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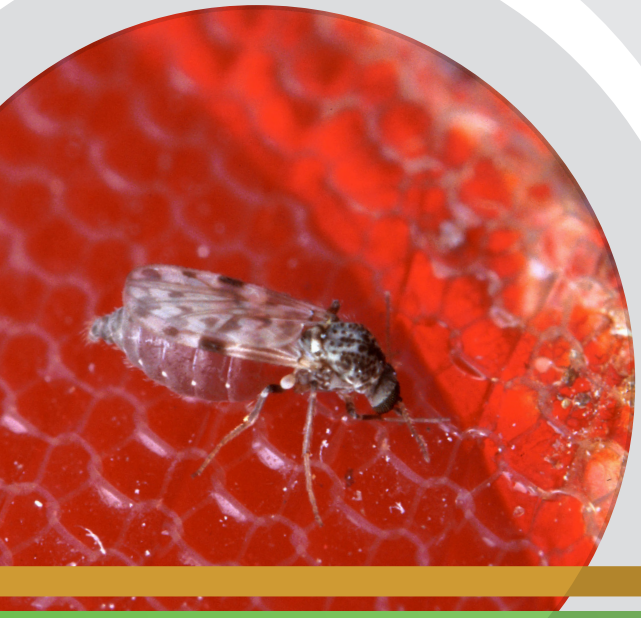

TECHNICAL REPORT

The importance of vector abundance and seasonality

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ECDC TECHNICAL REPORT

The importance of vector abundance and seasonality

Results from an expert consultation

This report by the European Centre for Disease Prevention and Control (ECDC) and the European Food Safety Authority (EFSA) was coordinated by Céline Gossner, and written and produced by the following contributors:

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Abbreviations

AHSV	African horse sickness virus
BTV	Bluetongue virus
CCHFV	Crimean-Congo haemorrhagic fever virus
CO_2	Carbon dioxide
ECDC	European Centre for Disease Prevention and Control
EEA	European Economic Area
EFSA	European Food Safety Authority
EID2	Enhanced Emerging Infectious Disease database
ESA	European Space Agency
E–W	East to west
GBIF	Global Biodiversity Information Facility
R_0	Basic reproduction number
S–N	South to north
TBD	Tick-borne disease
TBEV	Tick-borne encephalitis virus
WNV	West Nile virus
WNF	West Nile fever

Glossary

Abundance	Quantity (i.e. a number of specimens of a species in a site at a given time), which can be expressed in absolute terms, relative terms, as an index and as a rank or category.
Basic reproduction number	The number of secondary cases per case in a naïve population [1].
Human activity	Anthropogenic factors, which affect potential contact rate with vectors, as well as vector spread, and which may include farming practices, human behaviour and moving of animals.
Human biting rate	The number of bites received per day [2].
Intrinsic incubation period	The time taken by an organism to complete its development in the definitive host.
Longevity	A statistical measure of the average time an organism is expected to live [3].
Pathogen transmission by vectors	The process of a pathogen being passed from vector to host and vice versa.
Seasonality	The change in abundance of a species over the course of a calendar year. It is defined as the fluctuation of the active population over the period that it is present.
Vector-free period	Period of year when active (adult) vectors are not present.
Vector season	The period between the date from which active individuals are first recorded and the date after which it is no longer recorded (which is the end date of the season). It is also referred to as season length.

Executive summary

Knowing where vector species occur is crucial for the assessment of vector-borne disease risk. This was recognised by EFSA and ECDC, who, over the period 2014–2018, funded VectorNet, a European network for gathering and sharing data on the geographic distribution of arthropod vectors of disease agents affecting humans and livestock.

The VectorNet database contains distribution data on four vector groups: mosquitoes, sandflies, *Culicoides* midges and ticks. The majority of these data are on vector presence or absence, but since 2015, count data from a number of targeted field surveys, which used standardised sampling methods and that were funded through the network, have been added.

The objective of this document is to describe an assessment, for each vector group, of whether vector count data (abundance) and the way these change throughout the year (seasonality) can provide useful information about epidemiological processes of interest, and therefore, whether resources should be devoted to collecting such data. The document also summarises what measures of abundance and seasonality can be collected for each group, what gaps remain in the sampling coverage and what can be done to fill these gaps. Furthermore, it provides guidance for prioritising the acquisition of information.

For each vector group, expert opinion was canvassed to provide a semi-quantitative assessment of whether and how vector abundance and seasonality, each individually or in combination, are related to pathogen establishment, persistence, transmission and spread, are predictor variables useful for early warning, and are useful to spatially and temporally target vector or pathogen control.

Abundance and seasonality may each be closely related to pathogen establishment, persistence, transmission and spread, and thus each serve as epidemiologically relevant indicators. However, their significance may only become apparent when combined with each other or with other variables that are related to the vector's ability to transmit infection — for example, the proportion of vectors that are infected with the pathogen (the vector infection rate). The importance of abundance and seasonality was, therefore, considered for each in isolation and for both combined as well as both combined with other variables that may determine vector occurrence such as vector behaviour, vector infection rate and habitat.

The information needed to make the assessments was collated from dedicated VectorNet group discussions, field sampling studies, and both peer-reviewed and grey literature. Each vector group leader scored the importance of abundance and seasonality (alongside other vector-related characteristics) for the assessment of whether early warning of pathogen introduction must be issued, for the assessment of pathogen establishment and spread and to guide vector control strategies.

In the group discussions, experts assessed that abundance, by itself, plays a role in the epidemiological processes of most vector-borne infections, although the importance of the role varied among the vector groups. Seasonality was assessed to have relatively little influence on vector abundance but to be more important in determining the phenology of overwintering vector populations.

In all vector groups, abundance was considered to have an effect on pathogen establishment and transmission. This applied less to early warning systems and assessments of pathogen persistence. Abundance measures are routinely used for targeted control of mosquitoes, but this is not the case for the other vector groups.

For ticks, a special case exists: tick presence was considered to be a better indicator of risk of pathogen transmission than tick abundance if abundance is considered alone. Indeed, the number of ticks observed by itself cannot be considered an indicator of risk of infection. This changes when abundance is combined with vector infection rates. If information on abundance and seasonality is combined with other vector-related characteristics (such as vector infection rate), then abundance and seasonality are judged to be important.

This argues for acquiring both abundance and seasonality data on the disease vectors of public and animal health concern, alongside collecting and recording additional variables such as vector infection rates and biting rates.

While the VectorNet database already contains a substantial amount of vector abundance and seasonality data collected during targeted field surveys, important gaps at the continental scale remain. Additional data are, therefore, needed to fill these gaps, for example through additional field work and literature searches. Additionally, mechanistic, environmental and spatial distribution modelling may aid to maximise the use of the data currently available as well as help minimise the amount of additional information that would be needed to generate large-scale transmission risk maps. This report outlines the sampling strategies and prioritisation steps needed to acquire such information most efficiently.

Finally, in order to understand and ultimately reduce the potential risk of infection by (new) vector-borne pathogens, it is useful to compile comprehensive abundance and seasonality databases. Such a reduction of the potential risk of infection will, however, only be possible if there is the political will to support long-term transboundary programmes and if the necessary professional skills base is maintained.

Background

Knowing where a vector species occurs is crucial information for vector-borne disease risk assessment. This was recognised by EFSA and ECDC who funded VectorNet, the European Network for gathering and sharing data on the geographic distribution of arthropod vectors transmitting both human and animal disease agents (2014–2018). The maps generated under VectorNet are very widely used by the professional community and include published vector data, field data collected under targeted VectorNet field surveys, and information provided on a voluntary basis by the extensive expert network.

The VectorNet data database currently includes mainly presence/absence data on four vector groups: mosquitoes, sandflies, *Culicoides* midges, and ticks. Presence/absence data may be used as a first indication of potential risk for vector-borne pathogen transmission. The presence of a vector alone is, however, unlikely to be a reliable indicator of pathogen transmission, and it is reasonable to assume that measures of the number of vectors, also called abundance, would provide better indication of transmission risk.

In temperate regions, such as Europe, the importance of abundance and seasonality as factors in arthropod-borne (arbo) viral outbreaks vary widely from region to region [4]. In general, active vectors are less numerous or even absent during the winter time, whereas they are more numerous during the rest of the year and will show one or two peaks in abundance, usually in summer time. The timing and pattern of these abundance cycles, called seasonality, affects the impact of vectors on infection dynamics. In turn, the variation in vector numbers and in vector activity are related to environmental drivers such as temperature and humidity. Neither vector abundance nor seasonality can be measured by taking a single sample at a given time and place, and sequential samples during longitudinal studies are required to obtain information on seasonality.

A number of epidemiological indicators are relevant to the preparation of outbreak response and mitigation strategies and might be used for early warning of pathogen introduction, and as indicators of pathogen establishment, persistence, transmission and spread. These indicators are determined by a range of factors related to the vector, its hosts, the geographical location, and the characteristics of the pathogens themselves. Vector abundance and its associated seasonality are, therefore, only two of the epidemiological drivers, and the degree to which they are relevant varies between the vector groups and between the pathogens these vectors carry.

The objective of this document is to assess the degree to which estimates of vector abundance and seasonality, for each vector group, can be used to inform assessments of epidemiological concepts. It does not aim to be a comprehensive overview of the subject but rather to inform decision makers whether it is worth investing the resources needed to acquire abundance and seasonality information. The document also summarises what measures of abundance or seasonality can be collected for each group, and the extent to which these are available within the VectorNet database. The document also outlines what gaps remain and what can be done to fill them.

Types of measures of abundance and seasonality

Abundance. According to Eldridge and Edman [5], abundance is a general term that addresses the question: 'How many?'. In this report, the term abundance refers to a quantity (i.e. a number of specimens of a species in a site at a given time), and can be expressed in absolute terms, relative terms, as an index and as a rank or category. Density, expressed as the number of individuals per unit area or volume at a given time point, is one measure of abundance.

Absolute abundance. The number of specimens per unit area or volume is called the absolute population [6]. When it is the number of a species per unit of the habitat, e.g. per volume of water or per host, it is called 'population intensity' [6].

Relative abundance. The number of specimens collected in a specific trap or sampling method, which is a sample of the population. When vectors are sampled by traps containing an attractant (CO_2, light, odour, sound, animal or human bait) or by dragging or sticky papers, their relative abundance is expressed as numbers per standardised sample. Only when collection methods are standardised, it is possible to compare relative abundance estimates between different places and/or different times.

Index. Individual specimens are not necessarily counted, but their occurrence in a breeding site or habitat is recorded. This measure is expressed as the number of sampled sites with vector presence divided by the total number of sampled sites. The resulting estimate is the abundance index. Examples are the container index and the house index for yellow fever mosquito (*Aedes aegypti*) surveillance [7,8].

Rank/category. Sometimes, relative densities across a large study area (e.g. Europe) are collected and classified into categories (e.g. high, medium, low), when the collection methods are not standardised. This provides an indication of the rank of the abundance on such a large scale. This can only be achieved when the category limits are defined by taking the entire area into consideration. Categorical density estimates can be useful as input to risk assessment models such as the Rift Valley fever risk assessment for EFSA [8].

Seasonality. The change in abundance of a species over the course of a calendar year is called the seasonality, which is defined as the fluctuation of the active population over the period during which it is present. The season and seasonality can vary from year to year and is influenced by a variety of landscape-level drivers including climate, vegetation, and host availability. Especially for long-lived vectors such as most tick species, fluctuations in the number of active individuals may differ from fluctuations in the population as a whole.

The more practical term 'vector season' or 'season length' is defined as the period between the date from which active individuals are first recorded (which is the start date of the season) and the date after which they are no longer recorded (which is the end date of the season). The 'vector-free' period is then defined as a period when active (adult) vectors are not present.

Using abundance and seasonality data

Vector abundance and seasonality data may be used to inform a number of epidemiological concepts that are of particular public and veterinary health interest. These include the early warning of pathogen introduction, the potential for pathogen transmission, its establishment and persistence, the consequent spread of the pathogen to new localities and the control of pathogen spread (these are defined in the Methods section). Many factors may influence these concepts, including factors related to vector ecology and behaviour, and they interact in a non-linear way, as recognised by Ross in 1916 when he published the first mathematical vector-borne disease model for malaria infection [9].

The interaction of these factors (parameters) is also illustrated by the estimation of, for example, the basic reproduction number (R_0), which can be considered to be a measure of the likelihood of success of the pathogen's establishment [1]. For example, the R_0 of malaria can be calculated in a formula using as parameters the number of bites per human per day (human biting rate or aggressive density, *ma*), the number of bites per day by each female vector (feeding rate, *a*), the longevity of vectors, the length of the intrinsic incubation period and of the duration of pathogen presence in blood [10]. Under the model assumption of homogeneous mixing (each human has the same probability to be bitten by each vector), the aggressive density can be calculated as *ma* = [(number of vectors/number of humans) x biting rate], and vector numbers are therefore an integral part of this formula and linearly related to R_0.

R_0 can serve as an estimate of the level of (potential) pathogen circulation between vector and host.

In vector-borne disease systems in which the pathogen reservoir species is also the host of interest to public or veterinary health, R_0 and the risk of infection (in hosts of interest) are similar, correlating linearly with vector abundance. The linear relationship may not hold if, for example, the hosts in which infection is of interest are 'dead-end hosts' – i.e. hosts from which the pathogen cannot be transmitted onwards by the vector. An example is West Nile fever. A high transmission rate of West Nile virus (WNV) among birds by mosquitoes does not directly imply that horses or humans will become infected and sick. Horses and humans are dead-end hosts that do not contribute to the virus transmission cycle, and therefore are not part of 'classical' R_0 calculations. Another example is Lyme borreliosis. The causative agent of this disease (*Borrelia burgdorferi*) cycles between ticks and wildlife hosts such as small mammals and birds, while humans are dead-end hosts. Therefore, high transmission rates between ticks and wildlife do not necessarily imply a high risk of transmission between ticks and humans.

Methods

Abundance and seasonality cannot be considered in isolation from other vector characteristics and factors that influence the ability of vectors to carry and transmit pathogens. At the start of VectorNet, four experts were appointed as vector group leaders, each responsible for the management of data for one of the following vector groups: mosquitoes (Francis Schaffner), ticks (Jolyon Medlock), sandflies (Bulent Alten) and *Culicoides* biting midges (Thomas Balenghien). In order to assess the importance of abundance and seasonality in a wide context, these vector group leaders were asked to assess the importance of a range of vector characteristics to a series of epidemiological concepts. The group leaders were also asked to assess whether quantitative estimates of each vector characteristic are related to specific epidemiological parameters.

The approaches used to make the assessments were developed by consensus during a face-to-face meeting of the vector group leaders and members of the VectorNet consortium. This meeting was followed by a number of electronic exchanges in which parameters and epidemiological concepts were defined as outlined below.

Vector-related parameters

- Vector presence/absence. Whether a population of a species is present or not at any time of year. Vector presence data can be collected by ad hoc as well as systematic sampling efforts. Confirmation of absence requires a more intensive and standardised sampling regime.
- Vector abundance. Any measure of the number of vectors per sample, collected in a known and standardised way [11], at some point during a year. The vector may be sampled as epidemiologically active stages or inactive stages (e.g. mosquito eggs and larvae).
- Vector seasonality. Timing and duration of the period of vector activity or presence during the year, which embraces the start and end dates of the vector season and, by inference, the period when vectors are not present (the 'vector-free period').
- Vector infection rate. Proportion of vectors in which the pathogen has been detected (out of the total tested).
- Vector behavioural traits. Behavioural traits that may be related to a vector's host seeking and blood meal feeding efficiency. These include endo/exophagy, circadian activity, flight capacity, biting rate, longevity, etc. Many of these factors are incorporated into epidemiological models that quantify the risk of establishment and transmission of the pathogen.
- Reservoir host numbers. Any standardised indicator of numbers of one of more host species.
- Human activity. Anthropogenic factors, which affect potential contact rate with vectors, as well as vector spread, and which may include farming practices, human behaviour and moving of animals.
- Habitat change. Environmental changes affecting vector abundance or distributions.

Epidemiological concepts

- Early warning. Systems designed to provide advance warning of pathogen introduction or to detect pathogen circulation before the onset of disease in hosts of interest (on time to allow for implementation of prevention methods).
- Pathogen transmission by vectors. The process of a pathogen being passed from vector to host and vice versa.
- Pathogen establishment. A pathogen is considered to be established if there is at least one confirmed autochthonous case of transmission.
- Pathogen persistence. A pathogen is persistent if transmission in a given place continues from one transmission season to the next (by, for example virus overwintering).
- Pathogen spread. The movement of the pathogen to a previously pathogen free area. This includes, but is not limited to, vector-mediated spread.
- Pathogen/disease control. Any measures implemented to reduce levels of pathogen transmission, or disease prevalence. This includes control of the vector and of the disease in hosts.

As this document aims to provide an overview of the importance of abundance and seasonality of several groups of vectors of multiple diseases in relation to these epidemiological concepts, a scoring system, based on the VectorNet expert opinions and complemented with literature information, was applied. This scoring system, despite its limitations, was selected as the most appropriate method to achieve the objectives over more formal expert elicitation approaches such as Delphi elicitation. In addition to the expert opinion and data collected from peer-reviewed and grey literature, VectorNet experts also used material derived from a series of dedicated discussions among vector group network members at VectorNet annual general meetings and selected evidence from VectorNet field sampling studies.

The 'importance scores' assigned to each vector characteristic ranged from 0 to 4 (0: do not know, 1: no importance, 2: importance unlikely, 3: probably important, 4: certainly/almost certainly important). Each score was accompanied by a supporting comment which represented expert opinion unless formal references were supplied. A table was completed by each vector group leader (see Annexes).

To enable comparison between the vector groups and across the epidemiological concepts, the original scores from Tables in the Annexes were normalised so that the sum of scores for each vector group is 100. To provide some indication of the interaction between the various factors considered, these normalised scores for each vector characteristic were also summed for each epidemiological concept and each vector group.

Results and discussion

Assessment of the importance of abundance and seasonality

The group leaders' expert opinions and scoring are presented in Tables A1–A4, and the scoring is summarised in Table A5 in the Appendix. These tables have been condensed into two overview tables that summarise the results and highlight the similarities and contrasts between the different groups. Tables 1A and 1B provides a textual overview of the comments from each vector group, while Tables 2 and 3 give the normalised scores to help compare the assigned importance levels by epidemiological concept and vector group.

This series of tables suggests quite clearly that both abundance and seasonality (alone or in combination with other factors) are important for the majority of the epidemiological concepts for all vector groups and therefore should be included in any quantitative assessments of infection risk. This is not unexpected, particularly for abundance, given its central place in epidemiological models such as the one employed to calculate the reproductive number (R_0), outlined above.

There is thus a good case for acquiring quantitative data on these two parameters, and the data gathered can be used to provide useful quantitative estimates for a range of epidemiological concepts. The results also show, however, that the interpretation of abundance and seasonality data is not straightforward, as their contribution to infection dynamics is complex and often contradictory.

For ticks, vector numbers are unlikely to inform early warning. More tick vectors may, however, mean more chance of pathogen establishment in reservoir hosts and an increased likelihood of pathogen persistence. Tick abundance is weakly related to pathogen transmission as vector infection rates can be very variable and may compensate for low numbers. These interactions are illustrated by the example of rural and urban ticks and Lyme borreliosis provided in Box 1A. Pathogen spread is mediated largely by the movement of hosts and is more dependent on synchrony between vector and host than on vector abundance. Control tends to be focused on the host and is not dependent on vector numbers.

For mosquitoes, high abundance is likely to be linked to increased likelihood of pathogen establishment, and an increase in abundance may sometimes provide an early warning of potential pathogen establishment and transmission. However, this relationship is not necessarily linear, and high vector abundance does not necessarily mean that there is a high risk of pathogen transmission (see Box 1B), or that either vector or pathogen will spread. Control may be best targeted to areas of high mosquito abundance where the aim is to reduce vector numbers.

Because sandfly-borne disease and vector distributions usually match, a rise in abundance might provide some early warning of pathogen introduction, though there is too little direct evidence to consistently link sandfly numbers to increased pathogen establishment or infection risk (Box 1C). Vector abundance tends to be linked more closely to vector infection levels in outbreak situations than in situations where sandfly-borne diseases are considered to be endemic. The spread of sandfly-borne pathogens may be faster when populations are abundant, like with all vector-borne pathogens, but spread may be constrained by the heterogeneity of the local microhabitats (there might be barriers of unsuitable habitats that the vector cannot cross). Sandfly control is normally targeted to areas, and at times, where confirmed disease case numbers are high; it is usually not guided by vectors abundance.

For midges, populations rising above an abundance threshold may provide an early warning, and such events have been theoretically implicated in increased establishment of midge-borne pathogens like bluetongue (Box 1D). As is the case for other groups, abundance is a component of the basic reproductive number and vectorial capacity, which include transmission rates. Local spread of pathogens to surrounding areas may be high from farms with high midge abundance, and, as for ticks, control is most often focused on the pathogen within the host rather than the vector.

For all vector groups, seasonally unfavourable conditions in the environment may prevent activity or survival of vector life stages that are capable of transmission throughout the year. This affects pathogen persistence unless the pathogen survives the 'vector-free period' in the mammalian host or is transmitted vertically across vector life stages. Climatic seasonal changes are also closely linked to vector activity and development rate which will have some impact on vector numbers and pathogen transmission.

Table 1A. Summary of expert opinion of vector-related drivers of epidemiological concepts

Concept*	Early warning of pathogen introduction	Pathogen establishment	Pathogen persistence
Vector presence	Vector presence may not mean the pathogen is also present. For ticks, presence may not imply risk of infection, as ticks may not be established. Mosquitoes and midges may be present and established but not infected. Sandfly and disease distributions usually match.	For tick-borne pathogens, especially zoonotic ones, vectors are usually needed for transmission to hosts. Many midge-borne pathogens have multiple vectors, so the absence of one vector species does not prevent establishment of pathogens. For mosquitoes, presence is a prerequisite of establishment but this is highly influenced by other factors such as climate or host numbers. Sandfly-borne pathogens are found where there are vectors.	For all groups, pathogen persistence requires the presence of the vector. If a pathogen has multiple vectors, the link between persistence and a single vector may be less close. If hosts help to substantially amplify the pathogen (as for some tick-borne pathogens), persistence may be determined by host rather than vector.
Vector abundance	For less abundant vectors like ticks, vector infection rates are likely to be a better indicator of the risk of pathogen introduction than numbers of ticks. For more abundant species like midges and mosquitoes, populations rising above a threshold density may provide warning of potential transmission.	More vectors may mean more chance of establishment of tick-, mosquito- and midge-borne pathogens. There is little field evidence to link high sandfly numbers with increased pathogen establishment.	For many tick-borne pathogens, both vector and host abundance need to be high to lead to persistence. For all vector groups, pathogen persistence is likely to be linked to the vector's capability of surviving throughout the year as infected nymphs, larvae or adults, rather than survival of the pathogen in the host.
Vector seasonality	The start of seasonal increase of midge, sandfly and mosquito vector populations or feeding activity in ticks could provide some short-term warning of pathogen transmission.	Tick development may take several years, and longer seasons with suitable climate may encourage pathogen development. Pathogens of other vectors are more likely to establish themselves if there is no vector free period.	The longer the season, the more likely that vectors will become infected, be able to transmit pathogens to humans or reservoir hosts and will be able to overwinter to ensure pathogen persistence.
Vector infection rate	High vector infection rates are likely to provide early warning of pathogen introduction into uninfected host populations for all vector groups. For midges, vector infection rates are, however, generally too low for this to be a reliable early warning indicator.	High vector infection rates in all vector groups will increase likelihood of pathogen establishment, especially if there are overwintering infected vectors.	Vector infection rates are a good general indicator of the likelihood of pathogen persistence, where vectors are abundant, though less so for midges because of their low infection rates.
Vector behavioural traits	If accompanied by high vector abundance and vector infection rates, high biting rates provide warning of disease. Biting rates are unlikely to be a practical indicator for midges, as infection rates are often very low.	For ticks, only co-feeding by several stages is likely to increase establishment. For the other groups, biting rate and longevity combined with abundance may help identify where pathogen establishment is more likely.	For ticks, host rather than vector density or activity is the more important factor. For mosquitoes and sandflies, high biting rates combined with high abundance will lead to increased persistence.
Reservoir host numbers	Tick- and mosquito-, but not midge-borne pathogens are more likely to become introduced in areas with abundant hosts. Sudden increases in densities of hosts of sandflies may be followed by epidemics.	Tick- and mosquito-borne pathogens may be more likely to become established in areas supporting high (amplification) host densities. Rises in host densities may be followed by epidemics (sandflies).	Host density is linked to pathogen persistence in all vector groups, though only if it exceeds a threshold and particularly if the pathogen overwinters in the host.
Human activity	If human activity (e.g. trade, livestock farming and movement, tourism) determines contact rates with infected vectors, the occurrence of such activity might be used to identify where new infections are more likely.	Human activity may aim to prevent establishment and may create conditions such as concentrations of hosts, or vector overwintering sites where establishment is more likely.	Human activity may aim to prevent persistence, but it may also create conditions such as concentrations of hosts, or vector overwintering sites where persistence is more likely.
Habitat change	Habitat or environmental change can create areas that are suitable for vectors and are therefore known before the vectors become established. The reverse is also true. This is less important for mosquitoes and midges.	Habitat or environmental change can create new areas suitable for vectors and allow them to become established. The reverse is also true. This is least important for midges as they are less associated with specific natural habitats than other vectors.	Habitat or environmental change can create new areas that are suitable for vectors and allow them to persist. The reverse is also true. This is least important for midges.

**: for definitions, see Methods section.*

Table 1B. Summary of expert opinion of vector-related drivers of epidemiological concepts

	Pathogen transmission to hosts	Pathogen and vector spread	Pathogen transmission control (vector control and other)
Vector presence	Vector presence is not directly linked to pathogen transmission, especially if vectors are widespread. Vector role in transmission is reduced if there are other transmission routes (such as nosocomial) or via milk (e.g. tick-borne encephalitis).	Vector presence is not directly linked to pathogen spread, especially if the vectors are widespread. Vector presence in periendemic regions may not imply spread for sandfly-borne pathogens. As the vectors are limited by microhabitat conditions with very patchy suitability, this prevents spread from patch to another.	Control is by definition only needed where the vectors are present, but may not be needed everywhere they are present, especially if the vectors are not restricted to particular habitats or very abundant like midges and mosquitoes.
Vector abundance	For midges, low abundance restricts pathogen transmission, and vector abundance is a component of the basic reproductive number and vectorial capacity calculated for midges and mosquitoes. Tick abundance is less closely related to pathogen transmission and vector infection rates can be very variable and compensate for low numbers. For all vectors, however, pathogen transmission and disease occur when vectors are abundant and when they are not.	Vector abundance may enhance local spread, for example from farms with high midge abundance. Long-distance spread may be more affected by other factors like bird migration routes (ticks), wind and climate (midges), trade or animal movements (mosquitoes, midges). Sandfly spread is constrained by the patchiness of the local microhabitats.	Control may be best targeted on areas of high vector abundance especially of mosquitoes where the aim is to reduce vector numbers. For ticks and midges, the control is often focused on the hosts and may not primarily be intended to reduce vector numbers in the environment as a whole, and for sandfly-borne diseases the control is targeted on disease case numbers not vector abundance as most such diseases are asymptomatic.
Vector seasonality	The longer the season, the more likely that vectors will become infected, be able to transmit pathogens to humans or reservoir hosts and will be able to survive over the winter to ensure pathogen persistence.	The longer the season, the more chance for spread, provided the neighbouring habitat is suitable (for sandflies) and host and vector activity coincide (for ticks).	Vector-free periods determine when restrictions to animal movement are relaxed and vaccination campaigns can be run. Long seasons mean control programmes need to run for longer (sandflies and mosquitoes). Abundance cycles affect timing of public health measures against tick-borne diseases.
Vector infection rate	High infection rate is likely to increase pathogen transmission and disease risk. However, for very abundant groups like midges this relationship is not linear, so the impact of low infection rates can be offset by high abundance.	High vector infection rates will promote pathogen spread in all vector groups, but this may be counteracted by limited host numbers for ticks, and habitat unsuitability in sandflies.	Vector infection rate is a useful indicator for target control, providing sufficient sampling is practical.
Vector behavioural traits	For ticks, transmission is highest when human and vector activity are highest. High biting rate and high abundance of the other groups will increase transmission.	Ticks will spread fastest when high host density and vector activity coincide. For other vectors, high biting rate, longevity and abundance will promote spread.	Tick control is more effective if vectors are active. Biting rate of other vectors may help prioritise areas for control and be used as an indicator to assess impact.
Reservoir host numbers	The vectors rather than hosts drive the transmission of tick borne disease. However, high host density is associated with increased transmission rates of tick, midge and sandfly-borne pathogens.	Movement of infected hosts spreads pathogens. High host densities mean faster spread rates (midges).	Control of tick vectors on the hosts may reduce pathogen, but not if infection persists in the host. For the other vector groups control targeting is unlikely to be determined by host numbers.
Human activity	If human activity (trade, livestock farming and movement, tourism) determines contact rate with infected vectors, then it may promote transmission. Other human activities like vaccination, vector control or host treatment are meant to break the transmission cycle.	Human activity can lead to the movement of infected vectors, such as ticks on farmed animals and mosquitoes in trade goods, as well as the movement of infected hosts such as companion animals or livestock.	Not applicable.
Habitat change	Habitat or environmental change can increase or decrease the suitability of an area for vector development and activity, affecting pathogen transmission. This is least important for midges	Habitat or environmental changes, including urbanisation, can affect the suitability for hosts and vectors, creating areas into which they can spread, and where they can get established and persist. It is not relevant for midges.	Habitat change can be used to control vectors, for example modification of vegetation to control ticks or removal of larval breeding sites to control mosquitoes. It is not relevant for midges.

Box 1. Examples of the importance of abundance and seasonality for each vector group

A. Tick abundance and Lyme disease

The complexity of the interplay between tick density, tick infection rate and human exposure is illustrated by the rural and urban risks of Lyme disease, transmitted by the sheep tick *Ixodes ricinus*. Tick densities tend to be higher in rural areas, where there are also more large mammalian hosts (deer, livestock). Infection is not always transmitted from these larger animals to the ticks, so this can cause a dilution effect creating lower tick infection rates. With the relatively low human populations densities in rural areas, contact rates between humans and ticks may also be low, so that even where infected tick density may be high, few humans will get infected and the risk of infection at a population level is low [12].

In urban areas, the habitats suitable for ticks may have relatively few large animal hosts, but they do support small mammalian and bird hosts which can transmit infection to ticks. As a consequence, even if tick densities are low; the infection rates may be higher because infection rates are not diluted by large mammal hosts. Furthermore, in towns, the high human population densities may mean that more people come into contact with ticks with higher infection rates. Therefore, the main drivers of disease are neither tick density nor high infection rate alone, but the density of infected ticks coupled with levels human exposure to the vectors.

B. Mosquito abundance and West Nile fever

The severity of West Nile fever (WNF) outbreaks is determined by a complex interplay of avian host density, vector infection rate and human or animal exposure. For WNF, the numbers of human or horse cases are related to the numbers of bites by infected mosquitoes, and these numbers are themselves related to the intensity of pathogen transmission between birds and mosquitoes.

There is some limited field evidence to quantify the role of vector abundance in this system. During the 2012–2015 WNF outbreaks in Serbia, there was a close match between the distribution of clusters of infected mosquitoes, birds, horses and humans. There was also a strong positive correlation between both annual maximum and average mosquito abundance, and infection rate with annual incidence of WNF cases [13]. In the 2010 WNF outbreak in Maricopa County, USA, densities of the mosquito vector *Cx. quinquefasciatus* were also higher in outbreak areas than regions with no cases [14,15].

Despite these correlations, the relationship between vector abundance and infection rates is not consistent. The virus may be absent from areas of high mosquito density and WNF outbreaks may occur when vector abundance is low and the vector infection rate is high.

C. Sandfly abundance and leishmaniasis

In both outbreak (Madrid) and endemic (Murcia, Catalonia) situations in Spain, high vector abundance has been associated with high infection rates of *L. infantum* in the sandfly vectors, in humans or in dogs [16–18]. The outbreak in Madrid clearly showed that high sandfly abundance could be a major factor triggering a human leishmaniosis epidemic. However, this outbreak was epidemiologically unusual as it was associated with an explosion in the population of lagomorph hosts in the green amenity areas that were integrated into new housing developments built on agricultural land. Sandfly infection rates in endemic areas, however, seem to vary greatly, ranging from 4% or less in Portugal [19–23] to 39% in northwest Spain. None of these studies correlated sandfly abundance with *L. infantum* infection rate in vectors. Indeed there is evidence that high prevalence of human leishmaniasis was associated with a relatively low density of infected sandflies [24]. In this group, the relationship between vector abundance and infection rates is also inconsistent and contradictory.

D. Midge abundance and BTV infection

The case of bluetongue infection in Europe illustrates the relationships between midge vector abundance, seasonality and pathogen establishment, transmission and spread. Over two decades, several serotypes of bluetongue virus (BTV) have emerged in the Mediterranean Basin and (elsewhere) in Europe. Rise in temperature, due to climate change, is likely to have increased the abundance of the midge vector *C. imicola* populations in Spain, southern France and Italy during the 1990s, facilitating BTV emergence.

Rising temperatures have also led to changes in the biting rate and development rates of other midge species in north-western Europe making them more effective vectors [25]. After its introduction in 2006, BTV-8 was spread throughout northern Europe largely by wind-blown midge vectors [26]. The following year saw the disease spread from Belgium to the UK, Germany to Denmark and then to Sweden [27]. The speed of the BTV-8 spread in France was influenced by parameters linked to vector abundance, by land cover and by host density [28,29].

The interplay between abundance, seasonality and the other vector related factors provide the most insight into the drivers of epidemiological processes described by the concepts considered here. Table 2 shows the normalised scores summed for each vector related parameter by epidemiological concept and Table 3 shows the scores by vector group. The scoring in this table implies a fairly consistent pattern, as indicated by the distribution of the highest scores in red.

Table 2. Sum of normalised scores by epidemiological concept

Concept	Vector presence	Vector abundance	Infection rate	Behavioural traits	Seasonality	Reservoir host numbers	Human activity	Habitat change	Sum
Early warning	8.0	8.6	6.8	7.4	8.3	7.4	7.4	6.7	60.6
Pathogen establishment	7.7	**10.1**	**10.3**	**10.1**	7.6	8.9	7.0	8.0	69.7
Pathogen persistence	5.6	8.6	8.4	7.6	7.6	**9.9**	6.4	8.0	62.1
Pathogen transmission	7.4	**10.8**	**10.9**	**10.9**	8.3	**9.2**	8.9	8.9	75.3
Pathogen spread	6.7	**9.1**	**9.6**	7.6	7.6	**10.1**	**9.5**	8.9	69.1
Pathogen control	6.0	7.5	**10.0**	8.9	7.9	7.6	7.6	8.0	63.5
Total	41.3	**54.7**	**55.9**	**52.5**	47.2	53.1	46.8	48.5	400.0

Table 3. Sum of normalised scores by epidemiological concept and vector group

Vector group	Vector presence	Vector abundance	Infection rate	Behavioural traits	Seasonality	Reservoir host numbers	Human activity	Habitat change	Sum
Ticks	**14.3**	12.3	12.3	11.7	10.4	**14.9**	9.1	14.9	100
Mosquitoes	9.8	13.8	11.5	13.2	13.2	12.6	12.6	13.2	100
Midges	6.6	**17.9**	**15.1**	**14.2**	12.3	**14.2**	12.3	7.5	100
Sandflies	10.6	10.6	17.0	13.5	11.3	11.3	12.8	12.8	100
Total	41.3	**54.7**	**55.9**	**52.5**	47.2	**53.1**	46.8	48.5	400

Scores 9.0 or above in process and 14.0 or above in the vector group are shown in bold.

Abundance, vector infection rate, vector activity and behaviour, and host numbers are seen as the most important drivers of vector-borne disease epidemiology. By contrast, vector presence alone is seen as a relatively poor indicator (except for ticks), while the importance of seasonality and the effects of human activity and habitat change are considered to be of intermediate importance.

Abundance is to some degree important for all the epidemiological concepts, but most obviously in relation to establishment and transmission. Vector abundance matters most for midge- and mosquito-borne pathogens and somewhat less for those borne by ticks and sandflies. Seasonality alone is not generally seen as a frequent primary driver of any of the concepts. However, it is clear from Tables 2 and 3 that seasonality is considered a more important epidemiological driver for mosquitoes than the other groups and that it is an important determinant when combined with other drivers such as vector abundance. Vector season length is also not seen as a major driver of pathogen dynamics, except that it determines the vector-free period (when pathogen transmission by vectors is not possible).

These overarching patterns obviously conceal some characteristics of individual groups. Vector presence is most useful as an indicator of tick-borne disease, for which host abundance and the effect of the habitat on the vector are also key factors. This set of drivers highlights the difference between ticks and the other groups for which abundance, infection rate and vector behaviour are more widely identified as drivers of disease. The impact of anthropogenic influences on the vectors is considered to be comparatively small, especially for ticks.

Availability of abundance and seasonality data in the VectorNet database

It should be noted that much of the VectorNet database was compiled in the legacy of projects (TIGERMAPS, V-BORNE and VBORNET) and consists largely of presence/absence data for polygons, based on entomological observations, or on point data extracted from the literature or from national data surveillance programmes. While some of these data may have had numbers per trap or per sample, the earlier entries were converted to presence (or absence) per polygon or point location and recorded as such.

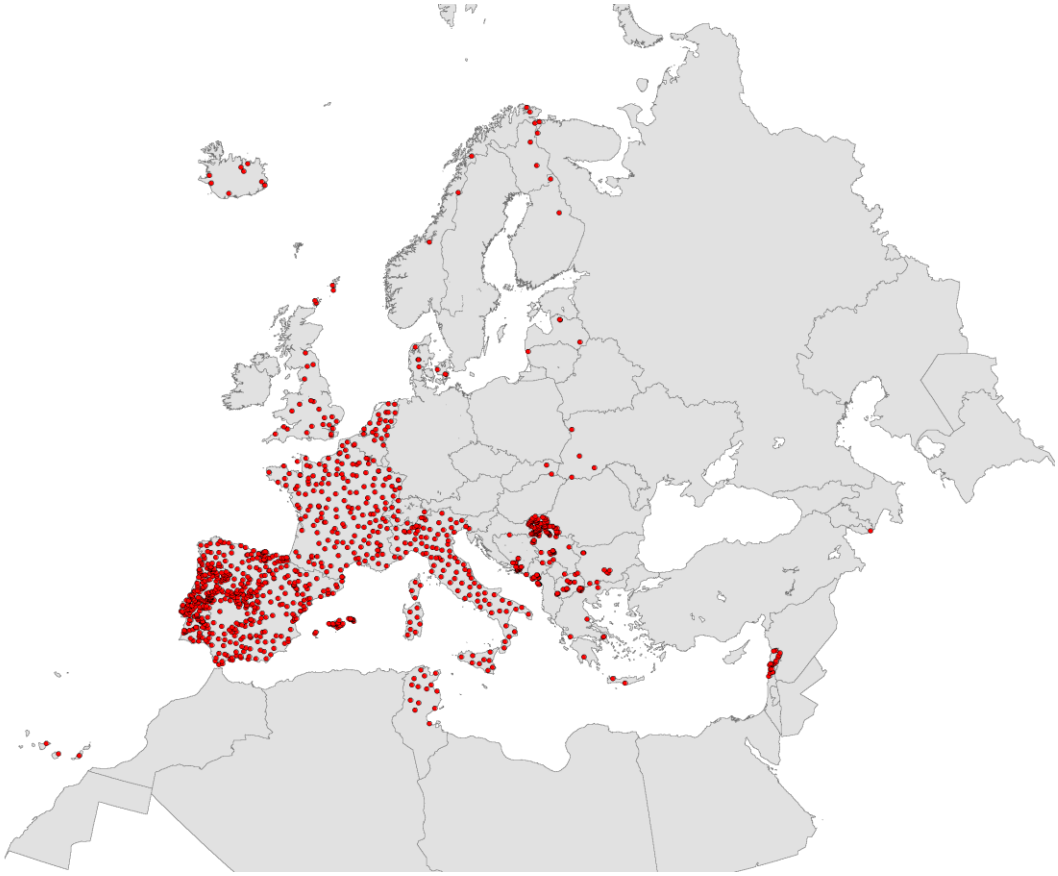
Collecting abundance data (numbers per sample) has only been a priority since 2016. An overview of the main methods used to sample abundance (and thus the potential for quantifying seasonality) of the four vector groups is provided in the Appendix. A summary of the data that have been assembled to date is provided below. While the field data in VectorNet were collected using standardised trapping techniques, and thus provide indicators of abundance per sample, most sites (with the exception of the *Culicoides* and the mosquito *Culex pipiens*) were sampled on a single date and were therefore not part of longitudinal studies. Therefore, they can only be used to provide indices of relative abundance within a group of sites sampled at the same time.

VectorNet funded substantial amounts of field sampling activities from 2014 until 2018, which were largely executed using standardised sampling or trapping methods and which yielded data on vector numbers with known denominators (per trap, per drag). In addition, many of the results from the wide-ranging national surveillance programmes for *Culicoides* species for much of western Europe have been incorporated into the database. These longitudinal surveys conducted in response to the outbreaks of bluetongue and Schmallenberg virus in the first decade of the new millennium.

All four vector groups have been sampled in several hundred locations as illustrated in Figure 1. Ticks and mosquitoes have been sampled throughout the continent, with a focus on northern and eastern Europe for ticks, and central and eastern countries for mosquitoes. Sandfly sampling in peri-Mediterranean countries, the Balkans and the Caucasus was informed by spatial distribution models produced in preceding projects. The *Culicoides* data obtained are concentrated in western Europe, supplemented by significant numbers of field samples in the Balkans and a transect crossing eastern Europe from north to south. Extensive *Culicoides* data have also been collected for other countries [30], focusing on species complexes rather than individual species. In order to integrate new data from these sources, VectorNet is continually contacting national surveillance authorities.

Figure 1. Locations with abundance values derived from standardised sampling of active vectors, VectorNet database, as of March 2018

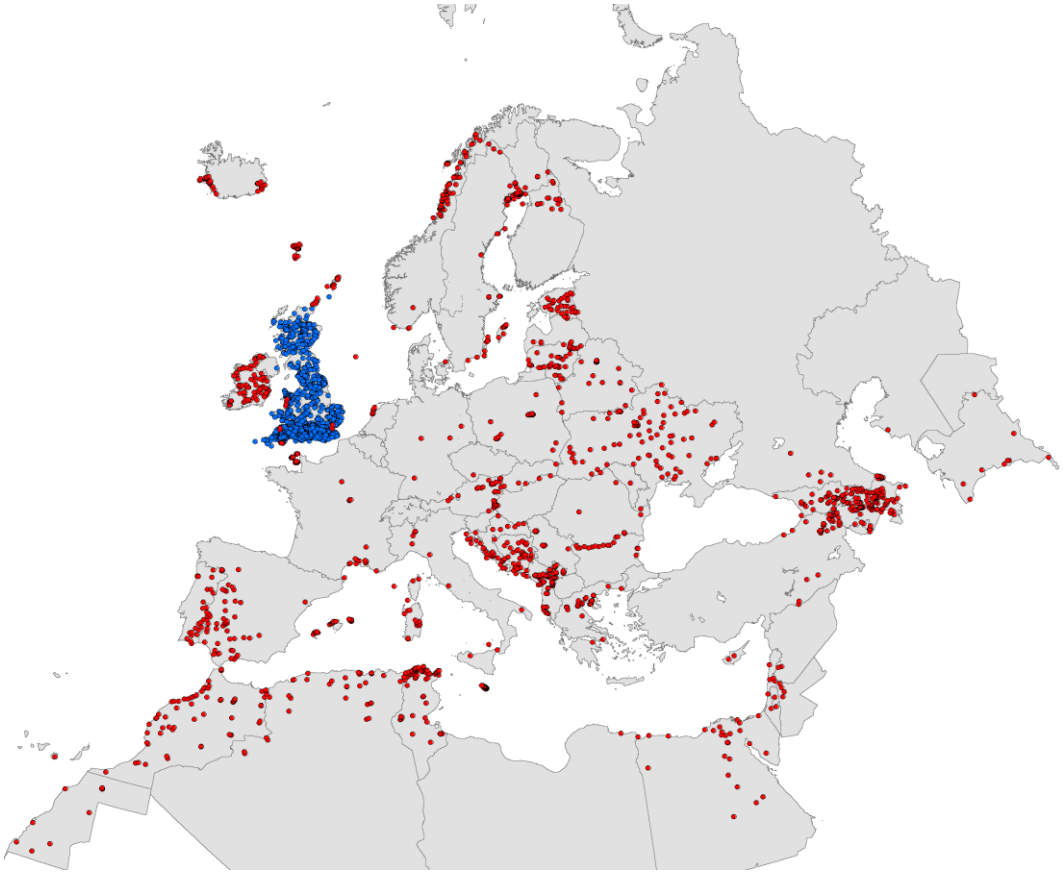
a) Midges



b) Mosquitoes

c) Sandflies

d) Ticks



Blue dots for ticks represent passive surveillance records.

For *Culicoides* midges, VectorNet holds rather extensive abundance data for much of Europe, and parts of northern Africa, though eastern European countries are less extensively sampled. These data therefore provide a reliable indicator of midge abundance in western Europe. For the other groups, few of the samples were longitudinal so there is little information on seasonality. There are, however, significant amounts of abundance data available for the four main tick species of interest, for some sandfly species, and for a few mosquito species (e.g. *Aedes albopictus*, *Culex pipiens*). For these groups, and for midges in the Balkans and some other areas, the standardisation of sampling provides at least some indication of abundance for the majority of sampled locations, even if it is only for a single date and a limited set of neighbouring locations. This resource may offer an opportunity to estimate abundance indices for limited regions or time periods, or perhaps provide opportunities for assessing the relationships between numbers and environmental drivers that could be used to generate models for larger areas. Additional information can be found in the section on spatial modelling of vector abundance and seasonality.

Requirements for abundance and seasonality assessments

The previous section demonstrates that the amount and coverage of vector abundance and seasonality data currently available for Europe and northern Africa are more complete for some groups than for others. With the exception of the *Culicoides* midges, longitudinal sampling efforts are available from relatively few locations at a continental scale, and both seasonality and harmonised abundance measures are comparatively rare. There remain, therefore, gaps in both the abundance and seasonality data for all groups. These gaps can be filled either by additional field sampling, or by model predictions that use environmental and existing distribution data to calculate consistent and complete coverage.

Field sampling

Field sampling, especially the longitudinal sampling needed for abundance and seasonality estimates, is expensive. Desk-based sampling methods are therefore likely to be the first port of call to acquire additional data. These methods include extraction from online databases such as EID2 [31] and systematic literature reviews. Though databases and literature reviews may provide useful information on abundance or seasonality, they are likely to focus on priority or high-profile species, and data for lower priority species tend to be excluded. Furthermore, neither method is guaranteed to provide information about particular areas of interest, and some form of further sampling or gap filling is likely to be necessary if continental level distribution maps are required.

Ways to prioritise which species and which locations should be sampled are set out in the Conclusions section below.

Overview of sampling strategies

A number of lessons have been learned during the VectorNet project. Sampling should be carried out using standardised or harmonised methods (which will be specific for each group) and run for several years to make sure that annual variation does not bias the outcomes. Transect sampling should be performed by standardised trapping starting at the beginning of season (potentially defined according to degree-days for each location) and continuing at regular two weekly intervals for the whole vector period that vectors are active. There should be sampling for consecutive weeks at 3–5 sites within each location.

Using large scale transects in Europe, S–N and E–W directed transects would reduce the amount of detailed sampling needed. If different trap types are used in different locations, conversion factors should be calculated from Latin square field comparisons or from evidence collated from the literature.

VectorNet experts from all vector groups were consistent in stating that it is not realistic to produce abundance (or seasonality) maps without substantially more resources than are needed for presence/absence maps with the same level of detail. Assuming, therefore, that the major aim of further field sampling is to fill the gaps in continental scale distributions (rather than, for example, to monitor the expansion of invasive species), sample or transect locations should be chosen to 'fill the gaps' and establish species distribution limits. If distribution models are available (see section on spatial modelling of vector abundance and seasonality), these can be used to determine where both the 'edges' and the major unsampled distribution foci are likely to be. Sample locations should also be well dispersed, rather than be close to regions for which data are available.

If, in addition to 'filling the gaps' in observed data, the objective of further sampling can be to feed spatial distribution models (see section on spatial modelling), then the target number of locations should be set accordingly. The main issues that limit spatial distribution modelling is the number of sample points available and whether they are sufficiently dispersed to be representative of the entire area for which the modelled map is required. There are no hard and fast rules to define the sample number needed to produce a reliable map, as it depends on the desired level of uncertainty, the method, the values themselves, and the strength of the statistical relationships between the target variable and the covariates used, which depends on group, species, and life stage as well as on habitat type, structure and other factors. As a guideline, at least one sample point every 100 km (i.e. 10 000 km^2) is required [32] for continental-scale areas, implying a minimum of 450 points for the EU.

There are a number of vector-group-specific issues that are summarised below.

Ticks

Earlier sections have suggested that ticks should be monitored by dragging of vegetation or estimating vector numbers on hosts. As for the other vector groups, sufficient longitudinal data will allow seasonal patterns in relative activity and relative abundance to be detected and can be compared with weather data on temperature and rainfall that can be robustly modelled (see section on spatial modelling below). A network of field stations where tick activity is monitored on a regular (preferably weekly) basis across the continent might be developed to generate data for a continent-wide temporal activity model. Data on tick seasonality and activity are likely to be more useful metrics to collect than vector abundance data, though these also require longitudinal sampling efforts.

Culicoides

Many extensive national schemes provide (or used to provide) seasonality and abundance estimates for *Culicoides* for much of western Europe. Annual maxima can be extracted from these data to compare abundance over time and locality, though additional information may be needed to establish seasonality as sampling dates may not have covered the start and end of the season. While many of these datasets have been incorporated into the VectorNet database, for several large countries, data on some species or species complexes exist but are not yet available to

the project. Future data acquisition efforts should be focussed on obtaining these existing datasets generated by existing surveillance programmes.

Though these data could most probably be used to generate reliable models for the whole VectorNet region (EU/EEA and neighbouring countries), there is a case for field sampling along the eastern and southern margins of this region from which *Culicoides* data are not readily available. Sampling should follow the protocols used for the national programmes such as those in France, namely longitudinal samples from selected farms every two weeks throughout the season, with the peak annual number per trap used as the abundance metric.

For *Culicoides*, in addition to climate, livestock density and land cover have been demonstrated to be determinants of species occurrence as well as where and how many vectors can be found [33]. An efficient strategy to limit the number of collection sites for assessment of abundance would be to use latitudinal and altitudinal transects, while sampling different classes of livestock and land cover. The number of collection time points needed per year would be dependent on the length of the activity period. The number of collections necessary to estimate maximum abundance could be reduced in areas where the *Culicoides* dynamics has been previously characterised by targeted trapping.

Searle also states '*Culicoides* surveillance methods should be adapted to focus on concentrated assessments of species-specific abundance during the start and end of seasonal activity in temperate regions to facilitate refinement of ruminant movement restrictions thereby reducing the impact of *Culicoides*-borne arboviruses' [33]. Searle also asserts that multi-species measures of diversity or richness are too variable to provide usable information [33].

Mosquitoes

Field work undertaken during VectorNet suggests a seasonal maximum of relative abundance might be the most suitable metric to describe continent-wide differences in basic 'risk' (Petric, personal communication) for pathogen transmission. Annual time series of relative abundance of eggs (e.g. *Aedes albopictus*) or adults (*Culex pipiens* complex) could be used to describe seasonality. Start and end date of vector activity (or vector-free period) can then be used to map the differences in seasonality across Europe.

A threshold level above which a vector's abundance is considered to pose a risk or be a nuisance is likely to vary regionally, as well as with pathogen and vector species. The threshold abundance to indicate WNV transmission onset in Italy was set to 300 specimens of *Cx. pipiens*/trap/night [34], while the citizen science programmes within the same area declared 150 specimens of *Cx. pipiens*/trap/night as a nuisance threshold.

At least for *C. pipiens,* VectorNet field sampling showed that one measurement at one location can be representative of a wider area and that a limited number of measurements per location at the beginning of the season gives a good indication of both seasonality and peak abundance later in the year. This has not been substantiated for other vector groups.

Sandflies

In rural areas, where sandflies are most common, they tend to concentrate where animals congregate, in farms and stables [35], but their abundance varies substantially with farm type [16]. Several sites of different type should therefore be sampled to get representative results. As with other species, standardised samples throughout the year can provide information on seasonality. As for mosquitoes, and indeed midges, annual maxima in numbers are likely to be a useful metric.

Light traps should be used and placed indoors in farms, close to walls and the floor, and within five meters of animal pens. Female sandflies are most abundant one to two meters from the animal group, and male sandflies may be more abundant four to five meters from the animal group [35]. Traps should be left for at least 24 hours. In order to estimate seasonality, sampling should be repeated at least every two weeks. Shorter sampling intervals will increase precision of the estimated seasonality and of the relationship between abundance and changing weather conditions.

Spatial modelling of vector abundance and seasonality

Mechanistic models

By using environmental determinants as proxies for vector presence or abundance, there are a number of ways in which vector distributions can be inferred. The simplest are the use of climatic thresholds to define areas where some aspect of development is limited or impossible. These thresholds can be applied as a determinant of absence (where for example species cannot overwinter and thus become fully established) or as a condition for development, which limits population growth to a specific season. This is well illustrated for *Culicoides* [30] and for the *Aedes* mosquitoes [36].

A number of more complex relationships between vector abundance or seasonality and environmental and other factors can be used to drive deterministic models. These models can be based on experimental or empirical determination of the relationships between the target variables and environmental (usually climatic) determinants. In particular, it may be possible to calibrate abundance models by matching contemporaneous climatic conditions with the standardised sample data already in the VectorNet database and make predictions for wider areas. Some examples of such relationships, investigated during the VectorNet project, are outlined below.

Temperature, and more generally climate, is an important determinant of the length of the activity period for most vectors [37]. For example, at the beginning of the year, activity starts when a threshold temperature is reached. Regional differences in the temperature thresholds that determine the start of the season for *C. pipiens* are recognised [38,39]. Risueño [16] reports a similar phenomenon for sandflies (e.g. *Phlebotomus perniciosus*; Central Spain: first occurrence early May (13.8 °C); northern Italy: first occurrence early June (14.3 °C). These thresholds are certain to be species specific.

Such relationships may be scale-dependent. Risueño et al. [16] report that sandfly (*P. perniciosus*) numbers are also related to micro-habitat, but that relative humidity, temperature and wind speed can be used to model numbers at a regional scale.

Apart from using simple temperature thresholds, some aspects of vector seasonality can be predicted using cumulative temperature or the number of day-degrees above a threshold. Examples include the questing activity of the tick *Ixodes ricinus* [40].

Relationships between environmental drivers and both seasonality and abundance may be affected by conditions which occurred several months earlier. An example is *I. ricinus* in Germany, where temperature and relative humidity determined vector densities 3–6 months later [41].

Other proxies for abundance may include vector hosts as well as environmental determinants. The number of tick larvae in Spain is related to the number of horses, as well as the temperature and the number of frost days, while nymphs are more dependent on temperature, rainfall and land cover type [42]. Deer numbers have also been linked to the number of ticks [43] and, therefore, tick numbers are likely to be low where there are no deer or where the livestock are treated with acaricides.

The types of models that can be constructed from such relationships are illustrated by an example from the VectorNet sandfly group. A recent article [44] describes the development of a discrete-time stochastic difference equations model to predict abundance and seasonality of the *Leishmania* vectors *P. neglectus, P. tobbi* and *P. papatasi* in eastern Mediterranean countries. The model includes four compartments, one for each life stage: egg, larvae, pupa and adult and models the flow between them dependent on environmental variables, including temperature and humidity. Basic survival, development and fecundity requirements are parameterised using experimental data obtained under controlled conditions [45]. Moreover, surveillance datasets from Turkey, Greece and Cyprus are used to adjust model parameters and validate the model.

These studies show that precise information on these parameters allows accurate prediction of field observations for sandfly populations in Turkey. The model and methodology used are extendable for predicting sandfly abundance and seasonality elsewhere, provided basic information on life history parameters are used for different vector species.

Clearly, such models are species specific and rely on a substantial amount of laboratory or field-based calibration, but they do provide an opportunity to produce distribution maps using readily available climatic indicators, such as those available from remotely sensed satellite imagery. As these become more widely available with, for example, the advent of the ESA Copernicus programme, such models may prove ever more cost efficient for a range of species.

Stochastic models

For those species for which information is not available to drive mechanistic models such as described above, the gaps in knowledge about distributions can be filled using long-established statistical spatial distribution modelling methods.

As for presence/absence modelling, there are a plethora of available methods suited for abundance modelling [46], three of the currently popular ones being boosted regression trees, random forest, and generalised linear mixed modelling. All the methods use the same principal: a statistical relationship is established between the known values from the sampled locations and the values of a series of predictor covariates at the sample locations. These equations are then applied to generate predictive maps using data layers of the identified covariates that cover the whole region of interest, usually at a fixed resolution of 0.25 to 10 km. It is also important to provide estimates of the uncertainty of the modelled predictions, either though inherent features of the modelling techniques (such as Bayesian) or by running the models a number of times.

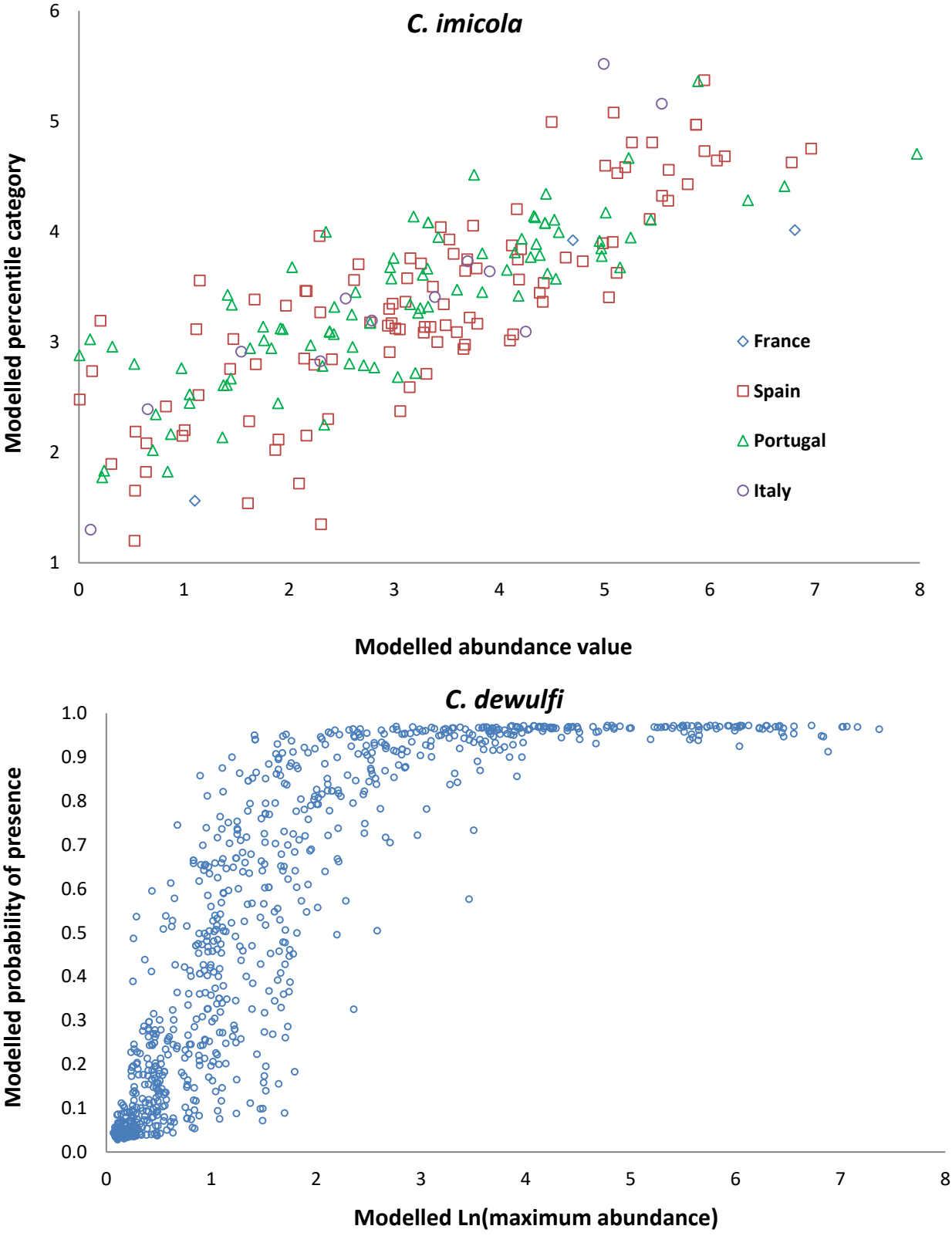
While modelling presence and absence does not rely on repeated samples throughout the year, it does need confirmed absence data. However, confirmed absence data (zero values) are not a prerequisite for abundance models, which use the whole range of values available and can predict absence (missing zero values) based on the assumption about the marginal statistical distribution (e.g. the negative binomial distribution). This simplifies the data gathering process significantly and means that fewer sample locations may be needed to fit an abundance or seasonality spatial model than a presence/absence one.

These techniques can be used on any datasets with numerical values, such as the standardised measures of abundance described above (the maximum number per trap and number per square meter are equally suitable). Given the difficulty of obtaining abundance data, there is a question as to whether proxy variables can be used to generate epidemiologically relevant spatial predictions.

Preliminary evaluations using the VectorNet *Culicoides* data suggest that, for most of the species, spatial model predictions of maximum abundance correlated well with model predictions of an outcome variable based on normalised abundance classes (which combine a number of different abundance value ranges; Figure 2, left). This implies that it might be possible, for some species, to calibrate some relative or ranked abundance measures in locations with reliable abundance values and use the resulting conversion factors to incorporate all relative or ranked abundance data into a single harmonised dataset. In addition, applying an appropriate threshold, model predictions of probability of presence, based on presence/absence data, could reliably be used to differentiate between low or zero abundance and medium or high abundance (Figure 2, right). For ticks, however, this was not found to be the case.

The 'standard' spatial modelling techniques and sample size requirement calculations used for abundance data can also be applied to indicators of seasonality, such as the length of the vector free period. These methods are also suited to model the start and end day of activity. For the date of peak activity, they may be less appropriate, as peak days may be difficult to define: there may be one or more peaks during the year, depending on climate or location.

Figure 2. Comparison of values extracted from spatially predicted surfaces of maximum abundance with ranked normalised abundance category for *Culicoides imicola* (top) and probability of presence of *C. dewulfi* (bottom)



The top panel of Figure 2 shows that the two models are very similar for all countries despite the fact that the abundance values are not measured the same way across countries. This means that converting abundance data into categorical data may be a way to standardise data from variable data sources. The bottom panel of Figure 2 shows that the modelled probability of presence, which uses presence/absence data as input, increases with the log maximum abundance value but saturates above a logged abundance value of two.

Conclusions and potential implications

Abundance and seasonality of vector activity play a role in the epidemiology of vector-borne diseases, even if that role is sometimes minor. Therefore, there is a case for collecting both abundance and seasonality data of vectors that carry pathogens of concern to public and animal health.

Collecting abundance and seasonality data through field sampling is, however, more expensive and time consuming than collecting most other vector-related data. With a few exceptions (such as for *C. pipiens*), multiple samples have to be taken throughout the year to ensure season start and end dates are adequately assessed and that seasonal peaks are detected. Furthermore, as vector distributions and abundance may change from one year to the next, sampling needs to be done over several years. As disease vectors typically occur in several countries, the production of maps requires continental scale approaches, which require standardisation among countries.

The importance of abundance and seasonality data varies considerably according to the vector group and the epidemiological concept of interest. Epidemiological concepts of tick-borne disease are less informed by abundance data than are those of the other vector groups, and presence/absence data of ticks may be sufficient if considered in conjunction with other factors. Abundance data are generally considered to be of relevance to pathogen establishment and transmission but less useful to inform early warning systems, estimates of the likelihood of pathogen persistence and – for sandflies, midges and ticks – to inform targeting of control measures.

Box 2. Prioritisation of abundance and seasonality sampling

Step 1. Desk study to define whether detailed abundance data are necessary and/or useful

- Define ecological concept of interest (early warning, pathogen transmission, spread, etc.).
- Define target variables for the study (abundance, start/end season, peak, etc.).
- Confirm that abundance is a useful epidemiological indicator (e.g. of transmission).
- Confirm whether or not seasonality metrics are useful.
- Assess whether the required outputs need precise abundance data or whether categorical are data sufficient.
- Check what data are available in existing databases (presence/absence data, standardised sample data, indicator dates).
- Assess whether a combination of other available data variables can be used to infer high risk (e.g. presence of host, habitat or climate).
- Determine whether there are species for which abundance is a more reliable indicator for risk.
- Assess whether proxies such as climate can be used to calculate the required metric.
- Define the time frame (snapshot, seasonal or change detection).

Step 2. Regionalisation (select from where these data are needed)

- The whole species range
- Pan-European
- Priority areas, e.g. outbreak areas or areas with a high risk
- Core areas
- Edges
- Specific habitats
- Locations optimised to calibrate models or maximise interpolation

Step 3. Assess the collection effort needed if precise abundance or seasonality data are required

- Define outcome measure and degree of precision required.
- Tailor sampling methods and outcome measures (e.g. number per trap or per square meter, maximum number per year) to selected species and region.
- Determine sample size, location and frequency required (using models if available).
- Use modelling of pre-existing (comparable) data to estimate the degree of extrapolation/interpolation possible.

While not generally amenable to large-scale regional or continental analyses, the majority of the abundance data in VectorNet may be suitable for localised analyses using proxy measures such as climate as predictors. Mechanistic, environmental and spatial distribution modelling can, through advanced interpolation and extrapolation techniques, make predictions for areas where data are sparse, and thus minimise the amount of field-collected data needed to fill gaps. Some models can generate maps that display the degree of uncertainty in the predictions, and where additional data are most needed. Despite this, there is a pressing need to reduce costs by prioritising among

abundance sampling strategies (Box 2). Essentially this involves 1) a desk study and extensive literature survey to define the programme, identify the target species and assess whether full-scale abundance surveys are really necessary; 2) if abundance surveys are required, selection of the areas where they are required; 3) an assessment of the sampling and data collection effort needed by defining sample strategy and required metrics.

Comprehensive abundance and seasonality surveys are clearly possible, as shown by a number of longitudinal sampling studies carried out as part of VectorNet and by the very extensive *Culicoides* surveillance programmes currently in place across much of Europe. Such large programmes are dependent on political will, which is often motivated by outbreaks, such as the unexpected emergence of bluetongue and Schmallenberg virus in Europe.

Other threats, such as the potential spread of vector-borne disease due to climate change and the potential emergence of new diseases, have yet to lead to similarly comprehensive monitoring efforts; in the latter category, the surveillance of invasive mosquitoes is the most extensive.

Finally, it must be emphasised that any form of extensive vector sampling depends not only on the provision of resources to fund the sampling programmes, but also on the availability of entomologists that have the skills to implement surveillance and monitoring programmes. The latter can only be guaranteed by continuous and sufficient strategic capacity building combined with career perspectives to attract recruits.

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Appendix 1. Vector groups

Vector group tables

Table A1. Expert opinion of vector-related drivers of epidemiological concepts: ticks

	Early warning of pathogen transmission	Pathogen establishment	Pathogen persistence
Vector presence	4	3	3
	A key pre-requisite, assuming vector establishment; e.g. *Hyalomma* ticks are frequently found in northern Europe, but they are not established [47], so their importation is not a sign of early warning of transmission [48,49].	Depends if the pathogen is zoonotic and whether the pathogen becomes established in hosts and amplifies within these hosts. Vectors are likely needed for transmission.	Persistence of a zoonotic pathogen may be reliant upon host presence and host density, but vectors are needed for transmission. It is possible that secondary vectors (e.g. I*xodes hexagonus* or *Ixodes uriae* [50,51] in Lyme borreliosis) play a role in establishing the pathogen (which may occur if no primary vector is present).
Vector abundance	2	3	2
	Less important, as outbreaks can start at low abundance. In cities, tick abundance may be low, but if there are high prevalence rates of *Borrelia* and high human exposure [12], pathogens may be transmitted.	More vectors mean possibly more opportunities for transmission to take place (depending upon prevalence rate), which increases the chance of pathogen establishment, particularly if this involves an animal reservoir of infection.	Vector abundance will not necessarily determine transmission, as it is host abundance that will determine persistence, unless vector is a key reservoir.
Infection rate	2	3	3
	Density of infected ticks is more important than prevalence rates, however no infection in ticks means no risk.	High density of ticks: higher infection rates increases chances of pathogen establishment.	Assuming a high density of ticks, higher infection rates increases chances of pathogen establishment.
Vector behavioural traits	4	3	2
	More activity/biting means more pathogen transmission. Very low activity can hinder pathogen transmission [52].	If pathogen is established in hosts and vectors, only activity determines transmission (e.g. for Lyme). However, co-incident feeding of tick stages can impact TBE transmission or local establishment.	Persistence of zoonotic tick-borne disease (TBD) is more linked to host presence/density than tick activity.
Seasonality	3	2	2
	Assuming vectors are the only route of transmission, pathogen transmission will not start until vectors are active, however, transmission may be linked to vector abundance, so vector season start may be less important. Pathogen transmission will cease once vectors stop biting, so season length can be important. However, vector abundance will be more important.	The season start does not determine establishment. The longer the season, the longer the chance of pathogen establishment; however, abundance and exposure are more important.	Only important if the length of the season determines the degree of disease transmission and hence the likelihood of the pathogen to persist in amplification hosts. Season start not likely to be important.
Reservoir host numbers	4	4	4
	If hosts are significant in amplifying the transmission, this is important. However, if vectors are required, this could be a constraining factor required for amplification.	In zoonotic TBD, reservoirs are important for pathogen establishment, particularly for *Borrelia*, *Babesia*.	In zoonotic TBD, reservoirs are important for pathogen persistence. *Borrelia* persists in small mammals and birds. For tick-borne encephalitis virus (TBEV), ticks play a greater role as reservoirs.

	Early warning of pathogen transmission	Pathogen establishment	Pathogen persistence
Human activity	4	1	1
	There may be aspects of human activity which determine transmission. If humans, for example, spend more time in the countryside (holidays, travel, events) and there is an ongoing outbreak in this area, transmission may be affected [53].	Humans are usually dead-end hosts, except in nosocomial transmission of Crimean–Congo haemorrhagic fever virus.	Humans are usually dead-end hosts.
Habitat change	3	4	4
	Changing a habitat may not immediately lead to an early outbreak warning. However, changes in vegetation (as part of the natural vegetation cycle) can be linked to a change in tick activity. This is often driven by climatic changes which change the habitat and also change tick activity.	If a habitat is changed from an unsuitable habitat (farmland) to a suitable habitat (woodland), amplification hosts and vectors may benefit.	Habitat change can be relevant if a habitat is managed in a way that allows vectors or amplification hosts to get established and flourish. Conversely, grubbing out a habitat and turning it into arable farmland negatively impacts persistence of the pathogen.

Table A1, continued

	Pathogen transmission	Pathogen/vector spread	Pathogen transmission control (vector control and other aspects)
Vector presence	4	4	4
	Important if mode of transmission is only vector-borne. Becomes less important for nosocomial transmission, e.g. Crimean–Congo haemorrhagic fever virus (CCHFV) [54] or transmission through milk, e.g. TBEV [55].	Presence can be due to importation. *Rhipicephalus* ticks were imported into northern Europe and are now infesting houses [56].	Knowledge of vector distribution in the risk area is important. Without data on vector distribution, it is difficult to take response measures. For example, defining the Lyme risk in a city is dependent upon mapping the presence of *Ixodes ricinus* [12]. Similarly, the presence of *Hyalomma marginatum* is important for CCHFV transmission. Being able to control ticks and transmission requires knowledge of vector distribution (assuming that nosocomial transmission is not relevant) [57].
Vector abundance	4	4	4
	More vectors may correlate with more transmission; this is, however, dependent on human exposure and infection rates.	More vectors can mean a higher likeliness for spread; however, spread is dependent on routes of spread, e.g. migratory birds, travelling pets [58,59].	The more ticks, the harder they are to control. Data on areas of high abundance may inform target control, but the key areas for control are those where exposure is also high [60].
Infection rate	3	4	4
	High infection rates are important if high exposure is combined with high tick density.	If more infected vectors are spreading, and more infected hosts are spreading [61].	R_0 will be higher if infection rate, density of ticks, and exposure are higher. This also has implications for vector control measures.
Vector behavioural traits	3	3	4
	Pathogen transmission generally occurs during times when humans are more active outdoors (e.g. in summer), which coincides with the time when (infected) ticks are also at their most active.	If ticks are active when hosts (e.g. migratory birds) are active, they will spread further [62].	Control of vectors is more efficient when they are biting/active (e.g. ticks on pets using acaracides, or *Hyalomma* on cattle). For *Ixodes*, management of vegetation may be important when ticks are not active (before or between periods of activity) [63].
Seasonality	3	2	4
	Season start determines when first transmission takes place (assuming it is only vector-borne); exposure, however, is just as important. Season length determines when pathogen transmission occurs and when it ends, but not the amount of transmission.	Again, if ticks start their activity after their hosts have migrated, season start is important; if not, it is negligible. Season length not very important for spread, unless ticks are active at a time of year when dissemination hosts are active.	Alerting the public/veterinarians at the start of the vector season to take precautions is standard procedure, so determining the season start is important [64]. The length of the vector season is also crucial in alerting the public/veterinarians to risk periods and can inform awareness campaigns [65,66].
Reservoir host numbers	3	4	4
	Hosts can amplify a pathogen, but for TBD it is the tick that drives transmission.	Dissemination of infected or infested vectors is important in spread of the pathogen or vector, e.g. migratory birds, dispersal of deer, movement of livestock [61].	Any attempt to control the vector will not necessarily control the persistence of the pathogen if the hosts remain abundant and infected.
Human activity	4	2	2
	Humans need to be exposed for disease transmission, so human activity is crucial for transmission to humans [similarly for livestock].	Unless humans can infect vectors or have a significant role in pathogen transfer, then human activity is not relevant. However, for Crimean–Congo haemorrhagic fever virus, there is nosocomial transmission, which is does not need a vector [54].	Unless vector/pathogen control depends on control measures, human activity is not relevant.
Habitat change	4	4	4
	If habitat changes lead to increased usage of that habitat by a range of animals, it will impact on pathogen transmission.	If habitats are changed so as to become connected, this provides corridors for vectors and their hosts to move into new areas and thus disperse the vector and pathogen along these corridors and exploit/infest/infect new habitats.	Managing vegetation is a key way of controlling human exposure to the vector by minimising public/animal exposure and/or making the habitat inimical for ticks.

Table A2. Expert opinion of vector-related drivers of epidemiological concepts: midges

	Early warning of pathogen transmission	Pathogen establishment	Pathogen persistence
Vector presence	1	2	1
	As *Culicoides* under interest are autochthonous species in some European and Mediterranean areas (no invasive species), detection of presence of species will not lead to an early warning. Moreover, presence does not necessary mean risk of transmission.	Probable bluetongue virus (BTV) vectors are present everywhere (at least one species) in European and Mediterranean areas, with the only exception of Iceland [67]. Absence of these *Culicoides* species in Iceland means probable absence of possible pathogen establishment. Up to now, *C. imicola* is considered the main vector in European and Mediterranean areas (as for BTV before BTV-8 emergence). Thus, *C. imicola* presence means that the area is at risk of African horse sickness virus (AHSV) establishment if introduced. However, as other species may be involved in AHSV transmission (with the previous example of BTV), absence of *C. imicola* does not mean necessary absence of risk of pathogen establishment.	As *Culicoides* are present everywhere (except Iceland for *Avaritia* or *Culicoides* species), vector presence could not be used to infer the suitability of specific areas for pathogen persistence. There could be other places where *Culicoides* are present, but the climate makes persistence of the pathogen unlikely.
Vector abundance	3	4	3
	Several publications compare vector abundance and BTV transmission in the United States, but not in Europe [68,69]. 'Aggressive density' assessed by CO_2-baited traps was correlated with the risk of BTV transmission (assessed by seroconversion follow-up) with a time-lag of four weeks [68]. Authors highlighted that seroconversion occurred only when 'aggressive density' was above a threshold of 60 *C. sonorensis* per host per night. These findings are compatible with those observed by Mayo et al. [69]. We can conclude that a certain threshold of abundance (as proxy for 'aggressive density') is necessary for the start of virus transmission and thus for disease onset. However, this abundance threshold is only meaningful in areas where virus is present and has overwintered. Practical use of abundance for an early disease warning system has never been implemented as a routine method.	*Culicoides* abundance (assessed by light traps) is related to the 'aggressive density' [70,71] and related to R_0. Some authors have developed an adapted R_0 formula to take into account the transmission of BTV among cattle and sheep populations [72]. It could thus be considered a key parameter to determine the possible risk of pathogen establishment after introduction. R_0 was used to assess the risk of BTV in the United Kingdom [73,74]. However, there is no experimental proof that abundance is directly correlated to the risk of pathogen establishment.	Mechanisms of overwintering and long-term persistence of *Culicoides*-borne viruses are not fully understood. Theoretically, virus could persist in vectors (through transovarial transmission and adult survival), in hosts (through direct transmission or long viraemia periods), and through continued transmission between vectors and hosts. Transovarial transmission has not been demonstrated in vectors and long viraemia periods in hosts are unlikely. Infected *Culicoides* were collected in winter [75], suggesting possible survival of infected females throughout winter. Long-term persistence is likely to occur through undetectable cycles of transmission and is more likely in areas of high *Culicoides* abundance.

	Early warning of pathogen transmission	Pathogen establishment	Pathogen persistence
Infection rate	3	3	3
	BTV has been detected in *Culicoides sonorensis* 2 to 6 weeks before the detection of infection in cattle [69]. Thus, following up on the infection rate in vector populations may allow for the detection of virus presence before the transmission to vertebrate hosts. However, the use of infection rates in an early warning system has never been implemented at a large scale due to low sensitivity, especially in light traps [76], costs, and the absence of practical prevention methods.	Infection rates cannot provide an indicator of the potential for a pathogen to establish in an area; detection of pathogens in vectors (especially at an early stage of the transmission season) may reflect the success of pathogen establishment.	Detection of infected midges during the winter would support the possibility of virus overwintering through infected females [69] or continuous transmission. However, due to the low infection rates, a systematic widespread assessment of infection rates cannot be used to routinely determine the suitability of areas for pathogen persistence.
Vector behavioural traits	1	4	2
	No information on which other behavioural traits may be used for an early warning system.	Both biting rate and longevity are important parameters of R_0. Assessing them may allow for determining the areas suitable for pathogen establishment, or more precisely, the period during which these areas are susceptible for pathogen establishment. Indeed, values for biting rate or longevity could be related to climatic variables, mainly temperature, and the relation between both parameters may be used to compute R_0 maps at a continental scale [25].	The capacity of infected vectors to survive several months during winter is a key parameter to assess the probability of a pathogen to survive through the winter months. However, these mechanisms are poorly understood and rarely investigated.
Seasonality	2	2	2
	Season length will define the time period during which transmission is possible. However, using season length as a measure will overestimate the time of the possible transmission, which will occur only in areas where the virus is present at the beginning of the season. Thus, season length is unlikely to be used as an indicator for an early warning system. In Europe, the concept of a 'vector-free' period, i.e. the period during which the abundance estimated by UV light traps remained under a threshold, has been used for more than a decade to manage animal movements under EU regulations and has demonstrated its utility. Thus, the season start could be considered for a rough estimate for an warning system, meaning that transmission may occur from the start of the season to the end of the year. However, this would not take into account the presence of the virus, which is essential for disease appearance, or the suitability of the area for pathogen transmission.	The longer the potential period of pathogen establishment, the higher is the probability of the actual establishment of the pathogen. Even in regions with a very short season, such as southern Scandinavia, the pathogen can become established and spread (e.g. BTV-8 in 2008) if the pathogen is introduced during the favourable period. Season start may only be used as a dichotomy: before the start of the season, establishment is unlikely; after it, it is possible.	In theory, the overwintering of pathogens is more likely to happen in areas with a long season because this implies a short winter, which makes it more likely that an infected vector survives. Moreover, in some Mediterranean areas, depending on the year, activity could be continuous through the year: overwintering seems more likely to occur under these conditions. However, from 2007 to 2008, BTV-8 has overwintered in more northern latitudes (e.g. Belgium, the Netherlands or Germany). Season start is not useful to indicate persistence.

	Early warning of pathogen transmission	Pathogen establishment	Pathogen persistence
Reservoir host numbers	1	2	3
	Changes in host numbers are not sufficient to infer an imminent increase in pathogen transmission.	After the introduction of an infected vertebrate or an infected vector, pathogen establishment is possible if $R_0>1$. Host density is not really a limiting factor if density is above a threshold that allows for the initiation of pathogen transmission. This threshold should be low, and thus host density should not be a limiting factor in most European and Mediterranean areas. There is, however, no experimental evidence for this.	Overwintering of the pathogen is related to the number of infected hosts and/or infected vectors at the beginning of winter. Thus, this number should be higher in locations with high host density than in those with low host density. Pathogen persistence over several years is likely linked to undetectable transmission cycles. These cycles are more likely to happen in areas of high vector density. There is, however, no experimental evidence for this.
Human activity	1	2	2
	No information on which changes in human activity may be used for an early warning system.	Although human activities such as vaccination, animal restriction, slaughtering, etc. may be efficient control measures to reduce pathogen establishment, it is difficult to identify human activities that result in areas that are suitable or unsuitable for pathogen establishment.	Though farming and animal movement may encourage establishment, only vaccination directly affects the probability of a *Culicoides*-borne pathogen to persist.
Habitat change	1	1	1
	No information on which changes in a habitat may be used for an early warning system.	Although habitat changes may modify the suitability of an area for pathogen establishment, there is no obvious habitat change that could transform a suitable area into a non-suitable area (the opposite is also true).	Although habitat changes may modify the suitability of an area for pathogen persistence, there is no obvious habitat change that could transform a suitable area into a non-suitable area (the opposite is also true).

Table A2, continued

	Pathogen transmission	Pathogen/vector spread	Pathogen transmission control (vector control and other)
Vector presence	1	1	1
	Areas suitable for pathogen transmission are by definition suitable for pathogen establishment. 'Vector presence' does therefore not add any additional information to pathogen transmission.	Pathogen spread can only occur from areas suitable for pathogen transmission, i.e. areas where vectors are present by definition. 'Vector presence' does therefore not add any additional information to the spread of the pathogen.	No specific control measures are implemented after the detection of *Culicoides* because *Culicoides* are virtually everywhere; presence does not necessary imply a risk of transmission.
Vector abundance	4	3	2
	As vector abundance is a component of R_0, it should also be a key parameter of pathogen transmission. R_0 was used to determine the BTV transmission in European and Mediterranean areas in the past decades [25] in order to predict BTV transmission under different climate change scenarios. Seroconversions occurred only in the two farms (of the four followed up) where *Culicoides* abundance was high. No seroconversion was detected in two farms: one farm where abundance was low (even though BTV could be isolated from *Culicoides* in the farm) and one farm where abundance was very low [69]. This shows that 'aggressive density' is linked to pathogen transmission. In Europe, abundance estimated by measuring with UV light traps have been used for more than a decade to manage animal movements under EU regulations, and this system has demonstrated its utility. Threshold values for low abundance have been routinely used to guarantee the (very likely) absence of disease during times of the year when low abundance could be verified.	Pathogen spread may be due to 1) active *Culicoides* dispersal, 2) *Culicoides* transported by wind, and 3) animal movements. Several journal articles have investigated the pathogen spread by modelling approaches [26,27,72,77,78]not exhaustive]. These papers highlight the importance of *Culicoides* dispersal in the spread of BTV, with *Culicoides* using both downwind and upwind movements, mainly at short and medium distances (below 31 km). This was also highlighted for Schmallenberg virus transmission [78]. Modelling results also suggested that pathogen spread is more likely to originate from farms favourable to vector abundance [78]. The importance of midges transported by wind was shown to explain the pathogen spread over large distances and over bodies of water [27]. These events are more likely to originate from areas of high *Culicoides* abundance.	Some control measures (application of pour-on insecticides) are mandatory for animal exportation when *Culicoides* populations are active, i.e. when *Culicoides* abundance is above a certain threshold. This is not required when *Culicoides* populations are 'inactive', i.e. when abundance remains under a certain threshold. Otherwise, control measures are not linked to the assessment of vector abundance. Moreover, control measures are usually not aimed at *Culicoides* abundance.
Infection rate	3	3	3
	Intensity of pathogen transmission is related to the infection rate of vector populations. However, the dynamics of infection rates do not necessary follow the dynamics of host infections [68,69], which is more related to 'aggressive density' or to the number of infected female *C. sonorensis* midges (mean number of female *C. sonorensis* midges captured per trap night × mean proportion of BTV-infected female *C. sonorensis* midges per trap night).	Pathogen spread from A to B by vector movement depends on the probability of a vector to move from A to B, the number of vectors at A, and the infection rate of vector population at A. Thus, pathogen spread is related to infection rate, however, very few studies have explored virus screening in vectors at a large scale, and if so, mostly with a retrospective perspective [79].	In theory, this is the most interesting indicator (detection of pathogens in vectors) to anticipate the imminence of pathogen transmission. However, it is quite impossible to carry out extensive and real-time assessments of infection rates. Thus, there are no examples where the detection of virus in vectors was used to implement control measures.

	Pathogen transmission	Pathogen/vector spread	Pathogen transmission control (vector control and other)
Vector behavioural traits	4	2	2
	Both biting rate and longevity are important parameters of R_0. Assessing them may allow for the detection of areas suitable for pathogen transmission, or more precisely, the period during which these areas are susceptible for pathogen transmission. Indeed, values for biting rate or longevity could be related to climatic variables, mainly temperature, and this could be used to compute monthly R_0 maps at a continental scale [25]).	The longer an infected vector lives, the farther it can spread the pathogen. However, there is no experimental evidence that variability of longevity (within the range of possible lifespan) has an impact on vector spread capacities.	Assessments of biting rates or longevity are used to evaluate the efficiency of some control measures (mainly application of insecticides on animals).
Seasonality	2	2	3
	BTV-8 has been successfully transmitted in areas where the season length is quite short, e.g. in southern Scandinavia. However, it is unlikely to find an area in Europe for which the temperature conditions are not favourable for at least three months per year. In Europe, the concept of a 'vector-free' period, i.e. the period during which the abundance estimated by UV light traps remains under a certain threshold, has been used for more than a decade to manage animal movements under EU regulations, and this system has demonstrated its utility. Thus, the date of the season start could be considered a rough index for transmission suitability, meaning that transmission may occur from the start of the season to the end of the year.	The longer the season, the higher the probability that a spread event occurs during this period. However, vector dispersal occurs throughout the season and seems sufficient to spread the pathogen. Before the start of the season, the spread is unlikely; after the start, it is possible.	Measures for disease management may be based on season length, restriction of animal movements, or authorisation of animal movements with insecticide applications, etc. This depends on the active/non-active status of *Culicoides* populations. The same applies to the use of attenuated vaccines, which should be limited to the period of vector inactivity.
Reservoir host numbers	3	4	2
	Even in areas where $R_0>1$, stochastic events may stop pathogen introduction. These events are more likely to happen in low density areas, where most of the hosts may become infected and then immune, leading to the absence of naïve hosts. Transmission may become endemic in areas where the host turnover or the pathogen circulation between different areas are sufficient to maintain a favourable number of naïve hosts. These conditions are more likely to happen in areas with high density, but there is no experimental evidence of that.	Several studies comparing BTV spread and a set of environmental variables identified cattle and sheep density as important factors of BTV spread [28,29,78,80]. Host density may have positive or negative effects on BTV spread velocity, depending on species and type of production, with high density of beef cattle being the most favourable condition for rapid spread [28,29].	Control measures do not depend on host density, but management decisions can, to a degree, be based on host density: if vaccine availability is limited, health authorities could decide to vaccinate those areas first that have the highest host density.
Human activity	2	4	2
	Although human activities such as vaccination, animal restriction, slaughtering, etc. may be efficient control measures to reduce pathogen establishment, it is difficult to identify human activities that result in areas that are suitable or unsuitable for pathogen establishment.	International trade and animal transhumance are known factors enhancing pathogen spread. BTV-8 or Schmallenberg viruses emerged in European hotspots for international trade (the route of introduction is still unknown). Exportation of animals are known to have been responsible for introduction of BTV-1 from southern to northern Spain, or of BTV-8 from France to Spain and Italy.	This is very difficult to assess because by definition, disease control is a human activity. If we ask whether some disease control measures are decided on the base of specific human activities (e.g. vaccination in a given production method, insecticide in another), the answer is no. The exception are specific control measures (regulations on animal movements) in areas where animals are exported.

	Pathogen transmission	Pathogen/vector spread	Pathogen transmission control (vector control and other)
Habitat change	2	2	1
	Although habitat changes may modify the suitability of an area for pathogen transmission, there is no obvious habitat change that strongly modifies the suitability of an area.	Land cover influenced the BTV spread of BTV-8 and BTV-1 in France [28,29]. Changes in the characteristics of the land cover may lead to changes in the pathogen spread conditions. However, these changes are unlikely to occur, and consequences are not easily predicted.	There are no examples of control decisions linked to habitat change.

Table A3. Expert opinion of vector-related drivers of epidemiological concepts: mosquitoes

	Early warning of pathogen transmission	Pathogen establishment	Pathogen persistence
Vector presence	4	3	1
	Basic requirement (risk or no risk), but to be completed for risk assessment by abundance of vector and pathogen presence/circulation or risk of introduction. Provided information is risk or no risk (not about level of risk), this is what public health asks when outbreak occurs in a neighbouring area.	Basic requirement (risk or no risk of establishment of pathogen), but to be completed for risk assessment by vector abundance, environmental factors (including host presence/number) and human activity (e.g. travel, habitat change).	Persistence requires establishment first and therefore vector presence is already demonstrated; further risk assessment would focus on vector abundance, environmental factors (including host presence/number) and human activity (e.g. habitat change).
Vector abundance	4	4	4
	Higher risk when vector is abundant [13,81]; standardisation of sampling procedures (VectorNet guidelines) and conversion ratios for different adult traps are necessary (not done yet).	Higher risk when vector is abundant [13,81]; standardisation of sampling procedures (VectorNet guidelines) and conversion ratios for different adult traps are necessary (not done yet).	Higher risk when vector is abundant [13,81]; standardisation of sampling procedures (VectorNet guidelines) and conversion ratios for different adult traps are necessary (not done yet).
Infection rate	3	3	3
	Early pathogen screening in vectors is relevant when pathogen can circulate in healthy hosts, e.g. West Nile yes, Dengue no [13,81].	When risk of pathogen maintenance/overwintering in vectors.	When risk of pathogen maintenance/overwintering in vectors.
Vector behavioural traits	3	4	4
	Related to vector abundance, with focus on pathogen-targeted host; more precise risk assessment but still need for data on pathogen circulation.	Related to vector abundance, with focus on pathogen-targeted host; Positively correlated; necessity to follow ethical rules.	Related to vector abundance, with focus on pathogen-targeted host; Positively correlated; necessity to follow ethical rules.
Seasonality	4	4	4
	Determines periods without or with risk; Also dependent to pathogen requirements. Earlier start of the season, earlier transmission should be logical output if pathogen is already present; seems that local vector population has great capacity for quick increase after adverse weather conditions (important but not yet evidenced).	Longer season increases chances of transmission when exotic pathogen is introduced. Earlier start of the season increases chances of transmission when a pathogen is introduced; also increases chances for early start of circulation.	Positively correlated; also dependent on pathogen requirements. More dependent on the timing of the pathogen introduction.
Reservoir host numbers	3	4	4
	Might intensify pathogen circulation and chances for early detection.	Positively correlated; travel and trade at risk for introduction.	Positively correlated.
Human activity	3	4	3
	If evidence about infected travellers coming to areas where vector is present and abundant are available.	Travel favours introduction; habitat change can favour establishment (of both vector and pathogen).	Changes can also decrease changes of persistence (both vector and pathogen).
Habitat change	3	4	4
	Temporary changes in habitat, for example flooding or evaporation of water bodies will affect larval and oviposition breeding sites. Rainfall has been used to predict some mosquito borne diseases such as Rift Valley Fever.	Habitat change can increase/decrease vector abundance (breeding site availability and flooding) and favour/reject pathogen introduction.	Increasing suitability for vector and host presence and abundance.

Table A3, continued

	Pathogen transmission	Pathogen/vector spread	Pathogen transmission control (vector control and other)
Vector presence	3	3	3
	Basic requirement (risk or no risk), but to be completed for risk assessment by vector abundance, environmental factors (including host presence/number) and human activity (e.g. habitat change, habits).	Basic requirement (risk or no risk), but to be completed for risk assessment by vector abundance, environmental factors (including host presence/number) and human activity (e.g. habitat change, habits).	Basic requirement (control to be implemented where vector is present), but to be completed by abundance for evaluation of needs and efficacy of control measures.
Vector abundance	4	4	4
	High mosquito densities have been associated with arboviral disease outbreaks [82,83]; thus, risk assessments involve estimating mosquito abundance [84–86]. However, high mosquito abundance may occur in the absence of virus or detectable virus amplification, and WNV outbreaks often occur when abundance is low but the mosquito population is older and the infection rate is high.	Higher risk when vector is abundant; Standardisation of sampling procedures (VectorNet guidelines) and conversion ratios for different adult traps are necessary (not done yet).	Important in particular when vector control aims at reducing abundance [87]; Standardisation of sampling procedures (VectorNet guidelines) and conversion ratios for different adult traps are necessary (not done yet); There is a need to determine abundance thresholds for pathogen transmission; Some standard procedures for evaluation of control efficacy are available [88], tailoring and harmonisation are needed.
Infection rate	4	4	3
	Outbreaks often occur when abundance is low but the mosquito population is older and the infection rate is high. The infection rate in a vector population is an estimate of the prevalence of infected mosquitoes in the population and is a good indicator of human risk Requires pathogen surveillance in vectors [13,81].	More vectors infected, more spreading of pathogen by vector movement. More vectors infected, more spreading of pathogen by vector movement.	By identifying thresholds are below levels associated with disease outbreaks, integrated vector management programs can institute proactive measures to maintain mosquito populations at levels below which amplification can occur. Requires pathogen surveillance in vectors [13,81].
Vector behavioural traits	4	4	4
	Related to vector abundance, with focus on pathogen-targeted host; positively correlated; Necessity to follow ethical rules.	High biting rate increases the risk of pathogen spread by travel and trade, e.g. infected *Aedes albopictus* entering vehicles by following hosts; Necessity to follow ethical rules.	Could be used as good quantifier of success of the control (but collectors should be protected from mosquito bites) [87].
Seasonality	4	4	3
	Positively correlated; Also dependent to pathogen requirements. Positively correlated; travel and trade a risk for introduction.	Positively correlated with the risk of dissemination to other regions; Also dependent to pathogen requirements for the region at risk for spread. Increased probability of establishment would stimulate the spread.	Longer season requires more resource-intensive control activities [87]. Intensive control pressure in that period might influence overall seasonal abundance of the vector (important but not yet evidenced) [87].
Reservoir host numbers	4	4	3
	Positively correlated; travel and trade at risk for introduction.	More hosts infected, more spreading of pathogen by host movement.	Control measure could focus where reservoirs or susceptible hosts are present [87].
Human activity	4	4	4
	Human daily activities can increase vector-host contact; habitat change can increase/decrease vector abundance (breeding site availability); some countries like Italy, France and Spain are more frequently visited by travellers from pathogen-endemic countries; hence, outbreaks are most frequent there compared with other countries with same vectors.	Travel and trade combined with environmental factors are the major drivers.	Private areas hardly accessible, major ordinance needed for successful control.
Habitat change	4	4	4
	Habitat change can increase/decrease vector abundance (breeding site availability and flooding).	Habitat change can increase/decrease vector and host movements.	Readjustment of vector control measures according to habitat changes.

Table A4. Expert opinion of vector-related drivers of epidemiological concepts: sandflies

	Early warning of pathogen transmission	Pathogen establishment	Pathogen persistence
Vector presence	3 (periendemic areas only)	3	3
	Leishmania is the main pathogen transmitted by sandflies. Sandfly and *Leishmania* infection distributions generally match, so we can assume that where there are vectors and hosts there is also *Leishmania* transmission [89], so the issue of 'early warning' is not relevant in endemic areas. It may be relevant in transition (periendemic) areas such as central France, southern Germany, etc. [90] where sandfly density is presently too low to maintain the parasite, but mere presence indicates potential for pathogen transmission and establishment.	Sandfly and *Leishmania* infection distributions generally match.	Sandfly and *Leishmania* infection distributions generally match.
Vector abundance	3 (periendemic areas only)	3	3
	As mentioned above, sandfly presence alone probably implies that *Leishmania* is present and being transmitted, so this is not relevant, except in periendemic areas where a rise in abundance would be a good early indicator of *Leishmania* transmission and establishment.	Sandfly and *Leishmania* infection distributions generally match.	Sandfly and *Leishmania* infection distributions generally match.
Infection rate	4	4 or 2 (periendemic areas)	4 or 2 (periendemic areas)
	High sandfly infection rates indicate efficient transmission, so finding infection in sandflies in transition areas clearly is a good early indicator of pathogen transmission.	Infection found in sandflies from endemic areas is a great indicator of *Leishmania* establishment. This may not necessarily be the case in transition areas (sporadic introductions).	Infection found in sandflies from endemic areas is a great indicator of *Leishmania* persistence. This may not necessarily be the case in transition areas.
Vector behavioural traits	4	4	4
	High biting rates are probably accompanied by high sandfly abundance. A sudden rise in sandfly biting rates would be a good early warning of *Leishmania* transmission in periendemic and endemic areas.	High biting rates probably mean there is high abundance and greater chances of *Leishmania* endemicity.	High biting rates probably mean high abundance and greater chances of *Leishmania* persistence.
Seasonality	3	3	3
	Increased length of active season usually means more cycles and sandfly generations. In periendemic areas, abundance may rise and reach the critical sandfly mass to allow *Leishmania* transmission, so it would be a good early indicator. Good early climatic conditions do not necessarily mean good conditions mid-way through the season and therefore high abundance. Having said that many areas with high abundance have early and long seasons.	Areas with long sandfly seasons are sandfly and *Leishmania* endemic.	Areas with long sandfly seasons are sandfly and *Leishmania* endemic.
Reservoir host numbers	3	3	3
	Sudden rises in host (wild lagomorphs) density associated with an epidemic of urban Leishmaniosis in southern Madrid, an otherwise endemic Leishmaniosis area [91]. Generally, sandflies in endemic areas thrive in animal farms and dog kennels, the latter also having a high risk of clinical cases.	Host density in endemic areas is positively correlated to sandfly abundance and establishment of *Leishmania* [91] and other vectors.	Host density in endemic areas is positively correlated to sandfly abundance and *Leishmania* persistence [91].

	Early warning of pathogen transmission	Pathogen establishment	Pathogen persistence
Human activity	3	3	3
	If non-immune people (e.g. urban people) move to new housing developments in rural, endemic areas in Europe then the risk of transmission and disease can be high. [91]. Dogs (and people to a lesser extent because they are not as sensitive as dogs) to non-endemic areas travelling from endemic areas may introduce Leishmaniosis into non-endemic areas and develop clinical signs [92].	*Leishmania* establishment depends on a critical mass of sandflies which is not often the case in non-endemic areas.	*Leishmania* transmission depends on a critical mass of sandflies which is not often the case in non-endemic areas.
Habitat change	3	3	3
	Habitat changes such as urbanisation of agricultural *Leishmania* endemic areas that incorporated green leisure areas led to a population explosion of hares and sandflies that fed on them and to an epidemic of Leishmaniosis in people [91]. Other land use changes may lead to a reduction in sandfly habitat and *Leishmania* risk. Climate change has expanded sandfly distribution in Europe northwards [93].	Habitat changes such as urbanisation of agricultural *Leishmania* endemic areas that incorporated green leisure areas led to a population explosion of hares and sandflies that fed on them and to an epidemic of Leishmaniosis in people [91]. Other land use changes may lead to a reduction in sandfly habitat and *Leishmania* risk. Climate change has expanded sandfly distribution in Europe northwards.	Sandfly and *Leishmania* establishment, persistence and transmission in periendemic areas is related to climate, allowing a critical mass of sandflies. Infection will be introduced by wildlife and infected dogs.

Table A4, continued

	Pathogen transmission	Pathogen/vector spread	Pathogen transmission control (vector control and other)
Vector presence	3	2	1
	Risk related to host immunity and transmission intensity, the latter depending on sandfly and host density and infection rates. [93]and expert opinion].	Low mark (2) because sandfly presence strongly depends on environmental/micro-environmental conditions, and neighbouring areas may not be adequate for *Leishmania* to spread into. This would be clearly the case in periendemic areas.	Control decisions are based on disease, i.e. people/dogs sick with *Leishmania*, not on vector abundance or even on infection prevalence because prevalence of asymptomatic Leishmaniosis is very high (60–80%) in endemic areas.
Vector abundance	3	2	1
	Sandfly and *Leishmania* infection distributions generally match. There is evidence that disease risk is positively correlated to sandfly abundance [16,19,92]. However, top mark (4) not given because sandfly abundance may be large in areas where non-susceptible hosts are the main source of blood for the sandflies. Also, there is evidence of high disease risk in areas with relatively low sandfly abundance and infection rates [24].	Sandfly presence depends on environmental conditions, and neighbouring areas may not be adequate for *Leishmania* to spread into. This would be clearly the case in periendemic areas.	Control decisions are based on disease (people sick with *Leishmania*) incidence, not on vector abundance or infection prevalence because prevalence of asymptomatic Leishmaniosis is very high (60–80%) in endemic areas.
Infection rate	4 or 2 (periendemic areas)	2-4	4
	Infection found in sandflies from endemic areas is a great indicator of *Leishmania* persistence. This may not necessarily be the case in transition areas. There is evidence that disease risk is positively correlated to sandfly infection rates [17–19]. However, disease depends very much on host factors.	Neighbouring areas may not necessarily be adequate for *Leishmania* to spread into. However, if they are, high infection rates would help pathogen spread	Important to carry out vector control interventions if sandfly infection rates are high because disease risk is likely to be high.
Vector behavioural traits	4	2-3	4
	High biting rates probably mean high abundance and greater chances of *Leishmania* transmission.	High biting rates probably mean high abundance and greater chances of spread, but only if neighbouring areas are environmentally suitable.	High biting rates may be sufficient to implement vector control to stop nuisance as well as disease risk.
Seasonality	3	2-3	1
	Areas with long sandfly seasons are sandfly and *Leishmania* endemic with ongoing *Leishmania* transmission takes. Host factors also important.	Neighbouring areas may not necessarily be adequate for *Leishmania* to spread into.	Control decisions are based on disease incidence and/or biting rates. Presence of sandflies at unexpected times (e.g. late fall) may extend the vector control period. In many Mediterranean countries where sandfly and Leishmaniosis are abundant, control starts before active season as a standard procedure.
Reservoir host numbers	3	2	2
	Host density in endemic areas is positively correlated to sandfly abundance and *Leishmania* transmission [16,91]. Most people and animals are resistant to developing clinical leishmaniosis, but high numbers mean more susceptible individuals.	Depends on whether neighbouring areas have suitable conditions and enough hosts.	Depends on disease incidence and/or biting rates.
Human activity	3	3	3
	Leishmania establishment depends on a critical mass of sandflies, which is not often the case in non-endemic areas.	*Leishmania* establishment depends on a critical mass of sandflies which is not often the case in non-endemic areas.	Control measures should be implemented when susceptible dogs (and people) are introduced to endemic areas, mainly using insecticides on the animal and domestically.

	Pathogen transmission	Pathogen/vector spread	Pathogen transmission control (vector control and other)
Habitat change	3	3	3
	Sandfly and *Leishmania* establishment, persistence and transmission in periendemic areas are related to climate, allowing a critical mass of sandflies. Infection is introduced by wildlife and infected dogs.	Spread to neighbouring areas depends on climatic conditions.	The epidemic in southern Madrid associated to a change in land use (urbanisation) led to the biggest epidemic of clinical human leishmaniosis in Europe.

Table A5. Expert scores of importance of drivers of epidemiological concepts

	Early warning				Pathogen establishment				Pathogen persistence			
	Tick	Mosq	Midge	Sand	Tick	Mosq	Midge	Sand	Tick	Mosq	Midge	Sand
Vector presence	4	4	*1*	3	3	3	2	3	3	1	1	3
Vector abundance	2	4	3	3	3	4	4	3	2	4	3	3
Vector infection rate	2	3	*1*	4	3	3	4	4	3	3	2	4
Behavioural traits	4	3	*1*	3	3	4	4	3	2	4	2	3
Vector seasonality	3	4	2	3	2	4	2	3	2	4	2	3
Host numbers	4	3	*1*	3	4	4	2	3	4	4	3	3
Human activity	4	3	*1*	3	1	4	2	3	1	3	2	3
Habitat change	3	3	*1*	3	4	4	1	3	4	4	1	3
	Pathogen transmission				**Disease spread**				**Pathogen control**			
	Tick	Mosq	Midge	Sand	Tick	Mosq	Midge	Sand	Tick	Mosq	Midge	Sand
Vector presence	4	3	1	3	4	3	1	2	4	3	1	1
Vector abundance	4	4	4	3	4	4	3	2	4	4	2	1
Vector infection rate	3	4	4	4	4	4	2	4	4	3	3	4
Behavioural traits	3	4	4	3	2	4	2	3	4	4	2	3
Vector seasonality	3	4	2	3	2	4	2	3	4	3	3	1
host numbers	3	4	3	3	4	4	4	2	4	3	2	2
Human activity	4	4	2	3	2	4	4	3	2	4	2	3
Habitat change	4	4	2	3	4	4	2	3	4	4	1	3

Tick = ticks
Mosq= mosquitoes
Midge = midges
Sand= sandflies.

Appendix 2. Overview of sampling methods

This section contains a brief overview of field sampling protocols, all of which are described in detail in the ECDC technical report 'Field sampling methods for mosquitoes, sandflies, biting midges and ticks' [11].

Ticks

Tick sampling aims to collect larvae, nymphs and adults, but not eggs. Abundance of ticks can be estimated by surveying the vegetation or potential hosts over specific periods of time [95,96]. Though *Ixodes* and *Dermacentor* species can be sampled from wildlife hosts, vegetation sampling is better able to provide accurate location and habitat data. There are a number of methods being used, but the most widely used in VectorNet has been vegetation flagging or dragging, which provides an indication of vector abundance in terms of number per square metre. All instars can be sampled in this way, but the number caught can be heavily influenced by vector activity patterns and vegetation structure [96].

Rhipicephalus species can also be sampled from the vegetation using flagging or dragging, but they are also commonly found on dogs, in their kennels, or the walls of homes where dogs are kept. Deploying a hair dryer over suspected resting sites will encourage the ticks to leave their resting sites so that they can be collected.

Hyalomma species are not amenable to flagging methods as they typically do not quest in the vegetation, but actively hunt for a host. They are best sampled directly from domestic and wild ungulate hosts. Collections from the ground are difficult as there is no reproducible way to collect *Hyalomma marginatum* with a standard flagging method.

Tick activity varies between European tick species, with some European species (e.g. *Dermacentor*) most active in the winter, others mainly in spring (e.g. *I. Haemaphysalis*) or late spring and summer (e.g. *Hyalomma*, *Rhipicephalus*). Even within a species, different life stages exhibit differing seasonality and each stage can vary in their potential to transmit disease. Ensuring that the correct stage of tick is monitored is important; larval *I. ricinus*, for example, present minimal disease risk while most Lyme cases result from of a bite by an infected nymph.

Culicoides midges

Most adult collections focus on flying adults, using passive aspiration traps such as Rothamsted suction traps or active traps such as truck traps [97]. However, UV light trap collections remain the most time-efficient and widespread method to assess *Culicoides* presence and abundance at a wide scale. UV light traps collect a fraction of the *Culicoides* populations, mostly host-seeking females. The assessed abundance depends to a large degree on the trap location, including distance to animals and height above ground level [99,100].

Mosquitoes

Sampling methods for mosquitoes are the most elaborate of the four vector groups, as all developmental stages (eggs, larvae, flying and resting adults) can be assessed. Which stage is sampled depends on the target species, the environmental conditions at the selected sampling sites, on the availability of resources and the objective of the sampling. The main methods used are: baited traps with or without light, mainly outdoors for flying adults; larval sampling for those species less attracted to light traps or baits; ovitraps, especially if resources are restricted, or in remote areas as they need only to be inspected relatively rarely. Resting adults (including males) are sampled manually and can yield seasonality data.

Sandflies

Sandfly sampling for abundance is limited to flying or resting adults as the immature stages are too small and too well hidden in the substrate to be assessed. Trapping host-seeking adults is based on light traps, sticky traps or CO_2 traps. Diurnal collections from sandfly resting sites in the vicinity of nocturnal trapping sites can reveal where these insects rest during the day. By design, the collection of resting sandflies does not require bait, rarely relies on traps, and supplies epidemiological rather than population-related information.

Light traps are ideal to investigate abundance of species attracted to light (which includes all important vector species) because the area of influence of the trap is known: 2–6 m for CDC-light traps [100] and abundance is expressed as number per trap-day. Sticky traps are cheap, collect an unbiased sample of species, and abundance is expressed per trap surface (m^2).

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