Invasion rate of deer ked depends on spatiotemporal variation in host density

C. M. Meier1*, D. Bonte2, A. Kaitala3 and O. Ovaskainen4

1Swiss Ornithological Institute, Seerose 1, CH-6204 Sempach, Switzerland: 2Terrestrial Ecology Unit, Department of Biology, Ghent University, K.L. Ledeganckstraat 35, 9000 Gent, Belgium: 3Animal Ecology, Department of Biology, University of Oulu, P.O. Box 3000, 90014, Finland: 4Metapopulation Research Group, Department of Biosciences, University of Helsinki, PO Box 65, 00014, Finland

Abstract

Invasive parasites are of great global concern. Understanding the factors influencing the spread of invading pest species is a first step in developing effective countermeasures. Growing empirical evidence suggests that spread rates are essentially influenced by spatiotemporal dynamics of host–parasite interactions, yet approaches modelling spread rate have typically assumed static environmental conditions. We analysed invasion history of the deer ked (Lipoptena cervi) in Finland with a diffusion–reaction model, which assumed either the movement rate, the population growth rate, or both rates may depend on spatial and temporal distribution of moose (Alces alces), the main host of deer ked. We fitted the model to the data in a Bayesian framework, and used the Bayesian information criterion to show that accounting for the variation in local moose density improved the model’s ability to describe the pattern of the invasion. The highest ranked model predicted higher movement rate and growth rate of deer ked with increasing moose density. Our results suggest that the historic increase in host density has facilitated the spread of the deer ked. Our approach illustrates how information about the ecology of an invasive species can be extracted from the spatial pattern of spread even with rather limited data.

Keywords: diffusion–reaction model, spatiotemporal spread rate, insect, range expansion

(Accepted 11 January 2014; First published online 13 February 2014)

Introduction

Biological invasions are considered as a major global threat for ecosystems and for human economics (Mack et al., 2000). A considerable fraction of current biological invasions is a consequence of human activity. Non-native species, for instance, spread as a result of ever-increasing trade and travel, changes in land-use and climate change (Lockwood et al., 2007). In order to manage and predict invasions, it is essential to understand how environmental variation in time and space affects species’ spread rates. Examining the patterns of spread in historical and still ongoing invasions might provide us with such insights.

Metapopulation or patch occupancy models have been much used to analyse the spatial pattern of biological invasions (Lockwood et al., 2007). Metapopulation models can account for environmental heterogeneity by letting the exchange rate of individuals between the spatial units (grid cells, habitat patches or hosts) depend on covariates (e.g. Kadoya & Washitani, 2010). Such models can be used to
predict in which order patches will become invaded (Eraud et al., 2007). If the landscape is assumed to consist of a regular grid of patches, patch occupancy models can be approximated by diffusion–reaction models (which assume local dispersal; Fisher, 1937; Skellam, 1951) or integrodifferential models (which allow for long-distance dispersal; Van den Bosch et al., 1990; Koo et al., 1996). Both model types express the spread rate with the help of two principal processes: the growth rate of local populations and the displacement of individuals in space (Hastings et al., 2005), both of which can be assumed to depend on covariates. Allowing for environmental heterogeneity makes the models mathematically intractable and they need to be solved numerically (Hastings et al., 2005). Because of this complication, most of the studies based on diffusion–reaction models have thus assumed homogeneous space, i.e. that the growth of local populations and the displacement of individuals are constant in space and time (though see, e.g. Turchin, 1998). This view has clearly been challenged by empirical studies that have reported high spatial variation in the spread rate (Kueffer et al., 2012), for independent invasions of the same species (Holway, 1998), or for different sections of the same invasion front (Evans & Gregoire, 2007; Tobin, 2007).

Predictive models of the influence of environmental heterogeneity on the spread rate of invasion are still few (With, 2002; Hastings et al., 2005; Lockwood et al., 2007) compared with the growing amount of data suggesting that such heterogeneity plays an important role. For instance, Cook et al. (2007) found different rates of colonization in Giant Hogweed Heracleum mantegazzianum for different types of habitats during the invasion in the UK. The invasions of the European Collard Dove in Europe and in the USA are associated with landscape elements related to human settlement such as parks, gardens and high road density (Fujisaki et al., 2010). Human-mediated transport explains the spread rate of many invertebrates, such as forest pests or water fleas (Daphnia lumholtzii) (Gilbert et al., 2004). The spread rate of the woody plant species Pseudotsuga taxifolia has been found to increase in areas disturbed by storm and to decrease in areas of active forest management (Sebert-Cuvillier et al., 2008). The spread rate of the invasive sugar cane toad in Australia is associated with high temperature, high precipitation, high moisture, availability of water bodies and high density of roads (Urban et al., 2008). The spread rates of gypsy moth, plant lice and bumblebees are affected by variation in forest composition and winter temperature (Evans & Gregoire, 2007; Kadoya & Washitani, 2010).

Although it is evident that habitat suitability for invasive species may change over time (Ficetola et al., 2010), most of the studies have described environmental heterogeneity by static maps, thus ignoring the temporal component of environmental variability (Thuiller et al., 2005). For instance, climatic and meteorological data are usually implemented as mean or maximum temperature during a certain biologically relevant time frame (Evans & Gregoire, 2007), and habitat cover is often assumed to remain static during the invasion history (e.g. Pitt et al., 2009). One major reason why spatiotemporal variability in environmental conditions is seldom accounted for in invasion studies is that the detailed information on the variability of the environment is labour intensive to collect (Lockwood et al., 2007). Often the invasion is not recognized and properly monitored until it becomes an economical concern and has already spread over a substantial area.

Empirical examples of spatiotemporally varying invasion rates are provided, for instance, by insects that invade new habitats opportunistically when conditions are favourable (Lloyd & Lushai, 1999). Such a spread can lead to alternative invasion trajectories and to jump dispersal, in which satellite populations are found in advance of the main front (Shigesada et al., 1995). A further complication with understanding and predicting invasion rates is that biotic interactions may exert a dominant role in governing distributional changes, especially at larger spatial scales (Araujo & Lüoto, 2007). Spatiotemporal variation in host density is recognized as one of the import factors driving epidemics (e.g. Keeling et al., 2001).

The example of the deer ked (Lipoptena cervi Hippoboscidae, Linnaeus 1758) invasion in Finland offers the opportunity to investigate if temporal and spatial variations in the environment, more specifically in the host density, has influenced the spread rate. Deer ked is a blood-sucking ectoparasitic louse fly (order of Diptera) of ungulates occurring in the Central Europe and Asia (Haarlov, 1964). Relatively little is known about the biology of deer ked. At its adult stage the deer ked is permanently attached to its host. Record numbers of 17,000 parasites on a single host have been counted (Paakkonen et al., 2010). Deer ked is viviparous, each female producing ca. 20–32 pupae during its lifetime. The pupae are dropped off the host, one at a time, over the entire reproductive period of 4–10 months (Haarlov, 1964). Pupae overwinter on the ground and are able to survive even harsh winter conditions (Häkkinen et al., 2010, 2012). Juveniles eclose as adults in late autumn of the consecutive year. Newly emerged adults wait passively until a potential host is close by and thereupon fly actively towards the host (Hackett et al., 1983). In Finland, the deer ked also often attacks mistakenly humans (Kortet et al., 2010), causing allergic reactions and may even propagate diseases such as Bartonella schoenbuchensis (Laukkanen et al., 2005; Duodu et al., 2013). This disturbing behaviour of the deer ked raised the attention of local people soon after the deer ked arrived in Finland, and specimens were sent to the Natural History Museum of Finland already at the early phase of the invasion. These specimens have later helped to reconstruct the invasion history of the ked.

The first observation of deer ked in Finland dates back to 1960 and since then it has made a rapid spread across half of the country (Hackett, 1972; Välimäki et al., 2010). In Finland, the primary host is Eurasian moose (Alces alces) and thus its density is likely to be an important factor affecting the spread of the ked (Kaitala et al., 2009). The Finnish moose populations have undergone great spatiotemporal fluctuations, mainly due to shifts in hunting and forest management (Tillikainen et al., 2012). Overhunting caused the number of moose to decline to such a low level in the 1950s that eventually moose was declared protected in 1969. The complete hunting ban lasted for 2 years (Luoma, 2002), after which hunting started in a regulated manner. The moose population recovered fast in the 1970s (Luoma, 2002) (fig. 1). Currently, the Finnish moose population consists of ca. 89,000–105,000 individuals (Pusenius et al., 2009).

This has led to the speculation that the fast increasing density of moose in Finland in the 1970s might have facilitated the deer ked invasion (Von Brander, 1976; Kaitala et al., 2009). As moose is a valuable game species, estimates of moose density are available from different hunting districts for most of the invasion periods of the deer ked. The spread of the deer ked is not systematically documented at a high spatial
resolution, but information of the spatial pattern at the invasion front is available (see below).

Our aim is to test if the spread rate of the deer ked varies with local moose density, and specifically the hypothesis that high moose density leads to a high spread rate. If the hypothesis is supported, our more refined aim is to test whether high moose density elevates the spread rate of the deer ked through increased local growth rate, through increased dispersal ability, or a combination of these two factors. To test these hypotheses, we fit to the observed data different versions of diffusion–reaction models, where the diffusion term, the reaction term or both of these terms are allowed us to depend on moose density. These spatiotemporally heterogeneous models are then compared with each other and to a spatiotemporally homogeneous model using the Bayesian information criterion (BIC) to examine which model is best supported by the data.

**Methods**

**Data on the distribution of the deer ked**

Data on the moose density

As a tool for hunting management, the size of the moose population has been estimated separately for each hunting district annually since the year 1974, covering all of the 298 hunting districts from 1976 onwards. Hunters estimate the moose density after the autumn hunting period on the basis of observation of tracks in the snow and by sighting of moose throughout the winter. We assumed that the district-based estimate of moose density is valid at the centre of each hunting district, and applied linear interpolation to obtain a continuously varying surface of moose density (fig. 2b). Prior to the year 1974, no systematic district-level counts are available. Nygrén (1987) estimated the total number of moose at winter time for the entire country based on various data sources, such as hunting permits, bagged moose, accidents and hunter reports. This is the best available information on moose density for the time between 1960 when the deer ked invasion started and 1974. Since the estimate of Nygrén (1987) does not include any information about the spatial distribution of moose density across Finland, we assumed that relative spatial distribution of the density of moose equalled that of the year 1976, which is the first year when moose density was collected for each hunting district.

Model of deer ked invasion

We model the spread of the deer ked following the diffusion–reaction model (Skellam, 1951; Turchin, 1998), which is a partial differential equation modelling both movement (diffusion term) and local growth (reaction term) as

\[
\frac{du(x, y, t)}{dt} = \nabla (D(x, y, t) \nabla u(x, y, t)) + r(x, y, t)u(x, y, t) \\
\times \left(1 - \frac{u(x, y, t)}{K(x, y, t)}\right)
\]

(1)

Here \(u(x, y, t)\) is the density of deer ked in space \((x, y)\) and time \((t)\), \(D(x, y, t)\) is the diffusion coefficient, \(r(x, y, t)\) is the population growth rate and \(K(x, y, t)\) is the carrying capacity. The derivative with respect to the two-dimensional space is written with the help of the Nabla-operator \(\nabla\). The full model in which all of these three parameters may vary arbitrarily is clearly overparameterized to be fitted to our limited data. We thus consider a simpler class of sub-models in which only the parameters \(D\) and \(r\) are allowed to vary in space and time in a manner that reflects the variation in the density of the host, the moose. As our data contain no information on deer ked abundance, we cannot estimate the carrying capacity \(K\). We thus standardize the equilibrium value of \(u(x, y, t)\) to 1 by setting \(K = 1\), so that \(u\) models the density of deer ked relative to the density that will be reached after the invasion when deer ked can be detected. We parameterized the following set of alternative models in which either (or both) of the diffusion and the reaction terms depend on moose density.

Model 0 (the null-model): \(D\) and \(r\) are independent of local moose density,

\[
\log(D(x, y, t)) = D_1 \\
r(x, y, t) = r_1
\]

Model 1: \(D\) depends on local moose density,

\[
\log(D(x, y, t)) = D_1 + D_2m(x, y, t) \\
r(x, y, t) = r_1
\]

Model 2: \(r\) depends on local moose density,

\[
\log(D(x, y, t)) = D_1 \\
r(x, y, t) = r_1 + r_2m(x, y, t)
\]

Model 3: Both \(D\) and \(r\) depend on local moose density,

\[
\log(D(x, y, t)) = D_1 + D_2m(x, y, t) \\
r(x, y, t) = r_1 + r_2m(x, y, t)
\]

Above, \(m(x, y, t)\) is the moose density, which we normalized to have zero mean and unit variance overall years and hunting districts. We assumed that the initial condition \(u(x, y, t_0) = 1\) if \((x, y)\) was within the range of the ked in the initial year \(t_0\), and otherwise \(u(x, y, t_0) = 0\). We used Matlab as a numerical solver of the diffusion–reaction model; see the appendix for the technical details of the implementation.
Table 1. Model selection – the marginal posterior distributions of model parameters summarized as means and the 95% credible intervals. $D_1$ is the log-transformed diffusion coefficient at mean moose density, and $D_2$ is the influence of moose density on diffusion. Similarly, the parameters $r_1$ and $r_2$ respectively model the growth rate at mean moose density and the effect of moose density on growth rate. $k$ denotes the number of model parameters, $L$ is the likelihood of the data, and BIC gives the value of the Bayesian information criterion on which model selection was based.

<table>
<thead>
<tr>
<th>Model</th>
<th>$D_1$</th>
<th>$D_2$</th>
<th>$r_1$</th>
<th>$r_2$</th>
<th>$k$</th>
<th>$\ln(L)$</th>
<th>BIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model 0</td>
<td>-2.665 (−2.809 to −2.515)</td>
<td>0.146 (0.129−0.163)</td>
<td>2</td>
<td>−592.3</td>
<td>1198.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model 1</td>
<td>-3.187 (−3.414 to −2.940)</td>
<td>0.151 (0.135–0.169)</td>
<td>3</td>
<td>−579.9</td>
<td>1180.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model 2</td>
<td>-2.674 (−2.818 to −2.522)</td>
<td>0.0676 (0.0298–0.102)</td>
<td>0.165 (0.106–0.224)</td>
<td>3</td>
<td>−577.3</td>
<td>1175.1</td>
<td></td>
</tr>
<tr>
<td>Model 3</td>
<td>-3.105 (−3.353 to −2.844)</td>
<td>0.502 (0.248–0.742)</td>
<td>0.0881 (0.0123–0.122)</td>
<td>0.132 (0.0732–0.191)</td>
<td>4</td>
<td>−570.4</td>
<td>1168.1</td>
</tr>
</tbody>
</table>

Parameter estimation

We initialized the model to correspond to the distribution of the deer ked in the first year $t_0=1960$ for which the data were available, and solved it with a yearly time step to produce an estimate of deer ked distribution for the next year $t=1964$ for which empirical data were available. At this point, we compared the predicted density with the observed density (see below), then initialized the model using the observed distribution in $t_0=1964$, and continued the procedure until the end of the entire study period. We did not have data about the spatial distribution of the deer ked or the density of moose in neighbouring countries, most importantly Russia. We assumed reflecting boundary conditions, and thus made the simplifying assumption that no further net immigration of deer ked occurred from Russia after 1960. This is a conservative assumption because any immigration that may have occurred from Russia will dilute the potential correlation between the spread rate of deer ked and the local moose density. The spread of deer ked occurs parallel to the Finnish–Russian border and thus deer keds moving across the border are less likely to contribute to the advance of the invasion front.

The diffusion–reaction model is a deterministic model describing how population density changes over time. To connect the model prediction to our data, we use the loose interpretation of $u(x, y, t)$ being the probability of the population being present at location $x$ and time $t$. Then the probability of observing the presence or absence of the species, $q(x, y, t)\in[0, 1]$ is

$$P(q|u) = u + (1 - q)(1 - u)$$

(10)

If a number of independent data points would be available at locations $(x_i, y_j)$ the total likelihood of the data would be a product of equation 10 over all those locations,

$$L(q|u) = \prod_i P(q(x_i, y_j)|u(x_i, y_j))$$

(11)

and thus the log-likelihood would be

$$\log(L(q|u)) = \sum_i \log(P(q(x_i, y_j)|u(x_i, y_j)))$$

(12)

Since our model and distributional data are in continuous space, we consider the limit

$$\log(L(q|u)) = \int_{\Omega} q(x, y, t)u(x, y, t)$$

$$+ (1 - q(x, y, t))(1 - u(x, y, t)) \, dx \, dy$$

(13)

where $n$ is the effective number of data points and $\Omega$ denotes the total area of Finland. Given the resolution of our raw data and the $\alpha$-hull technique used to smooth it (fig. 2a), we considered that the effective density of data points was one per $50 \, \text{km} \times 50 \, \text{km}$ (Supplementary fig. S1 in the appendix), giving $n = 135$ with $|\Omega| = 388,000 \, \text{km}^2$.

We applied the Bayesian parameter estimation through an adaptive Metropolis–Hastings MCMC algorithm (Ovaskainen et al., 2008). We assumed log-normal prior distributions for the parameters ($D_1$, $D_2$, $r_1$, $r_2$) with a mean of $\mu = -2$ and $\sigma = 0.01$ (for $D$ and $r$, respectively) and standard deviation of $\sigma = 3$ for both priors. The technical details of the Metropolis–Hastings algorithm as well as an assessment of the mixing of the MCMC chains are given in the appendix (Supplementary fig. S4 in the appendix).

We compared the four versions of the model with the BIC, which accounts for the fact that a model with a larger number of parameters is more flexible and thus always obtains a higher likelihood even if the added parameter is not of major importance (Schwarz, 1978). BIC penalizes for the number of model parameters by the formula $\text{BIC} = -2\ln(L) + k\ln(n)$, where $L$ is the likelihood, $k$ is the number of model parameters (table 1), and $n$ is the number of data points. We set $n = 7 \times 135 = 945$ as there were seven surveys against which the model prediction was evaluated, each of which was used to inform the model of the state of the invasion at 135 triangulation grid points (see above).

Results

The lowest BIC-value was obtained for the full model 3 in which both the diffusion coefficient and the growth rate were dependent on local moose density (table 1), whereas the spatially homogeneous null model obtained least support. In line with our hypothesis, both the diffusion coefficient and the growth rate increased with local moose density, the 95% credible intervals for the parameters $D_2$ and $r_2$ being strictly positive in all models in which they were allowed to vary (table 1). Model 2 performed a little better than model 1, suggesting that moose density operates more strongly through the growth rate than the movement rate.

Overall the spatially heterogeneous models fitted the data better than the spatially homogeneous models, but they could not outperform the alternative model in every year. In the survey of 1979 and 1987, the spatially homogeneous random diffusion model (model 0) fitted the data best (fig. 3 and Supplementary figs. S2 and S3 in the appendix). However, the spatially heterogeneous models were able to describe the data in years of a greater dynamic at the deer ked invasion front. Model 3 with growth rate and diffusion coefficient dependent on spatially heterogeneous moose data performed best in the year 1982 and 2008, when the front of the deer ked invasion advanced most. The same trend applied to model 1 and...
model 2, which performed intermediately for most surveys. Also model 2, with only growth rate dependent on moose, improved its fit in the second half of the invasion period, when the moose density was high (fig. 3).

The estimates of $D_1$, $D_2$, $r_1$ and $r_2$ of model 3 allow a calculation of the theoretical asymptotic spread rate $\sqrt{4Dr}$ (Skellam, 1951) of the deer ked in homogeneous environment (fig. 4). The mean estimate of average moose density in Finland varied between 0.104 and 0.479 counted moose per km$^2$ during the study period (fig. 1), with mean of 0.296. The mean moose density corresponds to the spread rates of 16.9 km/yr$^{-1}$ (posterior mean, with 95% credible interval 15.6–18.2). The lowest observed mean moose density corresponds to the spread rate of 4.0 km/yr$^{-1}$ (0.0–9.0), and the highest observed mean moose density to 28.5 km/yr$^{-1}$ (26.2–30.1). As the local moose density shows more variation than the mean density over the entire country, the numbers above probably underestimate the range of realized invasion speeds over the study period. The model predicts the threshold density of ca. 0.08 moose per km$^2$ below which the growth rate $r$ becomes negative (fig. 4), suggesting that the spread of deer ked across Finland would have been unlikely for moose densities below this level.

**Discussion**

Growing empirical evidence shows that spatiotemporal heterogeneity in environmental conditions can be important for determining the pace of biological invasions. For many parasites and diseases the density of the host is an important determinant of reproduction and dispersal. For example, the spread of the foot and mouth epidemic in France was facilitated by the aggregation of susceptible hosts in time and space (Pioz et al., 2012). Our work suggests that the spread of the deer ked through Finland was influenced by spatiotemporal changes in the density of its main host species, the moose. Our highest ranked model implies that the link between spread rate and host density was due to both the rate of movement (diffusion) and the rate of local growth (reaction) being increased with increasing host density. Adding spatiotemporal changes in the distribution of the host improves model fit, and comparison between the models with respectively $r$ and $D$ dependent on moose densities shows that those including host-dependent growth rates capture observations better than those with only diffusion dependent on local densities. Higher local moose densities mean higher host abundance and allow faster reproduction of deer ked, thus increasing the spread rate.
The highest ranked model predicts a minimal density of 0.08 moose per km² below which the growth rate becomes negative and the deer ked should not be able to spread. This moose density is slightly below the lowest observed value during the period we modelled. Before 1955, and hence before the invasion started, such low moose densities were the norm in Finland (Luoma, 2002). Our results are thus in line with the hypothesis that the low moose density was the main reason why the invasion of the deer ked in Finland did not start earlier than in 1960 (Von Brander, 1976; Kaitala et al., 2009).

Models for deer ked dynamics could be improved with more detailed knowledge about the movement patterns of moose in Finland. In North America, movement of moose occurs mainly within local populations and was restricted by roads (Vander Wal et al., 2012). In Norway, moose also migrates between different habitats during the year (Bjørneraas et al., 2011), which may explain part of the variation in the abundance of deer ked between habitats (Madslien et al., 2012).

An experiment conducted by Härkönen et al. (2010) shows that the deer ked has not yet reached its northern limit in terms of its tolerance to climatic conditions. Further spread north would introduce the deer ked to areas of commercial semi-domestic reindeer husbandry and concerns are that the parasite could cause an economical loss. Reindeer might be an alternative host to deer ked and occur at high densities in these areas (Kynkäänniemi et al., 2010; Välimäki et al., 2011). Reindeer forage as large herds with large-scale movements, and this behaviour is likely to increase the potential risk of the spread of the deer ked. However, deer ked reproductive success on reindeer is poorer than on moose and drugs are available to treat reindeer against deer ked (Kynkäänniemi et al., 2010). Large scale treatment or restricting the transport of reindeer could reduce the density of susceptible hosts and thus slow the pace of deer ked invasion or even stop it. The recent halt of the expansion of deer ked indicates that such a strategy could be effective (Välimäki et al., 2010). More generally, modifying environmental conditions in a way that slows down or stops invasion can be an effective management measure, especially in organisms in which per-capita reproduction rate increases with population density at low density (Tobin et al., 2011).

Although our model was successful in capturing the overall pattern of spread, it is clearly an oversimplification of reality. Firstly, the model is deterministic, and modelling movements through diffusion implies that displacement distances of all individual are distributed according to the normal distribution (Turchin, 1998). Thus, the model fails to account for the possibility of stochastic long-distance dispersal events. Empirically derived dispersal kernels often have a leptokurtic shape, i.e. a fat tail corresponding to a large number of long-distance dispersal events. Mathematical models that account for a leptokurtic shape of the dispersal kernel predict an increased spread rate (Kot et al., 1996). Stochastic long-distance dispersal events have often found to be of crucial importance for an invasion process (Hastings et al., 2005). Stochastic long-distance invasion events have been reported especially due to (often unintentional) human activities (Gilbert et al., 2004). The large-scale transportation patterns of reindeer might facilitate further spread of the deer ked in the future. However, to estimate for the frequency of such rare events would call for more detailed data than we had available. To mitigate the lack of long-distance dispersal in our model we employed the concept of stratified dispersal (Shigesada et al., 1995) by continuously updating information on deer ked ranges with available information from surveys, and thus accounted in the initial condition for satellite colonies in advance of the main invasion front.

Secondly, there is growing evidence that invasive species might evolve rapidly, leading to a change in growth rate and redistribution behaviour of the individuals ‘surfing’ the invasion front (Travis & Dytham, 2002; Phillips et al., 2008; Burton et al., 2010). Selection might therefore produce an unsteady spread rate at the invasion front, either through life-history parameters or through host use shifts (Phillips, 2012). Deer ked, for example, might adapt a better cold resistance at the pupae stage, which is the most critical stage during the parasite’s life cycle (Härkönen et al., 2013). This would result in an increase local population growth and hence lead to an increased spread rate at higher latitudes. Unfortunately, our data do not allow for testing for evolutionary changes during the spread. In Sweden, a separate population of deer ked is also spreading to the north but at much slower pace than in Finland. Moose density does not explain all of the variation in distributional patterns between the populations, since big uninfected moose populations exist in Sweden well beyond the northern boundary of L. cervi and changes in moose abundance have been more or less parallel across Fennoscandia (Välimäki et al., 2011). An explanation for the differential spread rate might be differential use of hosts (in Sweden deer ked commonly uses both moose and roe deer as major hosts), an evolutionary difference or a combination of these two (Välimäki et al., 2011).

In conclusion, assessing the links between environmental conditions and invasion processes is critical for gaining understanding on factors influencing invasions and in the development of effective control measures (Liebhold & Tobin, 2008). For many insects, the patterns of spread have been linked with climatic conditions, new colonies being established far from the current distribution during years of favourable conditions (Loxdale & Lushai, 1999; Hochkirch & Dameraru, 2009). In the case of the deer ked, a local peak in moose density can lead to a rapid expansion over an extensive area. Our analysis, based on mapping the dynamics of the invasion front of deer ked to spatiotemporal variation of host density, suggests that the spread rate of the ked varies substantially with host density, with a sevenfold difference between the years of lowest and highest host density in our data (fig. 4).

The appendix can be found in the supplementary material at http://www.journals.cambridge.org/BER

Acknowledgement

We thank Jyrki Pusenius and Tuire Nygrén from the Finnish Game and Fisheries Research Institute for providing us the data and insight on historical moose densities in Finland, and Kimmo Murto for the coordinates of the Finnish hunting districts. This work was supported by the Academy of Finland (C.M.M. 1114864, O.O. 250444); the European Research Council (O.O. ERC Starting Grant 205905); the FWO Research Network ‘Eco-evolutionary dynamics in natural and anthropogenic communities (Eve-Net)’ (D.B. G.0057.09); and FWO projects (C.M.M., D.B. 3G.0610.11).

References


