A framework to map abundance of tick metapopulations

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Abstract

This paper further explores a previously developed spatially explicit model that incorporates the effects of habitat topology and abiotic (climate) suitability on tick population density. The primary focus was to provide a parameterization of host dispersal, which is involved in the calculation of two critical parameters of the model, namely patch Traversability and Recruitment. We used a dispersal kernel that can accommodate a variety of dispersal patterns, varying the proportion of dispersing hosts as a function of patch size (v), and the dispersing range of hosts (r). Model values were compared with a set of tick densities from an actual landscape. Correlations were very poor for low v and r, but greatly improved (R² = 0.8–0.96, p = 0.0001) for high values of these parameters. This suggests the significance of long-range dispersers to keep this actual network of tick metapopulation patches. Further results of the dispersal kernel hint at the importance of short-range hosts in the maintenance of neighbouring, small, well-connected patches.

This abundance model involving climate suitability, habitat topology and host dispersal contributions, was applied to the tick *Ixodes ricinus* in a large area of northern Spain. The Recruitment at the patch level was calculated and used to forecast abundance of ticks across the study area. Sensitivity of every patch was defined as the response-range of Recruitment to quantitative changes in climate and topological features of the patch. To show how changes in the patch characteristics can dramatically alter the landscape composition and thence tick abundance, simulations were conducted in which the real landscape was modified by removing patches based on selected habitat features. The ecosystem was affected to the greatest extent by removal of patches of high sensitivity, large size, and high Recruitment. The proposed framework has particular utility for epidemiological studies aimed at evaluating the impact of climate change or habitat management on the survival of tick populations, and the health risks posed by ticks.

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1. Introduction

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patterns of environmental and biotic determinants. In the study of pathogens and vectors the guidelines provided by ecological risk assessment can be adapted to the risk mapping of vector-borne diseases, and are particularly suited to the study of emerging diseases and invasions of arthropods. In recent years there has been growing interest in how landscape affects the dispersion of ticks and the transmission of tick-borne diseases.

Although models have been developed to understand the effects of climate on tick dynamics, those models do not provide a framework within which to integrate the effects derived from abiotic (climate), topological (patch-derived) and biotic (host-related) factors on a metapopulation of ticks. Recently, efforts have been made to exploit metapopulation theory in the modelling of tick dynamics (Estrada-Peña, 2003). The distribution of ticks across a landscape is characterized by discrete patches of vegetation with high tick density interspersed with others where tick is present at low densities or even absent, all within a matrix of unsuitable habitat.

Prediction of the effects of climate and habitat modifications on tick populations requires a model that takes into account: (1) the abiotic properties, which reflect how ticks can survive and populate a site; (2) the movements of hosts through the landscape patches, which explain how tick populations are connected and how specimens are exchanged between patches. The persistence of ticks in any habitat will be influenced by the abiotic suitability of the habitat and the rescue effect produced by neighbouring populations through host interchange between patches. One shortcoming of previous models is that they ignore the effects of landscape configuration on tick populations.

A model explaining tick densities at the patch level including these aspects has been already built (Estrada-Peña, 2004). In this study we focused on parameterization of host dispersal across the landscape and its effects upon the predicted densities of ticks compared with actual tick counts. The model was applied to a large area to define the distribution of the metapopulation in terms of the abiotic features and patch connectivity. Simulations were then undertaken to demonstrate the effect of different scenarios of patch removal in this actual landscape on the persistence of disturbed populations.

2. Materials and methods

2.1. Parasitological and modelling background

The tick selected is *Ixodes ricinus* (L.) a prominent tick species in Europe that is responsible for the maintenance of several pathogens. In a previous study, two General Additive Models (GAMs) were developed and evaluated to predict the occurrence or abundance of *I. ricinus* in a set of patches. The occurrence model used remotely sensed data about temperature and vegetation stress. When applied to a test data set of 102 patches, it correctly classified 42 out of 46 (91.3%) sites known to be positive and 54 out of 56 (96.4%) sites known to be negative to the tick. According to the Area Under the Curve (AUC) method, 9 out of 10 pairs were correctly rated. The abundance model used one additional variable derived from the topology of the patches of the sampling area, called Traversability (TRA). According to graph theory (Urban and Keitt, 2001) the probability that an individual in patch *i* will disperse to patch *j* can be expressed in the form of a flux rate

\[
 f_{ij} = \frac{S_i}{\sum_{k} S_k} p'_{ij}
\]

where \(S_i\) is the area of patch *i*, \(S\) the sum of the areas of every available patch, and \(p'_{ij}\) the probability of dispersal from *i* to *j*, a direct function of the area of patches *i* and *j* and inversely related to the distance between patches. TRA is defined as the sum of partial dispersal flux probabilities for every link that is on at least on path connecting two given patches in the habitat. The output of the abundance models is the Recruitment (*R*), defined as

\[
 R = \sum_{i=1}^{m} S_i K_i TRA_i
\]

where \(S_i\) is the size of the patch *i*, \(K_i\) the abiotic suitability of that patch for ticks (as obtained by the occurrence model) and TRA the Traversability of that patch. The abundance model was able to explain much of the variation in the density of ticks found in a training set of 102 patches (*R^2* = 0.87, *p* = 0.001).
2.2 Sensitivity of the abundance model to host dispersal

Based on these previous developments, TRA emerged as a key variable for the abundance model. Ticks are passive dispersers depending upon host movements to invade other patches. Dispersal success then is a complex function of the amount of suitable habitat for host and ticks, the tick load on hosts and the dispersal rate of hosts between patches. The purpose of this part is to provide parameterization to the term $p_{ij}'$, in the definition of TRA, entering the abiotic and topological variables into the model and changing the variables in the equation below. It was assumed that habitat quality for hosts is homogeneous across the landscape and that the tick populations homogeneously use host species to disperse. To follow the spatial pattern of host dispersion and its rate of spread, we need detailed statistical data on dispersal distances together with the life history of the dispersing species. Because the catholic feeding habits of *I. ricinus* (Milne, 1949) of these data are currently unavailable for the whole range of animals used as hosts. Therefore, we used a dispersal kernel that can accommodate a variety of dispersal patterns (Clark et al., 1999)

$$p_{ij}' = \frac{v}{2\pi d_{ij}^2 \Gamma(2/v)} \exp \left( -\frac{r}{d_{ij}} \right)$$

where $d_{ij}$ is the distance between the centroids of patches, $r$ the mean dispersal distance of the host (km) and $\Gamma$ the gamma function. The parameter $\nu$ relates the proportion of dispersing hosts as a response to the patch size. It has been assumed that proportion of moving hosts has a simple inverse relationship with patch size (i.e. small patches allow high migration rates) and the $\nu$ parameter is simply a modifier of such a response in the gamma function. With decreases in $\nu$, the distribution has larger kurtosis. For example, when $\nu = 2$, it is a Gaussian with mean $\sqrt{\pi}d/2$. When $\nu = 1$ $\Gamma$ is an exponential damping function with a mean of $2d$, which is longer tailed than Gaussian.

Data on densities of ticks from an actual landscape of 204 patches (see Fig. 1) were used to assess the fit of the abundance model with variations of the parameters in the equation above. A range of values for $r$ and $\nu$ was obtained, TRA calculated for each patch and the abundance model for this actual landscape computed and checked against the actual tick densities. Spearman correlation was used to analyse the agreement between the outputs of the model and the actual abundance at every patch, whereas Pearson correlation was used to measure the amount of explained variation (Mittlböck and Schemper, 1996).

2.3. Ecological application

The purpose of the ecological application is to apply the model above to a wide area and check the effects of landscape composition and habitat loss on the persistence of a set of actual tick populations. A region in northern Spain (see Fig. 1) of about 500 x 300 km was selected. Climate and vegetation (NDVI) variables were obtained from the AVHRR sensor of the NOAA satellites. Quantitative data about temperature and vegetation were obtained daily between 1998 and 2000, and processed to obtain monthly composites. The set of temperature and vegetation variables providing the best fit includes yearly mean NDVI, absolute maximum NDVI, mean NDVI of the month with maximum values, yearly mean temperature, absolute maximum temperature, mean temperature of the warmest month and mean of maximum monthly temperatures. Other variables with potential interest had low contributions to the amount of variance explained and were discarded (Estrada-Peña, 2004).

Sensitivity is the rate of change in $R$ for a patch over a range of the variables governing this value, such as area, connectivity with other patches and TRA. Sensitivity is a powerful parameter measuring the range of response of a patch under an array of stimuli. Sensitivity was computed for each patch varying by ±10% (in steps of ±5%) the parameters of area, mean distance to connecting patches and each of the seven abiotic variable used in the model. Parameters were varied individually and the Recruitment for each patch recomputed for every combination of variables. Sensitivity is obtained as the difference within the maximum and minimum Recruitment values obtained for the group of varied parameters.

To assess how selective modifications of the habitat affect the $R$ values across the study region, we simulated habitat loss by removing carrying capacity. Various scenarios were considered. Two scenarios were constructed by removing the patches whose areas were within the 10% and 20% intervals of the smallest area values (AI10 and AI20), and another two scenarios...
were produced by removing the 10% and 20% of patches with the largest areas (AS10 and AS20). Two additional scenarios (HS10 and HS20) were obtained by removing patches in the upper 10% and 20% ranges of abiotic suitability values. In addition, four scenarios were considered in which patch removal was carried out based on the sensitivity. In two of these (S10 and S20), the 10% or 20% of patches with the highest sensitivity were removed. In the other two scenarios (C10 and C20), patches were removed based on a combination of parameters. In scenario C10, the removed patches were those that were simultaneously within the 10% of patches having the highest sensitivity, the 10% of patches with highest area, and the 10% of patches with the highest habitat suitability. Scenario C20 was similar to C10, except that the limits for all variables were set at 20%. Fragmentation was simulated in the present work by taking the 10% of patches with the highest area and dividing them into two contiguous patches with the same abiotic suitability (FRAG scenario).

For every scenario, the $R$ values were calculated for the new configuration of patches. The results of the removal analysis cannot be interpreted at the patch level; hence we overlaid the territory with a grid of 5 × 5 km. Patches enclosed by each cell of the grid were selected and the averaged values of total and mean patch area, total and mean length of links, number of links and total $R$ for each patch were obtained for all the patches contained within the cell. If a patch was not totally enclosed by a cell of the grid, area-proportional variables of the patch were included into the cells of the grid enclosing the patch. To understand how scenarios modify the initial data set, an ANOVA
was performed on various categories of variables in the original landscape. Cells of the grid were grouped into five equal-count categories according to their characteristics of total and mean area of patches, number and length of links, and total $R$. Then, ANOVA was performed separately for each category, to determine whether a given scenario has a greater effect on cells within a particular range of patch and link features.

### 3. Results

#### 3.1. Influence of dispersal behaviour on the predictive fit of the model

The correlations between the output of the model and actual tick density data for the range of values in the host dispersal kernel are shown in Fig. 2. Correlations are very poor at low values of $v$ (small proportion of dispersing hosts) and medium-large values of $r$ (dispersing range of hosts). Correlations are greatly improved ($R = 0.8–0.96, p = 0.001$) at high values of $v$. Highest correlations were obtained for the range of maximum $v$ (1.2–1.5) and $r$ (around 6–10 km). Interestingly, a region of medium correlations ($R = 0.6–0.8$) were obtained at low $r$ values (short dispersing hosts, 0.3–0.6 km) for the whole range of $v$ values.

#### 3.2. Ecological application

The ecological application provided a map of $R$ in the selected area. The visual inspection of that map shows three main zones in which $R > 0$ (Fig. 3) with different properties. The first zone is a large area in the north-west of the region, with a total of 24,405 patches, a mean patch area of 1566 ha (range: 1.29–1,476,493 ha) and a total of 30,439 possible links of mean length 477 m. This area has a mean $R$ of 79.54.

The eastern edge of this first zone is characterized

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Fig. 2. Correlations of actual tick densities vs. model predicted Recruitment values for the training set of patches as obtained with variable rates for $r$ (mean host dispersal rate, in km) and $v$ in the host dispersion kernel.
Fig. 3. Conditions of the *Ixodes ricinus* metapopulations in the area selected for the ecological application. The plates show the patches where $R > 0$. (A) Distribution of $R$ values (range 0–100), (B) area of each patch in ha, (C) sensitivity of each patch (range 0–1).
by a transition to scattered, large, loosely connected patches, largely unconnected with the first zone. A total of 910 patches with $R > 0$ were identified in this "eastern zone" (mean area: 1089 ha; range: 128–193,607 ha) with 1001 links (mean length: 1566 m). The mean $R$ of this zone was 53.47. This zone remains cohesive because of the large mean patch area and the presence of long-range links. However, the overall connectivity and $R$ in this zone are consistently low. The third zone of suitable habitat for $I. ricinus$ was detected to the south of the first, main zone. This "southern zone" had a total of 3054 patches with $R > 0$, with mean area of 2581 ha (range: 86.78–145,219 ha) and 3707 links (mean length 597 m). The mean $R$ of the region was 60.88. Mean sensitivity was low for the main northern zone, high in the eastern one and intermediate in the southern region.

The patch removal scenarios C10, C20, VM10, VM20, AS10, AS20, F10 and F20, but not scenarios AI10 and AI20, produced significant changes in $R$ at the 5 × 5 km grid level, as detected by ANOVA. Interestingly, the increased fragmentation through the FRAG scenario did not significantly affect $R$. Table 1 lists the values of the parameters characterizing the landscape (number of links and their total length, mean and total area, and total $R$) at the overlaid grid level for the original landscape as well as for the landscape modified according to the various scenarios. In zones whose original landscape was characterized by large patches or high original $R$ values, removal of patches via any

Table 1

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Cells in the grid were grouped into five equal-count categories according to the variable concerned. The column C indicates the category. The column "value" includes the mean values of the variable for that group of cells in the original landscape. The remaining columns give the percentage of the value of the variable retained by the cells of a category after the patch removal experiment. NS: no significant difference.

* $P < 0.5$.
** $P < 0.1$.
*** $P < 0.05$. 

...
scenario led to drastic changes in the mean area, total area, and total length of links and the total length of those links inside each cell of the grid were insensitive to patch removal.

Fig. 4 shows the geographical distribution of $R$ values at the 5 × 5 km grid level, together with the percent of $R$ retained for each grid cell after application of the various scenarios. All the scenarios displaying a significant ANOVA value had a clear effect on the distribution of areas suitable for tick colonization, even on the well-established populations in the north-west of the region. Scenario C20 produced a very large decrease in $R$, and resulted in the eradication of most patches suitable for tick colonization in the study area. The areas most drastically affected by patch removal were those in the southern and eastern parts of the study region, where the original landscape was characterized by smaller numbers of links and larger patch sizes. It is interesting to note that scenarios VM10 and VM20 had the smallest effect on the isolated eastern populations.

4. Discussion

This study further explores a model for mapping abundance of tick metapopulations at the patch level that includes the effects of habitat fragmentation, patch connectivity, and abiotic suitability. The proposed model yields the colonization probability of a tick species in a landscape, and hence can be used to elucidate the dependence of tick persistence on both the spatial structure of the landscape and the climate patterns. The form of the proposed model grew out of the results of previous fieldwork.

There is currently a lack of adequate, objective and reproducible methods to delineate the effects of climate and landscape configuration on the persistence and dissemination of tick metapopulations. Previously, models have been developed that predict the presence of ticks based on vegetation preferences (Daniel et al., 1998), climate alone (Estrada-Peña, 1999) or through the use of landscape and host-derived variables (Furlanello et al., 2003). However, vegetation-based methods are static in the sense that they provide a picture of the situation but are unable to account for changes in tick populations over time. Furthermore, both types of model ignore the fact that highly suitable patches may remain uncolonized if they lack adequate connections with other patches. The basic assumption on which the proposed model is built, namely that the landscape consists of a network of discrete patches among which ticks move by riding on host species, modulating the climatic suitability of each patch of vegetation, fits well with the situation in the field (Estrada-Peña, 2004). Landscape connectivity is the degree to which the landscape facilitates or impedes movement of organisms among source patches (Tischendorf and Fahrig, 2000). It is usually expressed as a function of the cost of moving between patches, usually assumed to be a function of the distance between patches. Ticks are passive dispersers in the sense that they cannot actively explore the different patches available in the habitat matrix; they can only move between patches while feeding on hosts. Dispersal success refers to the probability that an organism can locate suitable habitat on a landscape. Dispersal success is calculated as the fraction of individuals that successfully locate and occupy new habitat (Doak et al., 1992; With and King, 1999).

In ecological applications such as that considered here, straightforward ecological considerations suggest that the colonization and extinction rates should in general be related to the physical attributes of the patch network in which the metapopulation occurs (Hanski, 1994). If all other factors are the same, the population of a patch should scale with the area of the patch corrected for abiotic habitat quality. Given that the extinction rate generally decreases with increasing population size (Schoener, 1991), it follows that the risk of extinction also scales with the patch area. Thus, the smallest patches will make only small contributions to the connectivity of existing populations. Furthermore, increasing the distance of a source from a target patch will also decrease the contribution of the source to the target (Hanski, 1994). Parameterization of the dispersal kernel was done on the basis of straightforward ecological considerations.
above, entering into the model the abiotic and topological parameters of patches and exploring the effects of the variables included in the dispersal function on the predictive outputs. These experiments showed an improved fit to the actual tick density value in a range of $v = 1.2-1.6$ and for dispersal ranges around 6–10 km. Correlations of model output with actual data were very poor at other ranges of parameters, suggesting that host dispersal has a crucial impact on the maintenance of natural tick populations. It is evident that the ability of a metapopulation to persist in a fragmented landscape depends on the characteristics of both the species and the landscape. A habitat patch network that is very sparse will only be able to support highly dispersive species. Long-range dispersers (mostly ungulates) are common hosts for enzootic females of *I. ricinus*, which are seeders for a new generation of ticks, and thence important for the establishment into new habitat. Short-range animals feed commonly immature stages of the tick (Matuschka et al., 1991) which seem to be of smaller importance in the maintenance of the tick metapopulation. Probably, the later play a role while keeping small, contiguous, well-connected patches, allowing an interchange of immature ticks within local networks. This is observed as a medium (0.6-0.8) correlation values between predicted and actual tick densities in the range of short-dispersal hosts (0.3–0.6 km) for various values of the dispersal parameter $v$.

Sensitivity has been computed as a property inherent to the patch. It is a powerful parameter, which coupled with TRA, $R$, and abiotic suitability explains the most important features of each patch. Specifically, sensitiv-
ity is derived from the ability of a patch to retain its $R$ value under relatively narrow variations in abiotic and topological conditions. The geographical distribution of sensitivity values across a landscape clarifies the status of the population in the studied area. Sudden changes in population density, as a consequence of high sensitivity, should be expected in patches prone to rapid variations in climate or in areas subjected to habitat perturbation, allowing changes in patch connectivity. The habitat removal scenarios imposed upon the ecological system considered in the present study show how the areas that support permanent tick populations are characterized by many small patches structured around a few large patches, with many inter-patch links. Removal of patches from such areas produces only trivial changes in the $R$ at the grid level because new links emerge between the remaining patches. In contrast, removal of patches from systems containing only large, isolated patches tends to lead to the extinction of the tick metapopulation because the sensitivity is extreme due to the low number of links. The removal of a large patch also affects the smaller, contiguous patches, which depend on this “key patch”. Verboom et al. (2001) defined a key patch as one with a carrying capacity large enough to sustain a relatively large local population in a network, and close enough to other patches to maintain an exchange of individuals. The modelling results presented here strongly suggest that the colonization probability of *I. ricinus* is higher in physically highly heterogeneous habitats, with small patches (i.e., with many links), and in the vicinity of a large patch. Several field studies (Kitron, 1998) have shown that areas of extreme tick density are highly fragmented habitats, in some cases located near large patches of suitable habitat. Interestingly, scenarios AI10 and AI20 (removal of smallest patches) did not significantly affect $R$ because the removal of only small patches does not affect the main habitat features. Provided that a sufficient number of new links at the dispersal distance are created after patch removal. Severe effects on habitat configuration were observed when the patches with the highest fragility and highest $R$ were removed (scenarios C10 and C20). This highly selective removal procedure involves the removal of less than 5% of the number of patches from the landscape (because it selects patches with a given $R$ range within the initial selection of 10% or 20% of highest sensitivity), yet it has the most destructive effect on the overall metapopulation performance.

This is the first time a metapopulation-based spatially explicit model is applied to the prediction of tick abundance founded on the environmental niche of the tick populations, and showing that landscape patches have a contextual importance. The model presented herein explains the spatial variation of tick abundance in a given set of patches but is not adequate to depict the short-term temporal component of population change other than climate derived seasonal variation (abiotic component of the model). Important differences exist in the management of host characteristics compared with other metapopulation structured models of parasites (i.e. Singh et al., 2004). It has been recognized that temporal changes in host density as a consequence
of resource availability can account for large variations in tick abundance (Randolphi, 2001; Schaubert et al., 2005). Temporal changes in host density may be modelled for each patch when dealing only with a few local populations or with one species of host (Akçakaya and Sjögren-Gulve, 2000). However, if the number of habitat patches/local populations is hundreds or the modelled parasite uses a wide range of hosts, dealing with local host dynamics reliably becomes very difficult. The wide geographic range of I. ricinus renders parameterization of host abundance generalist and restricted to a direct relationship between patch area and resources for hosts.

It is widely acknowledged that corridors linking patches are pivotal to the structure of metapopulations (Jepsen et al., 2005). The model retains these features as derived from graph theory (i.e. Bunn et al., 2000) and utilizes different dispersion kernels to simulate the use of different types of hosts by the tick. Dispersal of animals has been adequately modelled (Reed and Levine, 2005) and remains a matter of incorporate behaviour into the host component of the model. This is another difference of the model introduced herein with other metapopulation-structured models, again as a consequence of the wide range of hosts used by the modelled tick species. Local unevenness in actual host use after host availability at each patch renders parasitic pressure on different host species complex to model for the whole landscape. Therefore, simple, direct relationships between hosts and parasites have been used herein.

The framework presented here has wide applications in the fields of epidemiology and vector risk mapping. A large amount of conjunctural work has been done on the effects of climate change on ticks. Perhaps the most important field of applicability is the use under scenarios of climate change, using explicit loads of ticks on hosts and exploring the effect of different patterns of climate on the abiotic parameters of the model, then displaying how the whole metapopulation is affected. In the control of tick-borne disease an actual landscape can be managed under selected conditions of climate change and landscape configuration, like the viable-habitat network developed by Nikolakaki and Dunnett (2005). Such risk maps can play a major role in refining research questions and surveillance needs, and in guiding control efforts and field studies.

References