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Towards a resource-based habitat approach for spatial modelling of vector-borne disease risks

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ABSTRACT

Given the veterinary and public health impact of vector-borne diseases, there is a clear need to assess the suitability of landscapes for the emergence and spread of these diseases. Current approaches for predicting disease risks neglect key features of the landscape as components of the functional habitat of vectors or hosts, and hence of the pathogen. Empirical–statistical methods do not explicitly incorporate biological mechanisms, whereas current mechanistic models are rarely spatially explicit; both methods ignore the way animals use the landscape (i.e. movement ecology). We argue that applying a functional concept for habitat, i.e. the resource-based habitat concept (RBHC), can solve these issues. The RBHC offers a framework to identify systematically the different ecological resources that are necessary for the completion of the transmission cycle and to relate these resources to (combinations of) landscape features and other environmental factors. The potential of the RBHC as a framework for identifying suitable habitats for vector-borne pathogens is explored and illustrated with the case of bluetongue virus, a midge-transmitted virus affecting ruminants. The concept facilitates the study of functional habitats of the interacting species (vectors as well as hosts) and provides new insight into spatial and temporal variation in transmission opportunities and exposure that ultimately determine disease risks. It may help to identify knowledge gaps and control options arising from changes in the spatial configuration of key resources across the landscape. The RBHC framework may act as a bridge between existing mechanistic and statistical modelling approaches.

Key words: novel framework, risk modelling and mapping, vector-borne diseases, functional habitats, conservation biology, biological resources, movement ecology.

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I. INTRODUCTION

(1) Vector-borne disease risks and the landscape

Vector-borne emerging diseases are a major threat to veterinary and public health (Jones *et al.*, 2008). Recent outbreaks of (re-)emerging vector-borne diseases throughout the world highlight the need for an increased understanding of the underlying mechanisms that explain the establishment, spread and persistence of diseases in natural and human-dominated landscapes. Examples of particular interest are bluetongue virus in Europe (Wilson & Mellor, 2009), West Nile virus in southern Europe and North America (Kramer, Styer & Ebel, 2008) and Chikungunya in various areas (Charrel, de Lamballerie & Raoult, 2007). The presence of a vector-borne disease depends on multiple factors including suitable climate for pathogen replication inside the vector, the suitability of the landscape as a habitat for the host(s) and the vector(s) and conditions that allow contact between the host and vector. Hence, vector-borne diseases are complex ecological systems that need an explicit framework for community interactions to predict disease risks under climate, landscape and biodiversity change (Gilman *et al.*, 2010; Keesing *et al.*, 2010; Randolph & Dobson, 2012). Landscape characteristics are likely to affect the spatial and temporal dynamics of several vector-borne diseases by influencing habitat suitability for vectors and hosts within a suitable climate envelope (Ostfeld, Glass & Keesing, 2005; Lambin *et al.*, 2010). While landscape composition affects the availability and quality of habitat of the different species that interact with the pathogen, landscape configuration and connectivity affect the spatial and temporal probability of contact between vectors and hosts, and are thus significant for understanding pathogen transmission and spread.

(2) Modelling and mapping of vector-borne disease risks

Models predicting disease distributions are needed to mitigate against current and future disease risks (Woolhouse, 2011). For regions where a disease is endemic, predictive tools may help public health experts and policy makers taking decisions about risk communication, prevention and control measures (Quine *et al.*, 2011). There is also a growing demand to assess the risks of introduction, establishment, spread and persistence of vector-borne pathogens outside endemic areas, especially in this era of increased trade and travel globalization (Tatem, Hay & Rogers, 2006). Furthermore, predictive models allow for scenario testing to assess the effects of climate change, land-use and biodiversity change and changes in disease control strategies and human resource-use priorities.

Two types of approaches for predicting risks related to vector-borne diseases can be distinguished; correlative approaches use statistical models of relationships between disease or vector incidence and environmental factors, whereas mechanistic approaches explicitly take into account different aspects of the biological and epidemiological processes of the system. However, both approaches fail to address a number of important features of vector-borne disease systems. The biological mechanisms underlying statistical associations between landscape characteristics and pathogen incidence are taken into account poorly by empirical–statistical models, which may select a predictor variable that has little to do with its biological role (as pointed out in e.g. Randolph, 2000). Hence, model transferability to different areas or periods is often limited (Elith & Leathwick, 2009). Most mechanistic models make very basic assumptions on habitat use of the vectors and hosts. The current approaches in landscape epidemiology have often been based on a human-biased perspective of the landscape, rather than on host- or vector-specific perceptions of the

landscape. Structural habitats (often referred to as biotopes) relate to vegetation or land-use types, but such typologies may not represent the spatial and temporal units of functional habitat of organisms, including pathogens (Kling, Juliano & Yee, 2007) Movements and population dynamics of hosts and vectors, and hence the dynamic spatio-temporal overlap between them, are rarely considered.

(3) Exploring the use of the resource-based habitat concept

Conceptual approaches of other fields can be interesting sources of inspiration for landscape epidemiology. Conservation biology and the field of vector-borne disease risk modelling share, for example, the challenges of mapping organisms and studying the environmental factors that help predict presence, abundance or dynamics of focal species. Concepts and tools to identify functional habitats from a mechanistic, biological viewpoint as developed for conservation (e.g. Dennis, Shreeve & Van Dyck, 2003) could therefore turn out to be highly useful to the field of vector-borne disease epidemiology. The aim of this review is to explore the potential of a conceptual framework of functional, resource-based habitat as developed in conservation biology for application to vector-borne disease systems.

First, we briefly review the approaches currently used in landscape epidemiology. Next, we introduce the resource-based habitat concept as developed and applied in conservation biology. We discuss the interest and feasibility of the concept to identify what actually is a functional habitat from the viewpoint of a vector-borne pathogen. Finally, we illustrate the resource-based habitat approach with the timely case of bluetongue, a midge-borne viral disease of ruminants. Until 1998, bluetongue occurred only sporadically in the European fringes of the Mediterranean, but in recent years several strains spread into Europe. The emergence of an unrelated bluetongue strain BTV8 in northern Europe in 2006 caused a large and costly epidemic in 2007 (Purse *et al.*, 2008).

II. LANDSCAPES AND MAPPING DISEASE RISKS: CLASSIC CONCEPTS AND CURRENT METHODS

Landscape epidemiology of vector-borne diseases can be defined as the study of the temporal dynamics of host, vector, and pathogen populations and their spatial interactions within a suitable environment for transmission (Reisen, 2010). The spatially defined focus – i.e. nidus – of transmission may be characterized by vegetation as well as by climate, latitude, elevation, and geology (Reisen, 2010). It is a long-standing idea that environmental and anthropogenic factors, including landscape characteristics, are significant for the distribution of vector-borne diseases. Over the course of the 20th century, scientists from various disciplinary backgrounds identified the role of

the ecological context in the occurrence of diseases. The French geographer Sorre (1933) and the American physician May (1950) were the first to reflect on ecological and human-related factors influencing the distribution of infectious diseases. The Russian ecologist Pavlovsky (1966) investigated the niche of zoonotic pathogens. In the late 20th century, significant technological progress (e.g. geographical information systems, remote sensing, powerful computers and statistical software) created new opportunities for quantitative, spatially explicit analyses in landscape epidemiology (Kitron, 1998; Meade & Emch, 2010). Most studies in the field adopt one of the two approaches: the inductive, top-down or deductive, bottom-up approach.

(1) Inductive, top-down approach

Searching for a combination of factors that together determine the distribution of vector-borne diseases forms the basic rationale of the inductive or top-down approach of several empirical–statistical methods in landscape epidemiology. Relationships between the pathogen and a number of environmental factors are quantified. The final statistical model is used to draw conclusions on ecological drivers and to map the distribution and intensity of risk by interpolation or extrapolation to different areas or time periods. Pathogen-related dependent variables are usually drawn from case data on human or domestic animal disease or from field data on infection prevalence in vectors or hosts. When these are not available, host or vector abundance data are sometimes used as a surrogate. A wide variety of data sources have been used to monitor environmental factors, often with remote sensing (e.g. vegetation, soils, climatic factors and landscape metrics; Rogers *et al.*, 2002). Recent studies have included social and biotic factors in addition to landscape and climate (e.g. Bui *et al.*, 2011). A range of different statistical techniques have been used, such as regression, discriminant analysis and machine-learning methods, such as ecological niche modelling (Elith *et al.*, 2006; Elith & Graham, 2009); the latter has re-emphasized the basic principles of the Hutchinson ecological niche, applicable to pathogen distribution modelling (Peterson, 2008). Many vector-borne disease transmission systems have been the subject of such statistical modelling studies (Rogers *et al.*, 2002; Purse *et al.*, 2012).

(2) Deductive, bottom-up approach

There is also a long tradition of mechanistic models for dealing with disease risk and spread, which are based on the basic elements and phases of the disease and the vector-borne system. Hence, this represents a more deductive and bottom-up approach. The basic rationale of the models is to divide populations into three or four categories of individuals: susceptible, exposed (in the case of a disease with an incubation period), infected, and recovered (or removed) (Kermack & McKendrick, 1927). An important concept for these models is the basic reproduction number R_0. It is defined as the average number of secondary cases

caused by one typical infectious individual arriving in a naïve population (Anderson & May, 1990; Diekmann, Heesterbeek & Metz, 1990). R_0 is a quantity that integrates, and weights in an ecologically realistic way, all factors that determine whether a pathogen can establish or not. In the case of a vector-borne disease, such factors include the contact rate between the vector and host, the length of the incubation period inside the vector, and the probability that an infected individual will survive to pass on the infection; all of which may be influenced by environmental factors. Since the early work of Ross and later Macdonald on the quantification of the transmission and control of malaria (Macdonald, 1957), R_0 models have been applied to a multitude of vector-borne diseases (Hartemink *et al.*, 2008, 2009; Reiner *et al.*, 2013).

There are also other bottom-up modelling approaches such as multi-criteria decision analysis, which makes use of expert judgement to identify and weigh the relative importance of different factors. The result can be visualized on a map [e.g. for avian influenza (Stevens, Gilbert & Pfeiffer, 2013) and vector-borne diseases (Hongoh *et al.*, 2011)].

Both approaches have contributed significantly to the field of vector-borne disease risk mapping, but they also have drawbacks. Empirical–statistical methods offer great flexibility in exploring environmental variables, but the variables used are typically proxies that have correlative, but not necessarily causal, relationships with the disease system (Messina & Pan, 2013). The variables can also be strongly interrelated (i.e. the problem of collinearity), posing problems for biologically relevant model selection and for model transferability among different areas (Dormann *et al.*, 2013). Most studies use structural habitat variables and usually ignore habitat connectivity. Moreover, empirical–statistical models rely on the actual distribution of the pathogen, which may obscure our ability to predict potential distributions and risks because pathogens in epidemic areas are unlikely to be in equilibrium with their environments as the actual distribution represents only a subset of the potential environmental conditions (Elith, Kearney & Phillips, 2010).

Mechanistic models are well-suited for scenario analysis and extrapolation, but are often not spatially explicit, and do not allow a straightforward incorporation of landscape factors. Empirical pathogen and vector life-cycle data required for application of such models may be lacking, particularly in ecosystem contexts where pathogens are newly emerging. There have been efforts to spatialize R_0 models, either by applying the R_0 principle to networks (e.g. Adams & Kapan, 2009) or by combining R_0 models with empirical statistical model outcomes (e.g. Hartemink *et al.*, 2011; Vanwambeke, Bennett & Kapan, 2011), but animal movements and functional habitat use are still ignored. For systems with several species, as is the case by definition for vector-borne pathogens, models can become complex. Hence, the development of reliable mechanistic, spatially explicit models to produce risk maps remains a challenge.

Tools to identify landscapes suitable for invasion, establishment and spread, as well as means to control diseases would ideally be explicit on the underlying mechanisms, as well as spatially explicit. This would allow us to examine more carefully the role of specific landscape factors in supporting the pathogen life cycle. An overarching framework incorporating functional habitat and movement issues of the interacting species in a vector-borne disease system has not been established yet. Here, we propose the framework of the resource-based habitat concept as a way to do so.

III. RESOURCE-BASED HABITAT CONCEPT (RBHC)

The recognition and spatio-temporal delineation of units of habitat is essential for basic and applied ecology. However, habitat is sometimes defined at a general vegetation-type level (e.g. deciduous forest, dry heathland) which may not precisely cover the specific zones that are significant to a particular species (Hall, Krausman & Morrison, 1997). Hence, conservation biologists have defended an organism-centred habitat concept based on the essential ecological resources and conditions the organism requires (Dennis *et al.*, 2003; Dennis, Shreeve & Van Dyck, 2006). Instead of assuming that general vegetation or land-use categories represent species-specific habitat in a top-down manner, the resource-based habitat concept (RBHC) assumes in a bottom-up manner that functional habitat 'arises' out of more fundamental ecological units, i.e. the ecological resources. Ecological resources include consumables (e.g. host plant for an herbivorous insect) and utilities (e.g. suitable microclimate, enemy-free space); they explicitly relate to functional relationships between the organism and elements of its environment. Some resources are essential in order to complete the focal organism's life cycle (Dennis *et al.*, 2003). Hence, the resource-based habitat concept reconnects with the multi-dimensional, classical ecological niche concept ('Hutchinson niche'); habitat is the spatial projection of this functional, biological space (Dennis *et al.*, 2006). As a consequence, functional habitat is not necessarily a physically visible 'patch' that corresponds to a polygon of a particular vegetation type, but rather an emergent entity of functional space that results from the overlap or contiguity of resources and the scale of movements between them.

The resource-based habitat approach has been applied to species of conservation interest to construct statistical distribution models, functional habitat maps and management maps to adapt nature reserve management relative to the presence, abundance and spatial and functional configuration of essential ecological resources for threatened insect species (e.g. Turlure *et al.*, 2010*a*,*b*; Kalarus, Skórka & Nowicki, 2013). Using standard geographic information system (GIS) tools, functional habitat is delineated based on several layers of information about key ecological resource distributions and on mobility estimates derived from mark–release–recapture programs to fix maximal distances between clusters of resources (for details, see Vanreusel & Van Dyck, 2007). Moreover, general linear models of distribution

using functional habitat factors performed significantly better than did models using classical, structural habitat factors (i.e. vegetation types) and the resource-based models also scored better for transferability to different areas within the same eco-region (Vanreusel, Maes & Van Dyck, 2007).

IV. APPLYING RBHC TO A VECTOR-BORNE PATHOGEN SYSTEM

(1) Pathogen level

Vector-borne pathogens have a complex ecological profile as they rely on different organisms for their persistence, i.e. hosts and vectors. Hence, the functional habitat of the pathogen ultimately needs to integrate the functional habitats of the vector(s) and the host(s). We propose to do this according to the resource-based habitat principles as discussed in Dennis *et al.* (2003) and applied in Vanreusel & Van Dyck (2007). The general approach is visualized in Fig. 1. Rather than focusing on vectors or hosts, we start by taking the pathogen as the focal organism, for which we identify the ecological resources related to key biological functions across its life cycle. We recognize three main functions: (*i*) replication in a host, (*ii*) replication in a vector, and (*iii*) successful transmission between host and vector. For most vector-borne diseases, the related resources will consist of the presence of the host, the vector and suitable thermal conditions for viral replication in the vector, since pathogen replication in the vector often proceeds more quickly at higher temperatures and stops completely when temperature drops below a threshold (Carpenter *et al.*, 2011).

(2) Vector and host level

In the next step, we apply the same approach to the vector and host species. The host and vector species each have their own specific ecological resources (e.g. food, shelter, meeting sites, etc.) that relate to their biological functions (e.g. foraging, resting, mating, etc.).

For arthropod vector species, these functions have to cover both the larval and adult resources: one needs to consider, within dispersal distances, suitable sites for larval development (often aquatic or semi-aquatic) and for adults blood feeding, mating, breeding, resting and feeding, all of which require suitable microclimate conditions since arthropods are poikilothermic and sensitive to desiccation.

For both vector and host species, the functional habitat can then be determined by integrating knowledge on the mobility of the species with information on the distribution of resources, e.g. from detailed land cover maps (Fig. 1). A spatial window, of a size determined by the mobility of the species, is used to determine whether or not all the required resources are present within the mobility range of the animal, for each area examined, as used by Vanreusel & Van Dyck (2007). This determines whether an area can be considered a suitable habitat from a functional perspective. Identifying specific habitat components directly from remotely sensed digital spatial data may not always be possible, especially when the habitat components are smaller than the pixel size of images (e.g. 30 m to 1 km). However, taking a bottom-up approach, we can often first identify the resources, then identify the related landscape features and then see whether these features can be captured by mapping tools and coarser scale spatial proxies. For instance, a landscape with small patches of vegetation can be characterized by a particular fragmentation index (Haines-Young & Chopping, 1996). Outlining the various functions and needs of the organisms involved, as is done in the RBHC framework, can help in interpreting results when indirect proxies have to be used, either in relation to the difficulty in collecting representative data on the vector, the host, the pathogen itself, or habitat features.

With growing sophistication of algorithms for data mining and greater availability of spatially extensive environmental data, many top-down or correlative studies of the environmental factors underpinning species distributions focus mainly on prediction using environmental data that are readily at hand, but fail to explain the relevance of selected predictors, and likely miss important ecological drivers (Elith & Leathwick, 2009). Incorporation of ecologically relevant, proximate predictors in top-down approaches improves ecological insight, reduces patterning in model residuals (Leathwick & Whitehead, 2001) and enhances model transferability (Austin, 2002). By focusing at the outset on species resources, the RBHC may give much better insight into the proximate factors driving disease transmission and generate more transferable models.

(3) Overlap of functional habitats

Finally, fulfilling the life cycle of the pathogen and making transmission possible requires the spatial and temporal co-occurrence of vectors and hosts (i.e. overlap of their functional habitats), in suitable climatic circumstances. Any susceptible vector or host for which the habitat range overlaps with this 'transmission zone', is at risk of being infected if the pathogen is present or introduced. The RBHC framework offers a method to distinguish the areas where these requirements are met. Note that the main difference between applying the RBHC in its original context (conservation biology, aimed at a single species) and the present application, to vector-borne pathogen systems, is that in the latter case, the RBHC is applied at two different levels: one level addresses the host, and separately, the vector as focal organisms, and another level addresses the pathogen as the focal organism using the results at the vector and host level as key inputs (Fig. 1). Pathogens may rely on several species of hosts and vectors such that the functional habitat of each must be considered.

V. APPLICATION OF THE RBHC TO BLUETONGUE VIRUS

We now illustrate the application of the RBHC to a vector-borne pathogen, using bluetongue disease as a case
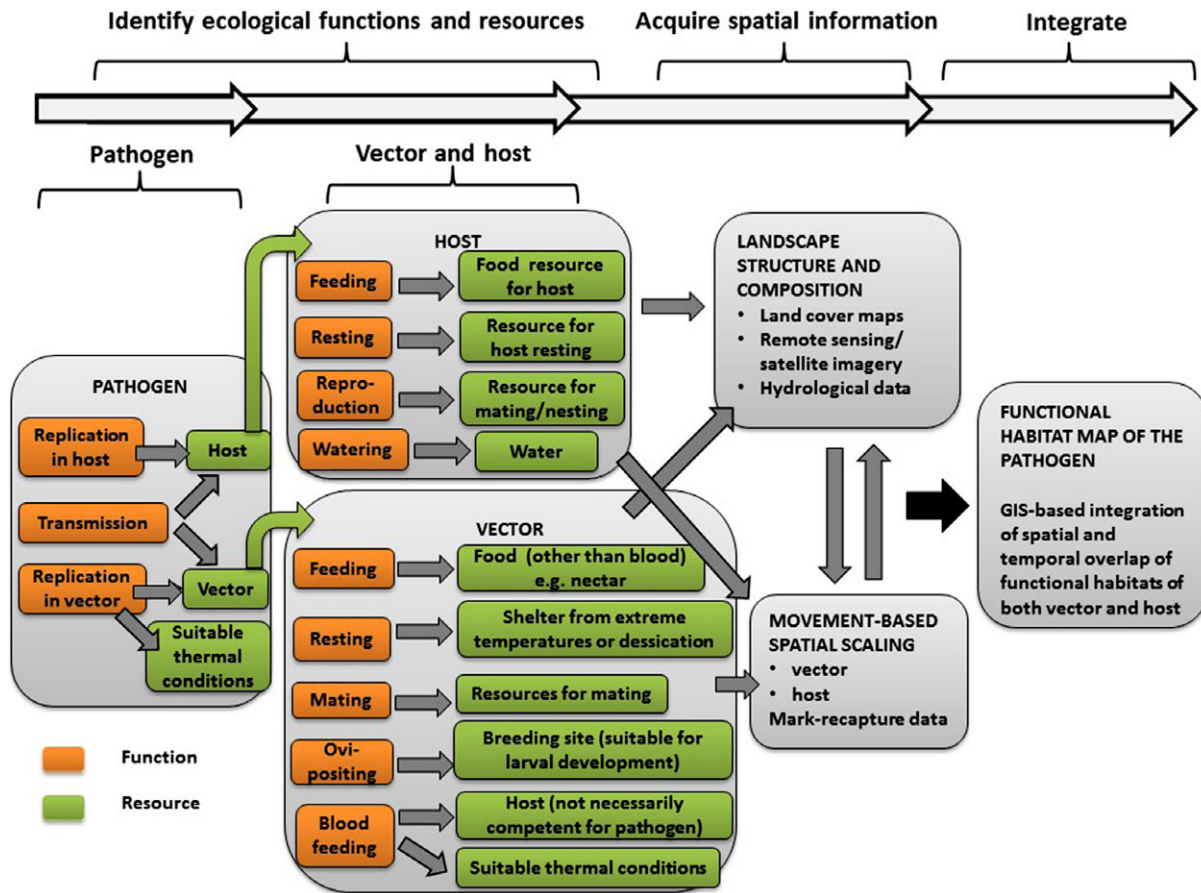
Fig. 1. Application of the resource-based habitat concept to vector-borne pathogens. Identification of the different functions (orange boxes) and associated resources (green boxes) is first done at the level of the pathogen and then at the level of both the vector and host. Information on the movement capacities of the species involved and on the structure and composition of the landscape together, and in mutual dependence, determine the functional habitats of vector and host species. That is, the movement range determines the distance that should be considered when looking at the accessibility of the different resources, whereas the type of terrain may affect the movement range. Transmission can take place where these functional habitats overlap.

study, starting with the identification of functions and resources at the pathogen, host and vector level. Regional variation in vector species, as described in Section V.4, leads to a number of epidemiologically different situations. In Section V.5, we apply the RBHC approach to three different situations and explore possible control measures.

(1) Pathogen level

Bluetongue virus (BTV) infects a wide range of ruminants but mainly affects sheep and cattle (Maclachlan *et al.*, 2009). A variety of wild ruminants have been found to be positive for antibodies to BTV, including red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and fallow deer (*Dama dama*), and virus titres can be comparable to those of cattle and sheep (López-Olvera *et al.*, 2010), suggesting that they could play a role in transmission (Falconi, López-Olvera & Gortázar, 2011). The biological vectors are adult female *Culicoides* spp. midges (Diptera: Ceratopogonidae) (Mellor, Boorman & Baylis, 2000). Virus transmission takes place

during the blood meals that female midges take to obtain proteins for egg production. Suitable thermal conditions, and hence sufficiently warm microclimates, are essential for viral replication in the infected midge (Carpenter *et al.*, 2011).

(2) Host level

Domestic ruminants are a special case of hosts, since their requirements in terms of resources are provided by farmers. Except for free-roaming sheep flocks, their functional habitat is equivalent to the pastures and farms in which they are kept. For wild ruminants, such as roe deer and red deer, it is known that they seek shelter in forested areas, forage both in forest and on pastures, particularly browsing along edges between these habitats (Saïd & Servanty, 2005; Pérez-Barbería, Hooper & Gordon, 2013) and require access to water for drinking (Vospernik & Reimoser, 2008; Godvik *et al.*, 2009).

(3) Vector level

Culicoides spp. need the availability of hosts for blood meals, but the hosts used are not all competent for BTV. Recent analyses of blood feeding patterns indicate that most of these mammophilic species feed opportunistically on a wide range of hosts including domestic and wild ruminants, people and even birds (Garros *et al.*, 2011; Ninio *et al.*, 2011; Lassen, Nielsen & Kristensen, 2012; Pettersson *et al.*, 2013). For oviposition and larval development, the availability of breeding sites is required. Although European *Culicoides* species have been found to breed in a wide array of potential sites (reviewed by Harrup *et al.*, 2013), some distinctions in breeding site preference can be made among species (see Table 1). Important breeding sites are organically enriched moist soil, mud at the soil–water interface, intact dung of large mammals and leaf litter. Furthermore, some species can tolerate shading of their breeding sites, such as *C. obsoletus* whose populations have been associated with forested areas (Conte *et al.*, 2007; Kluiters *et al.*, 2013; Rigot *et al.*, 2013). Resources needed for mating and resting are not well studied, although some species have been observed to shelter on tree trunks [Carpenter, Mordue & Mordue (Luntz), 2008*b*]. Male *Culicoides* spp. do not feed on blood and are known to use nectar as a food source (Mullens, 1985). Suitable thermal conditions, and hence sufficiently warm microclimates, are essential for the vectors to mature their eggs and go on to take further blood meals (Mullens *et al.*, 2004).

(4) Regional variation

There is geographic variation in the vectors involved in transmission and their ecological resources; we illustrate the use of the RBHC for several geographic regions, and discuss its advantages. The main vector in southern Europe is an African–Asian species *C. imicola*, whereas in northern Europe, potential vectors belong to two Palaearctic species complexes, the *C. obsoletus* group (*C. obsoletus s.s.* and *C. scoticus*) and closely related *C. dewulfi* and *C. chiopterus* species and the *C. pulicaris* group. In some cooler and wetter areas of southern Europe around the northern range margins of *C. imicola* (European Turkey; southern and eastern Spain, southern France and Corsica), these Palaearctic complexes may play a major role in transmission, either alongside or in the absence of *C. imicola* (Purse *et al.*, 2008).

(5) An instructive case study

Using the case of bluetongue virus, we illustrate how different landscape configurations may affect transmission risk by differentially promoting interactions between ruminant hosts and midges with diverse breeding habitat requirements. We consider three different epidemiological scenarios with differing midge community compositions, loosely corresponding to the situation in northern Europe with Palaearctic species only (Fig. 2A), southern Europe with *C. imicola* only (Fig. 2C) and an intermediate situation with Palaearctic species and *C. imicola* (Fig. 2E), each with an example of how removing or relocating a key resource could help to reduce transmission risk (Fig. 2B, D, F). These represent somewhat simplified situations [we assume for example that alternative breeding sites for these species such as silage and dung pats inside animal housing (Zimmer *et al.*, 2010, 2013) are not available in our landscapes], but are illustrative of the utility of the concept. We also assume that the key difference between *C. imicola* and palearctic Avaritia species like *C. obsoletus s.s.* (that both develop in moist-soil organically enriched habitats) is that the latter are more tolerant of shading by forest and can breed in leaf litter (Table 1, light versus dark purple circles Fig. 2). All potentially relevant species are considered as well as their (overlapping) functional habitats. This overcomes the problem of oversimplification of the system, e.g. by inferring risk only from vector presence or by looking at disease cases

Table 1. Characterisation of the breeding sites of potential European midge vector species of bluetongue virus (BTV)

| Species and subgenus	Region of Europe where incriminated in BTV transmission	Breeding sites
Avaritia subgenus		
Culicoides imicola	South	Organically enriched moist soil, e.g. water trough overflow, irrigation canal leaks and margins, mud-dung mixtures, often unvegetated or sparsely vegetated
C. obsoletus s.s.	North and south	Organically enriched moist soil, e.g. manure heaps, silage residue, and leaf litter
C. scoticus	North and south	Organically enriched moist soil, e.g. silage residue, rotting leaf litter
C. dewulfi Goetghebuer and *C. chiopterus* Meigen	North	Dung of large mammals
Monoculicoides subgenus		
C. pulicaris group (*C. pulicaris* L./*C. lupicaris* Downes & Kettle, *C. punctatus* Meigen)	North and south	Mud at the soil–water interface, e.g. pond margins, marshes, waterlogged meadows
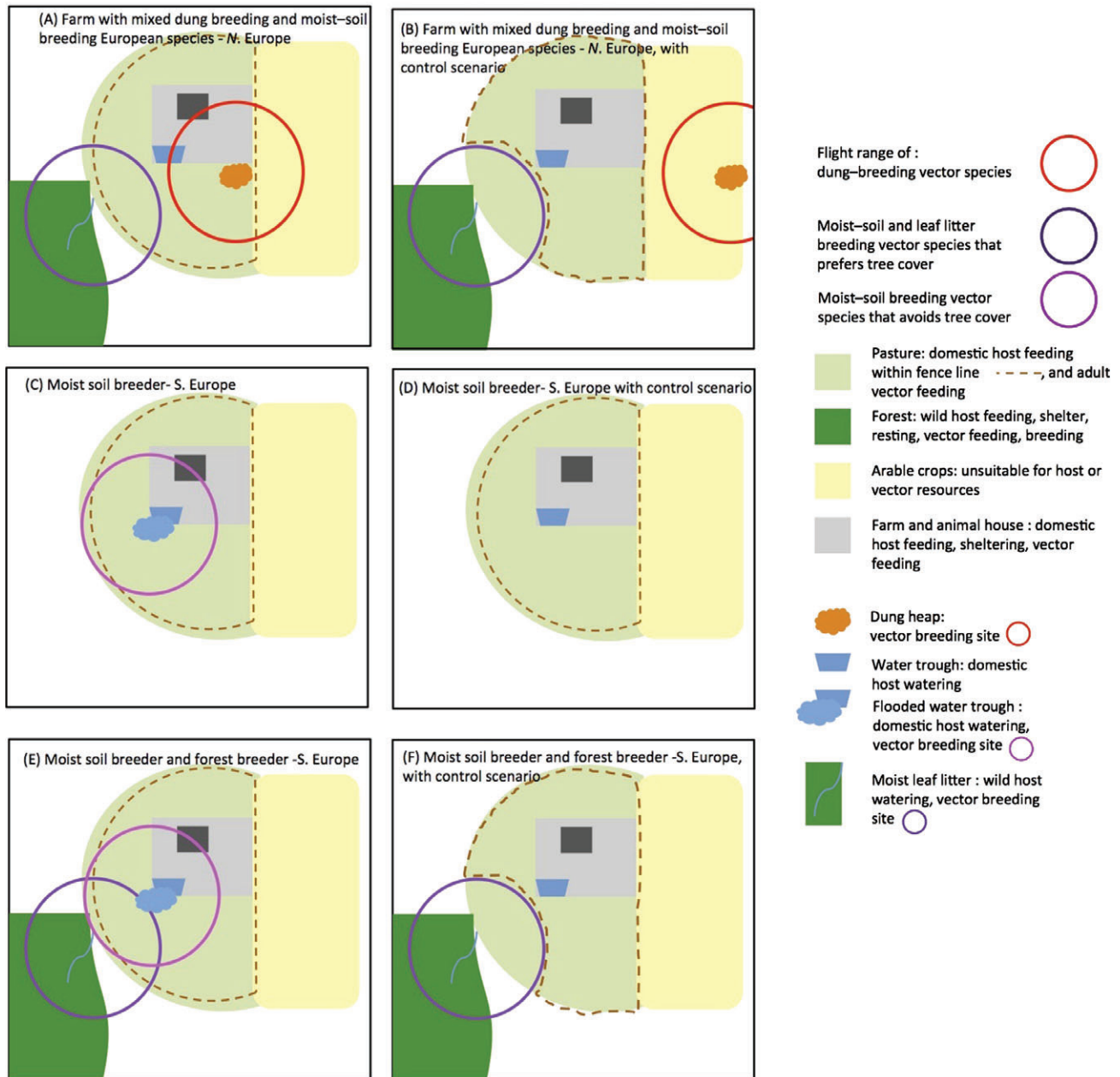
Fig. 2. Application of the resource-based habitat concept to bluetongue virus, with domestic ruminants as hosts and several species of biting midges as vector species. Scenarios represent the situation in northern Europe with Palaearctic species only (A), southern Europe with *C. imicola* only (C) and an intermediate situation with Palaearctic species and *C. imicola* (E), each with an example of how removing or relocating a key resource could help to reduce transmission risk (B, D and F, respectively).

data, that may be biased due to regional differences in level of host exposure or surveillance. It allows consideration of potential disease risk in advance of a pathogen arriving.

In Fig. 2A, domestic hosts are exposed to both dung-breeding and moist-soil-breeding species, as permitted by the spatial arrangements of features and movement capacity. Pathogens could be passed easily between domestic and wild hosts since both are bitten by moist-soil-breeding vectors. For the same landscape, in Fig. 2B, while all the same landscape elements are present, this potential has been

reduced by moving the dung pile breeding site far into the unsuitable arable area away from the farm and forest and by restricting grazing to areas close to the farm.

Figure 2C shows a situation where the moist soil breeder occurs alone (e.g. areas in southern Europe without forest where *C. imicola* is likely to be dominant over the *C. obsoletus* group species *cf.* Conte *et al.*, 2007). Removing the flooded area around the water trough should reduce the transmission risk (Fig. 2D).

Figure 2E displays a mixed population of moist soil breeders, one that prefers open conditions and a forest species that breeds in leaf litter or can tolerate shading of development sites. Domestic hosts are exposed to both and pathogens can again be transferred between domestic and wild ruminants. Measures accounting for functional features and movement, such as eliminating flooding around the water trough and restricting grazing to areas away from the forest, could reduce potential transmission (Fig. 2F).

(6) Advantages of the RBHC

These examples on bluetongue, based on the species described in Table 1, illustrate that the degree of spatial and temporal overlap between sets of pathogen resources is influenced by the spatial configuration of the resources of the vector (here mostly the breeding sites) and the host, but also by the dispersal capacity of the organisms, which for the midges is determined by their flight ranges and for the domestic hosts by the fence around the pasture. These illustrations show how the RBHC can be useful in differentiating between situations in which transmission is possible or not, in similar landscapes, depending on whether movement capacity of the vector and host and the location of the different resources allow for the completion of the life cycle of the pathogen. An explicit focus on the mobility of the vectors and hosts was adopted, considering local movements between resources. They determine the spatial scale at which the organisms functionally integrate physically separated clusters of (different) resources (Van Dyck & Baguette, 2005). Hence, the combination of resource distribution maps and knowledge about local movements of the organisms involved will allow assessment of the functional grain of landscapes (Baguette & Van Dyck, 2007). Animal movement also constitutes a key aspect of the spread of emerging diseases, since the permeability of a landscape for a pathogen will depend on whether vectors and hosts can disperse. Dispersal movements, and the way they are facilitated (or not) by landscape structure, may differ from routine types of movements to exploit resources locally (e.g. foraging) (Van Dyck & Baguette, 2005). Although the field of disease ecology is already multidisciplinary, collaborations with experts from the field of movement ecology may be very fruitful to improve modelling performance (Morales & Ellner, 2002; Davis *et al.*, 2008).

Note that even if the precise resources that are actually found in the (proximity of the) forest are not (yet) known the RBHC helps in identifying relevant landscape characteristics that present clusters of resource sets, such as pasture next to forest. The importance of forest in determining midge vector species composition has been suggested previously (Conte *et al.*, 2007) and by several participants in an online survey in the European research project EDENext (www.edenext.eu). Indeed, pasture and forest habitats represent key landscape elements where vectors feed on wild ruminants including roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) (Linden *et al.*, 2010; Lassen *et al.*, 2012); a high midge abundance at edges between pasture and forest has been confirmed by transect counts (Rigot *et al.*, 2013). Mixtures of pastures and forests can be easily identified on maps by looking at fragmentation indices, without detailed information on individual breeding sites or trees. Hence, even if we do not have full access to detailed autecological data, there is still scope to interpret vegetation maps from the functional viewpoint of the host, the vector and their interactions.

Another aspect of overlap that is not well captured by vegetation-type-based habitat approaches is temporal overlap. The RBHC helps us consider the spatio-temporal aspects of functional habitat overlap between the host and vector. For transmission to occur, vectors and hosts need to be present at the same time. An example of a disease where the temporal aspects of functional habitat overlap are crucial is Schmallenberg virus, another midge-borne virus. Schmallenberg virus only produces birth deformities if the female cow or sheep receives an infectious bite from a midge during a critical period of pregnancy. Bessell *et al.* (2013) showed that this critical period coincides with the end of the adult vector season in Scotland and that delaying mating by around 15 days could reduce the rate of malformations in sheep by moving the critical period into a time when adult vector populations are negligible.

The RBHC is based on an organism-centered approach, focusing on organism-specific ecological resources and their spatial–temporal configuration. The approach acknowledges that resource requirements can be realized in different ways under different conditions. For example, in an open area of pasture, a barn may be required for shelter, whereas in a small area of pasture between forest patches, shelter is provided by trees. In conservation biology, similar insights have been obtained as functional habitat may deviate from structural habitat as defined through the eyes of human observers (Van Dyck, 2012). For example, the grayling butterfly (*Hipparchia semele*) is a dune and dry heathland species in Belgium, but can be found in forests in Greece and Russia. These are structurally very different habitats, but both, locally, correspond to the thermal requirements of the species.

In Fig. 2, the right-hand panels illustrate how manipulation of landscape factors, such as removing or relocating dung heaps, changing the positions of fences around the pasture, and preventing spillage from water troughs, can locally reduce transmission risk. Removal of *Culicoides* spp. breeding sites has already been shown to be useful in reducing vector abundance in North America for *C. sonorensis* (Linley, Evans & Evans, 1970; Mullens & Rodriguez, 1989; Carpenter, Mellor & Torr, 2008a), even though this has not always translated into reduction of pathogen infection as measured by sero-conversion rate (Mayo *et al.*, 2012). In South America, transmission of oropouche virus was decreased by removing rotten banana stumps or cacao husks in the vicinity of houses since they act as ideal breeding sites for the main vector, *C. paraensis* (Hoch, Roberts & Pinheiro, 1986).

A valuable application of the RBHC framework concerns options for altering grazing areas and routes of domestic hosts on a farm-by-farm basis to minimize contact with wild

ruminant grazing areas and seasonally variable availability of vector breeding sites. A recent simulation model for the spread of bluetongue across pastoral landscapes in Denmark (Græsbøll *et al.*, 2012) showed that restricting grazing during outbreaks can reduce the overall number of infections in hosts and the size of the affected area in an epidemic. The RBHC could help to identify the key resources and the relevant scale at which movement restrictions and other measures, such as removal of breeding sites, should be implemented.

VI. DISCUSSION AND PERSPECTIVES

Vector-borne disease risk mapping has received much attention over recent years (Kalluri *et al.*, 2007; Reisen, 2010; Eisen & Eisen, 2011). Given the (re-) emergence of several vector-borne diseases due to globalization and global change, interest in this field is likely to increase. However, further conceptual and methodological progress appears to be hampered by the lack of a solid and applicable conceptual framework for landscape epidemiology. We suggest that the RBHC framework offers the opportunity to link mechanistic and statistical approaches in vector-borne disease risk modelling and mapping. It allows increasing biological realism by adopting the viewpoint of the organism, and by including spatial frames that correspond to the mobility of the organisms concerned. While the RBHC can be applied to any vector-borne disease, it is likely that it will be easier to apply to pathogens that use a restricted range of hosts and vectors, and for which the resource requirements of hosts and vectors are well studied and linked to specific landscape features. However, for pathogens for which the vector and host species are less specifically linked to certain vegetation types, but rather to a combination of landscape features, this framework may be even more useful.

Various paths exist for tapping the potential of the RBHC in vector-borne diseases, apart from the most immediate use suggested in Fig. 1. At the onset of studies, the RBHC can help in identifying the key components of the system under study. It provides an interesting avenue for guiding sampling campaigns, rather than carrying out opportunistic or random sampling, using maps of zones and seasons that are hypothetically more likely to contain suitable habitats from the pathogen's viewpoint. The RBHC can serve as a conceptual framework for agent-based models. From a methodological point of view, agent-based models may be a highly suitable modelling framework to integrate and explore the RBHC, particularly for integrating sociological and ecological processes underpinning transmission (Linard *et al.*, 2009). Agent-based models are both spatially explicit and mechanistic, and capable of incorporating animal movement and landscape features, and the RBHC could serve as a paradigm for this type of model; the systematic approach ensures that all relevant species, their interactions with the environment and with each other are taken into consideration.

Furthermore, the RBHC may facilitate collaboration among different scientific communities, including epidemiologists, geographers, landscape ecologists, zoologists, spatial modellers, public health specialists and policy makers. The RBHC can be used to assess systematically whether all relevant species, their life functions and associated resources (i.e. consumables and utilities) have been taken into account, and whether any knowledge or data gaps exist. Finally, because many pathogens considered here are shared among domestic animals, wild animals and humans, the RBHC may be a significant contribution to the implementation of the 'One Health' approach, interfacing veterinary and human health as well as other disciplines involved in the study of diseases with an ecological component (Zinsstag *et al.*, 2011).

Last but not least, the RBHC may be used to identify potential environmental control measures, as was illustrated with the BTV example above. Altering local landscape structure or land use may separate key resources spatially, so that not all resources needed to complete the life cycle are within the movement range of the organisms involved. Hence, by functional disruption of the life cycle of either the vector, or that of the pathogen, the risk of disease transmission may be reduced.

VII. CONCLUSIONS

(1) We argue that the RBHC offers promising scope to deal with spatial modelling of vector-borne disease risks.

(2) The framework incorporates the resources required by the interacting species (i.e. pathogen, vectors and hosts) and their functional relationships with specific environmental features at the landscape level.

(3) Using the movement capacities of the animals involved, the potential functional habitat range (i.e. the delineated zones that correspond to the combined and integrated information on resources, utilities and scale of movement) can be determined for each species, and the overlap between vectors and hosts, combined with climatic conditions, ultimately determines the habitat suitability for a vector-borne pathogen. In several cases additional research to provide better estimates of frequency distributions of movements, and hence of potential ranges of overlap among the different organisms, will be necessary.

(4) The RBHC allows for the integration of landscape factors in epidemiological spatial risk assessments and hence bridges the gap between existing mechanistic modelling approaches that ignore landscape factors and satellite image-based approaches that are based on statistical inference only.

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