



## UvA-DARE (Digital Academic Repository)

### A resource-based habitat concept for tick-borne diseases

Vanwambeke, S.O.; Li, S.; Hartemink, N.A.

**DOI**

[10.3920/978-90-8686-838-4\\_14](https://doi.org/10.3920/978-90-8686-838-4_14)

**Publication date**

2016

**Document Version**

Final published version

**Published in**

Ecology and prevention of Lyme borreliosis

[Link to publication](#)

**Citation for published version (APA):**

Vanwambeke, S. O., Li, S., & Hartemink, N. A. (2016). A resource-based habitat concept for tick-borne diseases. In M. A. H. Braks, S. E. van Wieren, W. Takken, & H. Sprong (Eds.), *Ecology and prevention of Lyme borreliosis: Ecology and control of vector-borne diseases* (Vol. 4, pp. 205-216). Wageningen Academic Publishers. [https://doi.org/10.3920/978-90-8686-838-4\\_14](https://doi.org/10.3920/978-90-8686-838-4_14)

**General rights**

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

**Disclaimer/Complaints regulations**

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

## 14. A resource-based habitat concept for tick-borne diseases

Sophie O. Vanwambeke<sup>1\*</sup>, Sen Li<sup>2</sup> and Nienke A. Hartemink<sup>3</sup>

<sup>1</sup>Université catholique de Louvain, Earth & Life Institute, Georges Lemaître Centre for Earth and Climate Research, Place Pasteur 3, 1348 Louvain-la-Neuve, Belgium; <sup>2</sup>Environmental Change Institute, University of Oxford, South Parks Road, Oxford OX1 3QY, United Kingdom; <sup>3</sup>Theoretical Ecology group, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, the Netherlands; [sophie.vanwambeke@uclouvain.be](mailto:sophie.vanwambeke@uclouvain.be)

### Abstract

Because tick and tick-borne disease distributions are so tightly linked to the environment, a robust conceptual background is necessary to build useful empirical and process-based models and to interpret results coherently with pathogen, vector and host ecology. This is especially pressing when considering that tick-borne pathogen circulation is a complex ecological system that has been studied in a great diversity of ways, producing results that may appear challenging to synthesise. We propose that a resource-based habitat concept can provide helpful leads to collect data, elaborate models and interpret and assemble upcoming and existing results. Two elements in the existing knowledge and its gaps, and in the current ecological context encourage us to explore such a conceptual framework. First, it is rare in the current practice to focus on the ecology of the pathogen, whereas this may be a key element in understanding the role of biodiversity in pathogen circulation. Second, the role of non-classical tick habitats (e.g. forest encroached areas and meadows) is getting more and more often highlighted, indicating that summarising tick habitat, or pathogen habitat, by a single vegetation class is not suitable. We revisit two simulation models (a cellular automata and an agent-based model) that focus on infected ticks and on tick population dynamics. In these models, the potential of a resource-based habitat concept can be highlighted. We then discuss how to implement this concept for studying the ecology of tick-borne pathogens.

**Keywords:** biological resources, environmental factors, functional habitats, movement ecology, tick-borne pathogens

### Introduction

Tick distribution and tick-borne disease transmission is closely tied to the environment (e.g. Medlock *et al.* 2013, Randolph 2001). This relates to the fact that ticks, the pathogens they may host, and the organisms they feed from all have specific habitat requirements. Identifying these requirements allows identifying and predicting the riskiest environments and, potentially, modifying these conditions to make them less suitable for pathogen circulation and transmission.

Studies investigating associations between environmental factors and elements of tick-borne disease transmission systems have been carried out in many different ways: examining different groups of environmental factors, using different entry points into the system (i.e. the variable to be explained or predicted by a quantitative model), or different methodologies. Environmental factors highlighted for ticks, their hosts, and their pathogens range from regional or continental-scale environmental factors to the micro-scale. At the regional or continental scale, environmental factors considered mostly aim at identifying the climatic envelope of ticks: where are climatic conditions suitable for ticks to survive and develop. These factors are mostly considered at a coarse scale and are monitored using remote sensing or interpolated weather station data such

as WorldClim (<http://www.worldclim.org>) (Estrada-Peña *et al.* 2006, 2016). At the landscape scale, focus usually shifts to the fine or mid-resolution habitat characteristics mostly related to vegetation. Land cover maps are often used and can be processed to describe various elements of the landscape such as composition (how much of a land cover) and configuration (how it is arranged) (Dobson *et al.* 2011b, Halos *et al.* 2010, Vanwambeke *et al.* 2010). Finally, some studies also focus on fine scale characteristics of the environment that can cover weather conditions (instantaneous or short-time scale temperature, relative humidity), fine scale vegetation and soil conditions, such as presence of ground vegetation or litter (Gassner *et al.* 2011, Randolph and Storey 1999, Tack *et al.* 2012). Few studies combine scales of studies (De Keukeleire *et al.* 2015, Jore *et al.* 2014, Li *et al.* 2012b).

Studies may also use different entry points, that is, look at different dependent variables or model outputs. Often used entry points are the presence and abundance of (infected) ticks, usually measured through flagging (Barandika *et al.* 2006, Boyard *et al.* 2011, Richter and Matuschka 2011). Other entry points related to the vector include counting ticks on hosts (Carpi *et al.* 2008, Claerebout *et al.* 2013), and reports by veterinarians (Jore *et al.* 2011). Other used or potential entry points include infected hosts (Juřicová and Hubálek 2009), tick bites (in a survey or in citizen or at-risk population reports) (De Keukeleire *et al.* 2015, Hugli *et al.* 2009), and human disease cases (Linard *et al.* 2007, Zeimes *et al.* 2014). The latter, using human case reports, is an attractive option as it relies on the most systematic, spatially exhaustive and temporally deep datasets available, whether the disease considered is reportable or not. However, it adds the important filter of reporting and exposure. Domestic animals serology libraries offer an interesting alternative with temporal depth (Jore *et al.* 2014), but an exposure filter persists for most domestic animals populations. The consequence of this diversity of measurements of the intensity of tick-borne disease transmission is that we are effectively looking at the process through keyholes, none of which allow us to get an extensive view of the phenomenon, either because it is practically difficult to get a large number of consistent measures, or because the measure can only report on a part of the system. This is why studies on tick-borne disease transmission are often considered to only assess the emerged part of an iceberg (Randolph and Šumilo, 2007).

Methods encountered include both empirical studies (most of the studies cited above), or process-based models that attempt to model the effect of host, host habitat, tick habitat or weather and climate variables on tick emergence and population dynamics (Dobson *et al.* 2011a, Hancock *et al.* 2011, Hoch *et al.* 2010, Ogden *et al.* 2005).

While a wealth of results has come out of such studies, our understanding of how the observed associations relate to the ecology of tick-borne disease transmission remains proportionally poor, and can be confusing to those less acquainted with ecological modelling. Results may appear contradictory, while they may simply reflect different local conditions, or a focus on a different part of the system. A striking example of this concerns habitats described in some areas as of intermediate suitability, whereas in some regions they may represent the best habitat available and therefore the most significant one (for an example on hantavirus, see Zeimes *et al.* 2015). Because some such habitats are related to intense human exposure to tick bites, they are of high relevance from a public health perspective. Also, the choice of a scale of study is often suggested as more advantageous than another, whereas they are complementary, as is the case in most ecological processes (Forman 1995).

In this paper, we identify and discuss two specific challenges that are currently poorly addressed in most empirical studies, such as those cited above, or the less numerous process-based studies.

First, few studies include the ecology of the pathogen in their focus. This is a key element for modelling tick-borne disease transmission, particularly considering the role of biodiversity on the circulation of pathogens. This is beginning to be conceptually formalised but it is still poorly represented in models, with many studies producing apparently idiosyncratic results. Second, more and more studies are pointing towards the role of non-classic environments for ticks, primarily non-forest habitats (Hartemink and Takken 2016, Rizzoli *et al.* 2014, Špitalská *et al.* 2016, Uspensky 2014). Several reasons can be highlighted for their possible role: they are suitable habitat for tick hosts; transitional environments (e.g. bushy areas, forest encroached areas, grasslands) are a major feature of landscapes in some regions, or one that is expanding (Estel *et al.* 2015, Meyfroidt and Lambin 2011, Navarro and Pereira 2015); or these areas are highly suitable for human exposure to infected ticks. It is becoming clear that there is not just one type of vegetation or land cover that is linked to tick-borne pathogen (TBP) transmission. This highlights the need for a new perspective on the role of the landscape in shaping the risk of TBP transmission. Focusing only on forests as risk areas is clearly not sufficient, we need to look at other vegetation and land cover types as well, provided that the conditions in those areas are suitable for TBP transmission. Assessing whether this is the case, requires a framework that incorporates the link between landscape factors and the functional ecology of the actors involved in TBP transmission (ticks, hosts and pathogens).

We propose that a habitat concept focusing on ecological functions and their associated resources for all species involved – not only for the vector or for the hosts, but also for the pathogen – as drawn from conservation ecology, can bring a robust and useful perspective on these questions and help consolidate both existing knowledge and future studies. In our conceptual model, the organism of focus is the pathogen considered. After presenting the concept and its adaptation to tick-borne pathogens transmission systems, we revisit existing models in the light of the resource-based habitat concept and discuss a few lines for implementation of the concept to better understand the ecology of these diseases.

### **The perspective of functional ecology: the resource based-habitat concept**

In a functional ecology perspective, we adopt a focus on the organism and its ecological requirements, rather than approaching it from the angle of habitat characteristics or classes such as vegetation types. Initially proposed in the field of conservation biology (Dennis *et al.* 2003, 2006), this approach has been conceptually adapted to deal with vector-borne diseases (Hartemink *et al.* 2015) and illustrated with the case of bluetongue virus. At various life stages, an organism needs to be able to carry out a certain number of functions (e.g. feeding, mating, diapausing). These functions can be associated to specific resources found in the environment, which can be either a consumable (e.g. host plant for an herbivorous insect) or utility (e.g. suitable micro-climate). The resource-based habitat concept (RBHC), in line with the classical ecological niche concept, considers in a bottom-up way the ecological resources needed by the organism of interest (here, the pathogen) to complete its life cycle, from which a functional habitat arises. In order to determine whether a habitat is suitable for an organism, the RBHC explicitly takes into account the movement capacity of animals and the distance between the different resources needed during all life stages of the organism. This means that a habitat may not correspond to a single land cover or landscape patch type, but rather to a combination of different land cover types or landscape elements, that offer all required resources within a range than can be covered by the individual.

## A resource-based habitat concept for tick-borne diseases

The primary purpose of RBHC is to set up a conceptual framework, which can subsequently be used in various ways to support modelling (Hartemink *et al.* 2015). Here we present the structure of the concept as adapted to TBP, generally, illustrated with *Borrelia* spp. The concept is illustrated in Figure 1. In this general model, we focus on fine-scale environmental features and ecological interactions, and assume climatic conditions favourable to pathogen, vectors, and hosts.

### Pathogen level

Three essential functions are identified for vector-borne pathogens: replication in the host, replication in the vector and transmission. This can be identified for any TBP. Two resources are thus necessary to complete the life cycle: reservoir hosts and vectors. Their functional habitat needs to be considered as well. In the case of *Ixodes*-borne diseases, many reservoir hosts need to be considered, also depending on which pathogen is considered. For *Borrelia burgdorferi* genospecies of public health relevance, the role of rodents can be highlighted, especially *Apodemus* spp., particularly as vectors of genospecies *Borrelia afzelii*, and of birds (*Borrelia garinii*, *Borrelia valaisiana*) (Lommano *et al.* 2014, Mannelli *et al.* 2012).

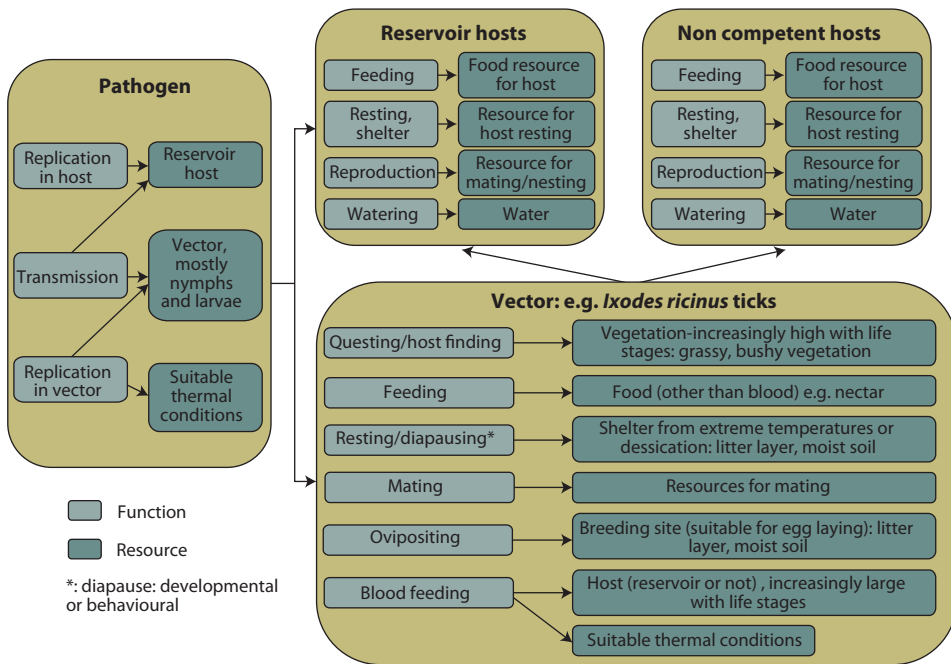


Figure 1. Application of the resource-based habitat to tick-borne pathogens. Identification of the functions (light grey boxes) and resources (grey boxes) is first done at the level of the pathogen and then at the level of both the vector and hosts. A box for non-competent hosts is added to account for their role in tick reproduction and population dynamics.

### Vector level

Vectors are a necessary resource for the vector-borne pathogen functions of transmission and replication in the vector, and vectors have their own functions and resources that need to be accounted for, which include hosts. For *Ixodes* vectors, a number of functions will be the same for all motile life-stages (larvae, nymph, adult) but correspond to different resources (Figure 1), with older life-stages generally feeding on gradually larger hosts, and questing higher on the vegetation. Larvae quest on low, grassy vegetation and feed primarily on small mammals and birds – among which many reservoir host species are found, while adults quest also on bushes and on larger animals, such as deer, often as a result considered as key for reproduction. Each stage takes a single blood meal over three to seven days. When not questing or attached to a host, for oviposition, for eggs to moult into larvae, ticks require a protective layer of litter, such as what can be found on the ground of deciduous forest. Tick movement is extremely restricted and mostly vertical along the vegetation. Ticks can however end up far from their place of hatching as their feeding hosts can move considerable distances – host movement capacity is therefore the main component for tick spread.

### Host level

While their functions and resources may not differ greatly, or not differ in relation to this divide, we need to consider two types of tick hosts: those competent for supporting pathogen functions (that are thus a pathogen resource as well as a tick resource) and those that are not competent (i.e. in which no systemic infection/pathogen replication is observed) and that only support tick functions. As some tick species, in particular those considered here in priority (*Ixodes* spp.), are opportunistic feeders, it is not feasible to list here all possible host species and their associated resources but when looking at *Borrelia burgdorferi* we can make a general distinction between reservoir hosts (including many rodent species) and non-competent hosts (that include e.g. red deer, roe deer). It is necessary and useful to assess which areas of the landscape, including in the sense of a combination of spatially explicit land cover or vegetation types, contain the set of resources for possible hosts. This will lead to consider specifically host movement capacity, permitting or not to access the necessary combination of resources for survival. Likely, it is a combination of land covers that holds the resources making up a host's habitat, also considering that resources will be needed in sufficient quantities.

This brief outline focuses on the general concept and did not outline precisely the functions and resources of specific species concerned here, which would be beyond our scope. Our main purpose is to present the concept and highlight its potential when studying TBP. Also, considering the resource needs of the vector(s) as well as of the hosts sheds light on why such diverse habitats have been identified as favourable for tick-borne disease transmission in the general sense of the term.

### Cellular automata and agent-based models to implement RBHC

We here revisit two simulation models that have implicitly integrated RBHC principles as outlined above and examine their set-up and results in the light of the RBHC.

### Landscape fragmentation and transitional habitats

Li *et al.* (2012a) elaborated a cellular automata model to assess the role of landscape fragmentation on tick abundance and infection prevalence (for a schematic overview of the model see Figure 2). This model explicitly represented the movements and habitat preferences of two types of host species. A generic small reservoir host, calibrated following bank voles *Myodes glareolus*, is assumed to move small distances and stay in the forest, whereas the other host type, a generic large 'reproduction' host (i.e. that provides blood meals but does not become infected), calibrated following roe deer *Capreolus capreolus*, moves across larger distances and used forests (mostly for shelter) as well as grassland (for foraging). The composition and configuration of the highly suitable tick and host habitat (assumed to be forest) was modified in the different simulations: the proportion of 'forest' – highly suitable habitat, that is resource-rich habitat – varied between 20 and 80% and forest patch ('block') size varied between 1 and 100 ha. Non-forest areas were 'non-vegetated' (low or no resources), or 'grassland' (medium level of resources for hosts).

Depending on whether the areas surrounding the forest were grassland or non-vegetated areas, the outcomes in terms of the effect of fragmentation of the forest patches were radically different. When the forest is surrounded by grassland, the model predicts the density of infected nymphs to be highest in large patches of forest, whereas if the surrounding areas consist of non-vegetated areas (unsuitable habitat for deer), the density of infected nymphs was highest in the scenarios with few and small patches of forest. These seemingly contrasting outcomes are a direct result of the underlying assumptions of the model. In case of forest surrounded by grassland, deer will move into the grassland for foraging and also drop off ticks there. Ticks have a lower survival in grassland compared to forest (due to an increased desiccation risk). More grassland thus means more deer movements into grassland, more ticks being dropped off in grassland and lower survival

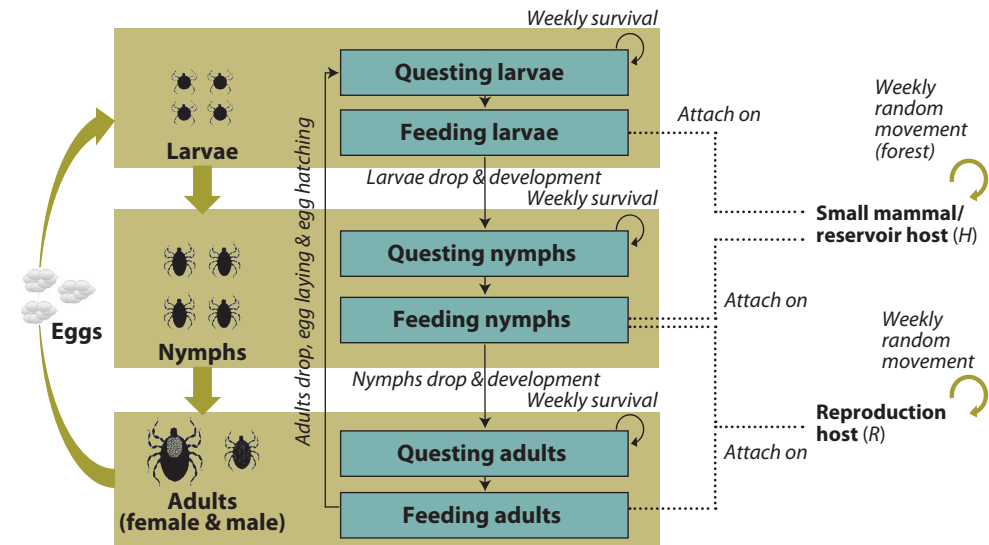


Figure 2. General structure of the simulation models revisited (modified from Li *et al.* 2012a, 2014, where details of the models can be found).

\$(protocol)://www.wageningenacademic.com/doi/pdf/10.3920/978-90-8686-838-4\_14 - Wednesday, August 15, 2018 4:17:47 AM - IP Address: 145.18.108.49

for ticks (grassland basically acts as a 'sink' for ticks), which hampers TBP transmission. In contrast, if the forest is surrounded by unsuitable areas for deer, the deer will stay in the forest, as will the ticks, and the interaction between ticks, small hosts and deer intensifies as the area of forest (patches) becomes smaller, which increases TBP transmission. This shows that the assumptions made in such a simulation model heavily affect the simulation results, and a robust ecological base is therefore absolutely necessary.

The cellular automata model presented in Li *et al.* (2012a) thus implicitly incorporates several aspects of the RBHC approach, such as the focus on the movement capacities and use of the landscape of the different hosts and the results underline in a striking manner that tick dynamics are heavily impacted by how hosts of various types may effectively use the landscape. However, now that we can use the RBHC framework to provide a 'checklist' of the relevant actors (i.e. ticks, pathogens and hosts), resources and mechanisms, it becomes clear that the biological realism of this and other models can still be improved. For example, including more specific resources, possibly associated to vegetation types more easily addressed by mapping and land management, would allow better nuancing of scenarios and results. Rather than dividing the area in just forest and grassland, or forest and non-vegetated areas, it would be useful to include the ecological functions of the border zones, the so-called ecotones, with their own specific resources. Also, the amount of resources needed per individual need to be taken into account. The results of the cellular automata model may have been different if the resource availability had been modelled explicitly, since resources may not be available in sufficient amounts in very small forest patches as those assumed in the model. Making such small forest patches unusable by deer would thus improve the biological realism of the model. Another straightforward next step is to increase the host diversity in the model, as long as information on resource/landscape use, movement capacity and interaction with ticks are known.

### **Feeding host control: impact of deer management on ticks**

Li *et al.* (2014) used an agent-based simulation to examine the consequences of deer management, through scenarios modifying mortality or movement, on the spatial dynamics of *Ixodes ricinus* (Li *et al.* 2014). The main focus concerned a realistic representation of deer movement, and scenarios based on existing or foreseen practices related to game or disease risk management. Ticks were also included in the model, including a detailed life cycle and attachment on (a generic) small mammal, and (generic) deer. Pathogen transmission was not considered. Deer movements were calibrated based on existing knowledge concerning roe deer and red deer movements and included two types of movements: home ranging (short distance movement for e.g. foraging) and displacement (long range movements to other, e.g. less populated, habitats). These two types of movement correspond to specific sets of rule that include several steps ('phases') and are constrained by movement capacity – which is longer in displacement than in home ranging. Animals moved around an artificial landscape made out of three patches of woodland and a matrix of grassland. Four scenarios were considered: (1) reducing local deer density through hunting (across the landscape or in a local woodland patch); (2) controlling deer grazing intensity in grassland (applied by reducing movement capacity and time spent in the grassland matrix in home ranging); (3) translocation and reintroduction of deer; and (4) controlling human disturbances and deer displacement (reducing displacement caused by human disturbances). This therefore, from a RBHC point of view, considers tick resources as well as deer resources and movement capacity to access diverse resources.



This multi-host, multi-land cover model underlines the need to consider host movement capacity in order to understand tick population dynamics at the landscape level, and that the range of movement, combined with the landscape fragmentation, modifies the outcome of scenarios. The results indicated that the effect of locally controlling deer population on tick population differs according to the movement capacity of deer: if it allows deer to reach patches where control was applied, the effect on tick population is greatly reduced. The second scenario tested the effect of a decrease of the use of grassland by deer. This reduced tick abundance in grassland, but increased it in woodland, where ticks may thus feed more often on reservoir species. The third scenario indicated that suppressing deer in an area does not suppress ticks, which can still feed on other hosts. The suppression of deer may result in an increase in small mammal densities, and once deer are reintroduced, density levels can reach higher level than at the start of the simulation. The decrease in deer displacement applied in the fourth scenario indicated resulted in a decrease in overall and maximum tick density, which may relate to the model set up for use of grassland, where tick mortality is higher, and to movement rules (choice of a destination cell). Still, it does point at relevant public health implication of the establishment of 'quiet zones' (areas excluding human disturbances) in isolated areas – as movement capacity and landscape structure, as presented above, modify the effect, in terms of tick abundance and locations, of such processes. Results were consistent with other studies, both empirical and of simulation (see Li *et al.* 2014).

A full RBHC perspective as presented above would need to have the pathogen as its main organism of focus. This is feasible as the pathogen's resources (host and vector) are effectively present in the model. Concerning host and vector, several resources are included (e.g. grassland as a key element for feeding; hosts for ticks). However, the results do highlight that movement capacity, as well as landscape structure (are landscape features, such as woodlands, accessible?) do affect the outcome of a change in pathogen resource abundance. The results raise the issue of substitutions between resources – or else the need to carefully assess the potential of various animals or landscape features to serve as resources. A model set up such as this one indeed allows testing the effect of substitution or the lack thereof. In the context of dynamic landscapes that are subjected to managements by diverse public health authorities, this is an important issue, and one that a conceptual framework such as RBHC can usefully address.

### **Discussion: challenges and perspectives for RBHC in understanding and management of disease risk**

At the most basic level, RBHC underlines two major ideas. First, that, often, a single vegetation type cannot represent the entire habitat, whatever the species concerned. Any host, vector, pathogen species we may consider in the context of vector-borne and zoonotic diseases, including tick-borne diseases, has a range of functions that requires specific resources in order to be fulfilled. Second, as Figure 1 makes very clear, the habitat of a pathogen, does not equate to the habitat of the vector. Far from approaching the issue of environmental suitability for TBP in an overly complicated and detailed fashion, the structure that RBHC encourages to build offers keys to understand a complex system.

Operational constraints clearly remain, such as those generated by the information content of existing environmental databases or what is currently possible to monitor when it comes to vectors, hosts or the TBP themselves. This should not preclude the use of a RBHC concept, and may help in directing data collection in a resource tight context. It does not require mapping resources specifically, but primarily encourages the identification of any vegetation type or landscape feature that could provide them, rather than the element providing it mostly. Then,

examining the distribution of these features through the lens of host movement completes the picture. Such operationalisation of the concept have been demonstrated previously for insects (Kalarus *et al.* 2013, Turlure *et al.* 2009, 2010). Across a continent such as Europe, the suitability of vegetation types can vary for the transmission of zoonotic pathogens, with some vegetation types classically assessed as unfavourable in some areas that are found suitable in others. This was found for hantavirus by Zeimes *et al.* (2015). Medlock *et al.* (2008) found that grass/dwarf heath likely offers better protection from desiccation for ticks than the nearby deciduous forest. Considering resources available rather than vegetation types allows making such interpretations in diverse environments. In existing models, RBHC offers additional perspectives on results that may appear unexpected, and in areas where the primary habitat of *I. ricinus* ticks, deciduous forest, is poorly represented (Vanwambeke *et al.* 2016).

A major challenge, but also a major opportunity, for the application of RBHC to TBP is the opportunistic feeding behaviour of ticks, which may feed on reservoir or non-competent hosts. Models are currently unlikely, in relation to parameterisation and computing, to accommodate a representation of the full palette of hosts that ticks feed on. However, the use of scenarios that offer more or fewer reservoir hosts, on which ticks would therefore feed more or less often, opens interesting opportunities. Such models have been elaborated in the past but in a non-spatial way (Levi *et al.* 2016, Ogden and Tsao 2009). The results by Li *et al.* (2012a, 2014) suggest the very core of the RBHC: availability and accessibility of the resources do modify these outcomes, and including them may help solve some of the current questions. Also, as indicated by that model, the time spent in an area (e.g. grassland) does affect the importance each will play in providing resources and in distribution vectors across the landscape. Some research also has indicated that hosts may affect vector resources (other than blood meal) by e.g. keeping the vegetation low or by keeping key reproduction hosts away, this lowering tick abundance (Steigedal *et al.* 2013).

Understanding the details of a pathogen's habitat bears relevance also when considering humans, exposure and prevention. Two pathways can be highlighted for this. First, as outlined in Hartemink *et al.* (2015) concerning blue tongue virus transmission, key resources in the system can be identified that lend themselves to removal or displacement, making them inaccessible and therefore unusable. Second, the concept can be easily extended to include the resources required for human ecological functions that would lead to exposure to tick bites. Like other ecological resources, recreational resources (or related to other exposure activities) can be mapped in relation to other resources of the TBP and their accessibility through host movement. Those resources (e.g. signposted walks, recreational equipment) could potentially be placed in areas where infected tick abundance is lower, information is focused and/or control applied. The use of RBHC in formalised models such as those reviewed here allows exploring the effect of such interventions on exposure and on risk.

## Conclusion

A great wealth of knowledge has been accumulated thanks to decades of research and modelling of the suitability of diverse landscapes for tick-borne disease transmission. Because many datasets represent keyholes that only offer a limited insight into what are complex ecological systems, the coherence, beyond the most obvious results related to primary habitats, can be difficult to see. The RBHC approach offers a promising perspective to consolidate existing knowledge, to guide further data acquisition and modelling. Beyond the scientific interest of the concept, its potential use for understanding the risk of zoonotic tick-borne diseases for humans and for exploring options for prevention and control is significant.

## Public health relevance

- Model outcomes can be challenging to interpret for non-modellers. We believe a strong conceptual background for models would help make complex quantitative results more accessible to decision-makers and risk managers.
- Tick-borne pathogen transmission systems are complex. The resource-based habitat concept permits to identify relevant links between landscape elements and the suitability of an area as habitat for hosts, vectors and ultimately the pathogen of interest. This will help to build ecological simulation models that capture the essence of the (spatial aspects of the) eco-epidemiology of the pathogen.
- The resource-based habitat concept also bears potential for communicating the ecological complexity of this system to a broad diversity of audiences.

## References

- Barandika JF, Berriatua E, Barral M, Juste RA, Anda P and Garcia-Perez AL (2006) Risk factors associated with ixodid tick species distributions in the Basque region in Spain. *Med Vet Entomol* 20: 177-188.
- Boyard C, Barnouin J, Bord S, Gasqui P and Vourc'h G (2011) Reproducibility of local environmental factors for the abundance of questing *Ixodes ricinus* nymphs on pastures. *Ticks Tick-Borne Dis* 2: 104-110.
- Carpí G, Cagnacci F, Neteler M and Rizzoli A (2008) Tick infestation on roe deer in relation to geographic and remotely sensed climatic variables in a tick-borne encephalitis endemic area. *Epidemiol. Infect.* 136.
- Claerebout E, Losson B, Cochez C, Casaert S, Dalemans A-C, De Cat A, Madder M, Saegerman C, Heyman P and Lempereur L (2013) Ticks and associated pathogens collected from dogs and cats in Belgium. *Parasit Vectors* 6: 183.
- De Keukeleire M, Vanwambeke SO, Somassé E, Kabamba B, Luyasu V and Robert A (2015) Scouts, forests, and ticks: impact of landscapes on human-tick contacts. *Ticks Tick-Borne Dis* 6: 636-644.
- Dennis RLH, Shreeve TG and Van Dyck H (2003) Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. *Oikos* 102: 417-426.
- Dennis RLH, Shreeve TG and Van Dyck H (2006). Habitats and resources: the need for a resource-based definition to conserve butterflies. *Biodivers Conserv* 15: 1943-1966.
- Dobson ADM, Finnie TJR and Randolph SE (2011a) A modified matrix model to describe the seasonal population ecology of the European tick *Ixodes ricinus*: *Ixodes ricinus* population model. *J Appl Ecol* 48: 1017-1028.
- Dobson ADM, Taylor JL and Randolph SE (2011b) Tick (*Ixodes ricinus*) abundance and seasonality at recreational sites in the UK: hazards in relation to fine-scale habitat types revealed by complementary sampling methods. *Ticks Tick-Borne Dis* 2: 67-74.
- Estel S, Kuemmerle T, Alcántara C, Levers C, Prishchepov A and Hostert P (2015) Mapping farmland abandonment and recultivation across Europe using MODIS NDVI time series. *Remote Sens Environ* 163: 312-325.
- Estrada-Peña A, Alexander N and Wint GRW (2016) Perspectives on modelling the distribution of ticks for large areas: so far so good? *Parasit Vectors* 9: 1.
- Estrada-Peña A, Venzal JM and Sanchez Acedo C (2006) The tick *Ixodes ricinus*: distribution and climate preferences in the western Palaearctic. *Med Vet Entomol* 20: 189-197.
- Forman RTT (1995) *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press, Cambridge, UK, New York, USA.

- Gassner F, Van Vliet AJH, Burgers SLGE, Jacobs F, Verbaarschot P, Hovius EKE, Mulder S, Verhulst NO, Van Overbeek LS and Takken W (2011) Geographic and temporal variations in population dynamics of *Ixodes ricinus* and associated *Borrelia* Infections in the Netherlands. *Vector-Borne Zoonotic Dis* 11: 523-532.
- Halos L, Bord S, Cotte V, Gasqui P, Abrial D, Barnouin J, Boulouis H-J, Vayssier-Taussat M, and Vourc'h G (2010) Ecological factors characterizing the prevalence of bacterial tick-borne pathogens in *Ixodes ricinus* ticks in pastures and woodlands. *Appl Environ Microbiol* 76: 4413-4420.
- Hancock PA, Brackley R and Palmer SCF (2011) Modelling the effect of temperature variation on the seasonal dynamics of *Ixodes ricinus* tick populations. *Int J Parasitol* 41: 513-522.
- Hartemink N and Takken W (2016) Trends in tick population dynamics and pathogen transmission in emerging tick-borne pathogens in Europe: an introduction. *Exp Appl Acarol* 68: 269-278.
- Hartemink N, Vanwambeke SO, Purse BV, Gilbert M, and Van Dyck H (2015) Towards a resource-based habitat approach for spatial modelling of vector-borne disease risks: resource-based habitats for vector-borne diseases. *Biol Rev* 90: 1151-1162.
- Hoch T, Monnet Y and Agoulon A (2010) Influence of host migration between woodland and pasture on the population dynamics of the tick *Ixodes ricinus*: a modelling approach. *Ecol Model* 221: 1798-1806.
- Hugli D, Moret J, Rais O, Moosmann Y, Erard P, Malinverni R and Gern L (2009) Tick bites in a Lyme borreliosis highly endemic area in Switzerland. *Int J Med Microbiol* 299: 155-160.
- Jore S, Vanwambeke SO, Viljugrein H, Isaksen K, Kristoffersen AB, Woldehiwet Z, Johansen B, Brun E, Brun-Hansen H, Westermann S, Larsen I-L, Ytrehus B and Hofshagen M (2014) Climate and environmental change drives *Ixodes ricinus* geographical expansion at the northern range margin. *Parasit Vectors* 7: 11.
- Jore S, Viljugrein H, Hofshagen M, Brun-Hansen H, Kristoffersen AB, Nygård K, Brun E, Ottesen P, Sævik BK and Ytrehus B (2011) Multi-source analysis reveals latitudinal and altitudinal shifts in range of *Ixodes ricinus* at its northern distribution limit. *Parasit Vectors* 4: 84.
- Juřicová Z and Hubálek Z (2009) Serologic survey of the wild boar (*Sus scrofa*) for *Borrelia burgdorferi* sensu lato. *Vector-Borne Zoonotic Dis* 9: 479-482.
- Kalarus K, Skórka P and Nowicki P (2013) Resource use in two contrasting habitat types raises different challenges for the conservation of the dryad butterfly *Minois dryas*. *J Insect Conserv* 17: 777-786.
- Levi T, Keesing F, Holt RD, Barfield M and Ostfeld RS (2016) Quantifying dilution and amplification in a community of hosts for tick-borne pathogens. *Ecol Appl* 26: 484-498.
- Li S, Hartemink N, Speybroeck N and Vanwambeke SO (2012a) Consequences of landscape fragmentation on lyme disease risk: a cellular automata approach. *PLoS ONE* 7: e39612.
- Li S, Heyman P, Cochez C, Simons L and Vanwambeke SO (2012b) A multi-level analysis of the relationship between environmental factors and questing *Ixodes ricinus* dynamics in Belgium. *Parasit Vectors* 5: 149.
- Li S, Vanwambeke SO, Licoppe AM and Speybroeck N (2014) Impacts of deer management practices on the spatial dynamics of the tick *Ixodes ricinus*: a scenario analysis. *Ecol Model* 276: 1-13.
- Linard C, Lamarque P, Heyman P, Ducoffre G, Luyasu V, Tersago K, Vanwambeke SO and Lambin EF (2007) Determinants of the geographic distribution of Puumala virus and Lyme borreliosis infections in Belgium. *Int J Health Geogr* 6: 15.
- Lommano E, Dvořák C, Vallotton L, Jenni L and Gern L (2014) Tick-borne pathogens in ticks collected from breeding and migratory birds in Switzerland. *Ticks Tick-Borne Dis* 5: 871-882.
- Mannelli A, Bertolotti L, Gern, L and Gray J (2012) Ecology of *Borrelia burgdorferi* sensu lato in Europe: transmission dynamics in multi-host systems, influence of molecular processes and effects of climate change. *FEMS Microbiol Rev* 36: 837-861.
- Medlock JM, Hansford KM, Bormane A, Derdakova M, Estrada-Peña A, George J-C, Golovljova I, Jaenson TGT, Jensen J-K, Jensen PM, Kazimirova M, Oteo JA, Papa A, Pfister K, Plantard O, Randolph SE, Rizzoli A, Santos-Silva MM, Sprong H, Vial L, Hendrickx G, Zeller H and Van Bortel W (2013) Driving forces for changes in geographical distribution of *Ixodes ricinus* ticks in Europe. *Parasit. Parasit. Vectors* 6: 1.
- Medlock JM, Pietzsch ME, Rice NVP, Jones L, Kerrod E, Avenell D, Los S, Ratcliffe N, Leach, S and Butt T (2008) Investigation of ecological and environmental determinants for the presence of questing *Ixodes ricinus* (Acari: Ixodidae) on Gower, South Wales. *J Med Entomol* 45: 314-325.

- Meyfroidt P and Lambin EF (2011) Global forest transition: prospects for an end to deforestation. *Annu Rev Environ Resource* 36: 343-371.
- Navarro LM and Pereira HM (2015) Rewilding abandoned landscapes in Europe. In: Pereira HM and Navarro LM (eds.) *Rewilding European landscapes*. Springer International Publishing, New York, USA.
- Ogden NH and Tsao JI (2009) Biodiversity and Lyme disease: dilution or amplification? *Epidemics* 1: 196-206.
- Ogden NH, Bigras-Poulin M, O'Callaghan CJ, Barker IK, Lindsay LR, Maarouf A, Smoyer-Tomic KE, Waltner-Toews D and Charron D (2005) A dynamic population model to investigate effects of climate on geographic range and seasonality of the tick *Ixodes scapularis*. *Int J Parasitol* 35: 375-389.
- Randolph SE (2001) The shifting landscape of tick-borne zoonoses: tick-borne encephalitis and Lyme borreliosis in Europe. *Philos Trans R Soc B Biol Sci* 356: 1045-1056.
- Randolph SE and Storey K (1999) Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): implications for parasite transmission. *J Med Entomol* 36: 741-748.
- Randolph SE and Šumilo D (2007) Tick-borne encephalitis in Europe: dynamics of changing risk. In: Takken W and Knols BGJ (eds.) *Emerging pests and vector-borne disease in Europe. Ecology and Control of Vector-borne diseases, Volume 1*. Wageningen Academic Publishers, Wageningen, the Netherlands.
- Richter D and Matuschka FR (2011). Differential risk for Lyme disease along hiking trail. *Emerg Infect Dis* 17, 1704-1706.
- Rizzoli A, Silaghi C, Obiegala A, Rudolf I, Hubalek Z, Foldvari G, Plantard O, Vayssier-Taussat M, Bonnet S, Špitalská E and Kazimírová M. (2014) *Ixodes ricinus* and its transmitted pathogens in urban and peri-urban areas in Europe: new hazards and relevance for public health. *Front Public Health* 2: 251-251..
- Špitalská E, Stanko M, Mošanský L, Kraljik J, Miklisová D, Mahríková L, Bona M and Kazimírová M (2016) Seasonal analysis of Rickettsia species in ticks in an agricultural site of Slovakia. *Exp Appl Acarol* 68: 315-324.
- Steigedal HH, Loe LE, Grøva L and Myrsetrud A (2013) The effect of sheep (*Ovis aries*) presence on the abundance of ticks (*Ixodes ricinus*). *Acta Agric Scand Sect – Anim Sci* 63: 111-120.
- Tack W, Madder M, Baeten L, Vanhellemont M, Gruwez R and Verheyen K (2012) Local habitat and landscape affect *Ixodes ricinus* tick abundances in forests on poor, sandy soils. *For Ecol Manag* 265: 30-36.
- Turlure C, Choutt J, Baguette M and Van Dyck H (2009) Microclimatic buffering and resource-based habitat in a glacial relict butterfly: significance for conservation under climate change. *Glob Change Biol* 16: 1883-1893.
- Turlure C, Choutt J, Van Dyck H, Baguette M and Schtickzelle N (2010) Functional habitat area as a reliable proxy for population size: case study using two butterfly species of conservation concern. *J Insect Conserv* 14: 379-388.
- Uspensky I (2014) Tick pests and vectors (Acari: Ixodoidea) in European towns: introduction, persistence and management. *Ticks Tick-Borne Dis* 5: 41-47.
- Vanwambeke SO, Šumilo D, Bormane A, Lambin EF and Randolph SE (2010) Landscape predictors of tick-borne encephalitis in Latvia: land cover, land use, and land ownership. *Vector-Borne Zoonotic Dis* 10: 497-506.
- Vanwambeke SO, Van Doninck J, Artois J, Davidson RK, Meyfroidt P and Jore S (2016) Forest classes and tree cover gradient: tick habitat in encroached areas of southern Norway. *Exp Appl Acarol* 68: 375-385.
- Zeimes CB, Olsson GE, Hjertqvist M and Vanwambeke SO (2014) Shaping zoonosis risk: landscape ecology vs. landscape attractiveness for people, the case of tick-borne encephalitis in Sweden. *Parasit Vectors* 7: 370.
- Zeimes CB, Quoilin S, Henttonen H, Lyytikäinen O, Vapalahti O, Reynes J-M, Reusken C, Swart AN, Vainio K, Hjertqvist M and Vanwambeke SO (2015) Landscape and regional environmental analysis of the spatial distribution of hantavirus human cases in Europe. *Front Public Health* 3: 54.