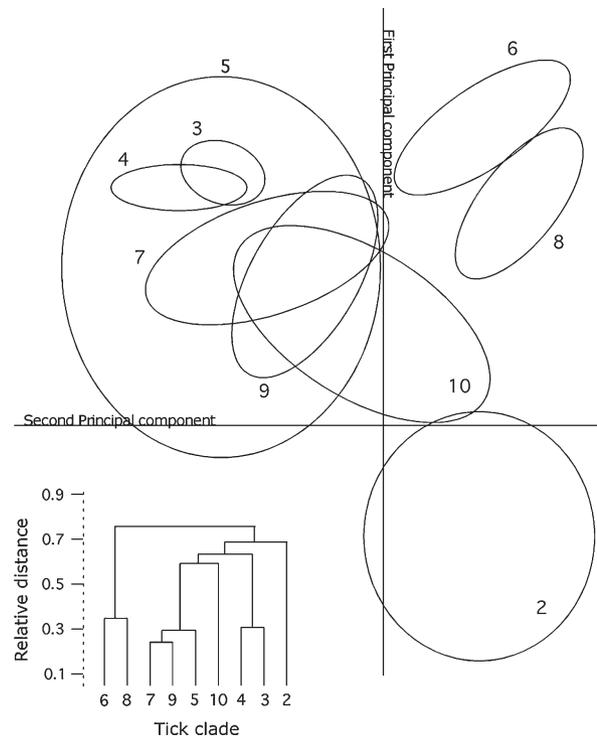


Fig. 3. Spatial distribution in the multivariate factorial space of the clades of *Ixodes ricinus* (components 1 and 2) detected in the western Palaearctic according to the climate predictor variables. The graph below shows the relative distances between clades. Each clade has the same numbering as the ecoregions in Fig. 1, to identify adequately their geographical distribution.

introduced in the research of arthropod-borne diseases (Costa *et al.*, 2002; Peterson & Shaw, 2003) or to understand the patterns of speciation of arthropod-borne pathogens (Randolph & Rogers, 2002). Although encompassing only a few possible niche dimensions, the environmental data set used in the present study covers many of the major physical variables that influence the distribution of ticks. These results demonstrate that tick populations as separated here represent different regions of the multivariate space of climate and not a casual representation of random patterns of distribution. A recent study on cuticular hydrocarbons of *I. ricinus*, used as phenotypic markers in arthropods, revealed the existence of several populations of this tick (Estrada-Peña *et al.*, 1996). These results provide a pattern of phenotypic distances between populations that is similar to the climate-derived patterns obtained in the present study. These parallel patterns of phenotypic- and climate-derived differentiation suggest that current processes of population segregation occur in several evolutionary dimensions, including ecological ones. The wide range of variation recorded for climate variables critical for different phases of the tick life cycle is highly suggestive of a varied pattern of ecologically related processes in the area of tick distribution. For example, the response of ticks to accumulated daily temperatures is responsible for the activation of questing stages and can modulate the effect of the sunlight on the onset of diapause (Gray, 2002). Large differences in

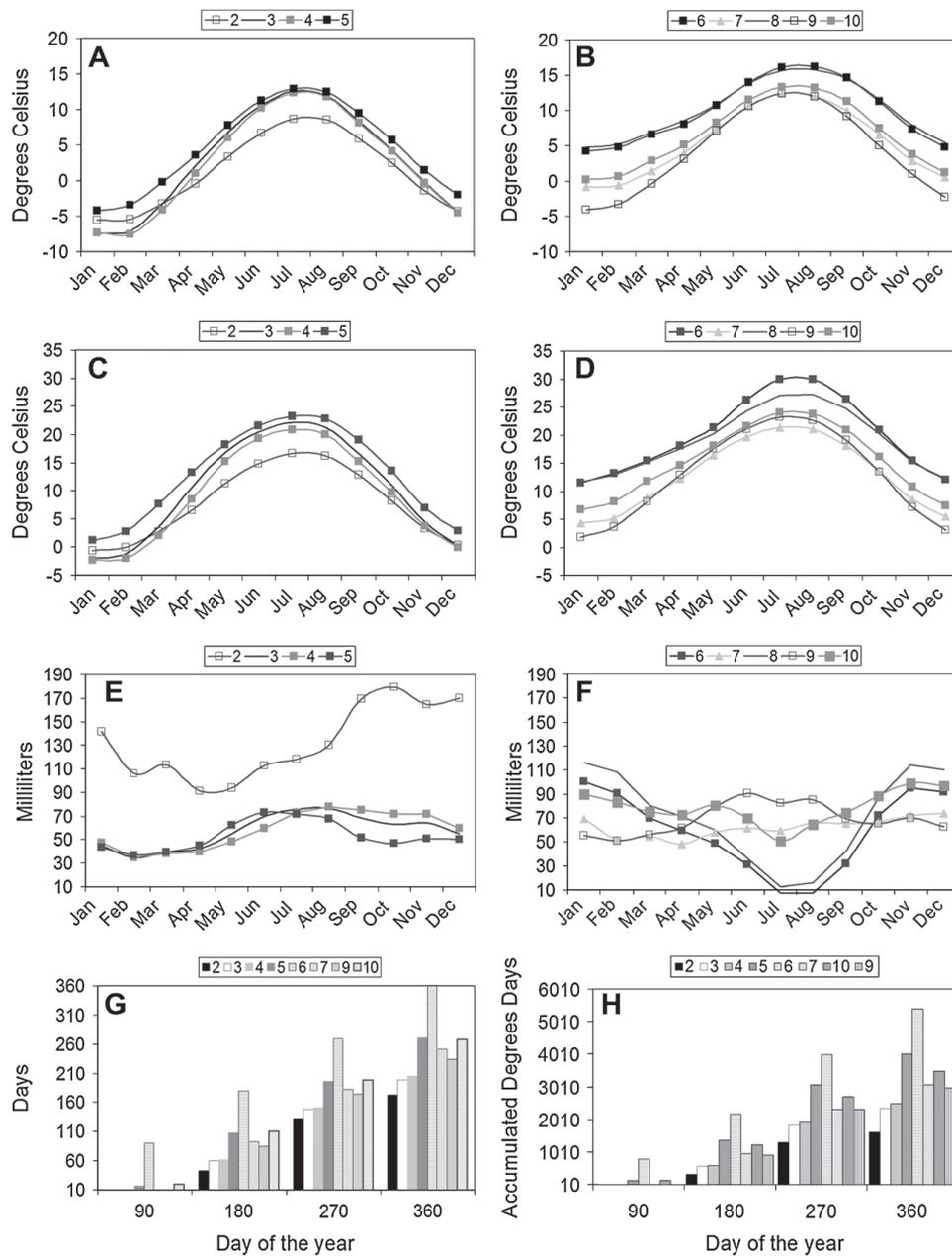


Fig. 4. Climate variables experienced by the different clades of *Ixodes ricinus* as associated. The figure includes monthly minimum temperatures (A and B), monthly maximum temperatures (C and D), monthly accumulated rainfall (E and F), number of days with temperatures above 6°C (G) and the total accumulated °Celsius above 6° (H) at days of the year 90, 180, 270 and 360. The legend includes the number of each population, being the same for clades in Fig. 3 and ecoregions of Fig. 1.

developmental rates have also been reported for a population of *I. ricinus* collected in the southern part of its distribution range (Estrada-Peña *et al.*, 2004) in comparison with developmental rates in northern populations (Walker, 2001; Randolph *et al.*, 2002). Most important, the biological response to climate-derived constraints, such as mortality, should be different for each clade, to accommodate the relatively few observed seasonal patterns to the wide range of climate niches recorded in

the current study. This represents an additional difficulty when environmental models are used to map the potential distribution of the species as well as its invasive abilities or life cycle constraints, as the marginality of the populations is diverse and there are significantly different distances in the multivariate space between populations. The performances of these populations under diverse climate conditions, together with adequate population genetic studies, should be addressed in the laboratory

Table 2. Cohen's kappa values computed using single ecoregions (left column numbers) to build models and predict habitat suitability for *Ixodes ricinus* at single ecoregions (top row headings) or for the complete western Palaearctic (right column) using only records from that particular ecoregion (each row). The bottom row includes the kappa values obtained for single ecoregions using the model built from the combined use of every ecoregion ('local predictability'). Bottom row right column is the kappa obtained for the predictions over the whole area of study using the models built for every single ecoregion and averaged for the whole area of study (italics and bold). Diagonal line (in bold) includes the kappa values when data from every single ecoregion are used to predict that particular ecoregion.

	2	3	4	5	6	7	8	9	10	All
2	0.60	0.41	0.38	0.29	0.20	0.15	0.45	0.41	0.44	0.31
3	0.21	0.77	0.76	0.51	0.35	0.41	0.32	0.61	0.54	0.34
4	0.21	0.61	0.78	0.38	0.29	0.42	0.31	0.49	0.37	0.38
5	0.22	0.67	0.69	0.81	0.39	0.51	0.49	0.58	0.51	0.51
6	0.11	0.19	0.21	0.25	0.79	0.31	0.69	0.59	0.49	0.44
7	0.24	0.67	0.67	0.61	0.31	0.88	0.49	0.79	0.76	0.49
8	0.18	0.34	0.39	0.58	0.75	0.54	0.83	0.59	0.69	0.30
9	0.27	0.69	0.70	0.72	0.33	0.78	0.41	0.79	0.68	0.41
10	0.16	0.51	0.64	0.75	0.49	0.79	0.49	0.74	0.84	0.44
All	0.69	0.89	0.92	0.94	0.81	0.90	0.81	0.84	0.81	0.83

to understand the ecological forces that drive the spatiotemporal patterns of tick distribution.

Partitioning of spatial data improves distribution models because it better accounts for regional variations in the data set (Osborne & Suárez-Seoane, 2002). This has previously been ascribed to geographical heterogeneity in predictor variables, but it is also important to consider geographical variation in behaviour and its interaction with environmental heterogeneity. It has been demonstrated in this study that predictive maps of habitat suitability constructed from records from a single ecoregion may have variable predictive power within that region, but predictability is invariably low if data from the single ecoregion are applied to the whole area of study. However, predictive maps are much improved if partial suitability maps are assembled from individual ecoregions and then averaged to obtain a final composite. If data partitioning improves model performance, then statistically superior models should result from the process of extrapolating results for each ecoregion, producing separate maps for each ecoregion, and then collating the different maps. The ecoregions and associated tick clades connected as formulated in the present study should be considered dynamic entities, although studies show that the main environmental boundaries in Europe remain stable over time (Metzger *et al.*, 2005). As the environmental multivariate niche to which each population is associated changes in space or as a consequence of long-term climate changes, the population adapts accordingly, either to close conditions in the multivariate space (specimens in the periphery of an ecoregion) or to the new conditions (specimens closer to the centroid of the ecological space of the population). Therefore, although statistically better, the use of 'static' ecoregions as geographically limited territories to receive the predictive output is not recommended here. Although not explicitly addressed in this study, the development of total-range models from the ecoregions using data partitioning would be considerably improved if an ecologically derived weighting technique were used to influence each ecoregion in terms of the total environmental niche of the species.

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