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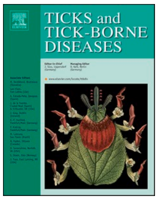

Original article

Exploring the influence of host community composition on the outbreak potential of *Anaplasma phagocytophilum* and *Borrelia burgdorferi* s.l.

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ABSTRACT

In large parts of the northern hemisphere, multiple deer species coexist, and management actions can strongly influence wild deer communities. Such changes may also indirectly influence other species in the community, such as small mammals and birds, because deer can have strong effects on their habitats and resources. Deer, small mammals and birds play an important role in the dynamics of tick-borne zoonotic diseases. It is, however, relatively underexplored how the abundance and composition of vertebrate communities may affect the outbreak potential, maintenance and circulation of tick-borne pathogens. In this study we focus on the outbreak potential by exploring how the basic reproduction number R_0 for different tick-borne pathogens depends on host community composition. We used published data on co-varying roe deer (*Capreolus capreolus*) and fallow deer (*Dama dama*) densities following a hunting ban, and different small mammal and bird densities, to investigate how the change in host community influences the R_0 of four tick-borne pathogens: one non-zoonotic, namely *Anaplasma phagocytophilum* ecotype 2, and three zoonotic, namely *A. phagocytophilum* ecotype 1, *Borrelia afzelii* and *Borrelia garinii*. We calculated R_0 using a next generation matrix approach, and used elasticities to quantify the contributions to R_0 of the different groups of host species. The value of R_0 for *A. phagocytophilum* ecotype 1 was higher with high fallow deer density and low roe deer density, while it was the other way round for *A. phagocytophilum* ecotype 2. For *B. afzelii*, R_0 was mostly related to the density of small mammals and for *B. garinii* it was mostly determined by bird density. Our results show that the effect of species composition is substantial in the outbreak potential of tick-borne pathogens. This implies that also management actions that change this composition, can (indirectly and unintentionally) affect the outbreak potential of tick-borne diseases.

1. Introduction

During the last decades, deer species have increased in density and have expanded their ranges across Europe (Apollonio et al., 2010; Deinet et al., 2013; Spitzer, 2019). These changes can be attributed to several factors, one of which is wildlife management. Wildlife management can influence deer communities through several actions, including hunting, the introduction (or elimination) of natural predators, fencing and supplementary feeding (Mysterud, 2010; Ripple and Beschta, 2012). Such actions may not only influence the overall densities of deer populations but may also affect the relative abundance of different deer species in the community. For example, in several locations in Europe it has been observed that the introduction of fallow deer (*Dama dama*), red deer (*Cervus elaphus*) and sika deer (*Cervus nippon*) led to decreasing densities of roe deer (*Capreolus capreolus*) (reviewed in Ferretti and Mori, 2020). This decrease can be attributed to

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the fact that these species occupy the same niche and interact over shared resources. Furthermore, the influence of management actions can cascade through the ecosystem over and across trophic levels. It has been shown that changes in deer populations can be linked to changes in bird (e.g., Palmer et al., 2015) and small mammal communities (e.g., Buesching et al., 2011), possibly through the effects that deer have on the vegetation through, for example, trampling and foraging. It is relatively underexplored how differences in the abundance and composition of vertebrate communities may affect the outbreak potential, maintenance, and circulation of tick-borne pathogens (but see e.g., Takumi et al., 2019). This information, however, could be vital in understanding the implications of certain management decisions on the transmission of tick-borne pathogens.

Two widespread and heavily managed European deer species are fallow deer and roe deer (Spitzer, 2019). Several studies suggest that these two species frequently engage in negative behavioural interactions, where fallow deer displace roe deer (Elofsson et al., 2017; Ferreti, 2011; Ferretti et al., 2011; Focardi et al., 2006). Aggression during feeding by fallow deer has been shown to drive roe deer away from their feeding sites (Ferretti et al., 2011). Also, competition over food forces roe deer to disappear. Roe deer are selective feeders and prefer high quality food, while fallow deer are more grazing generalists (Spitzer et al., 2020). In a shared environment fallow deer also eat the high-quality food, reducing the food resources for roe deer (Elofsson et al., 2017). Management actions that potentially increase fallow deer densities, could thus have a negative impact on roe deer densities. Indeed, in two nature areas in the Netherlands, 'Amsterdamse waterleidingduinen' and 'Deelerwoud', hunting bans led to increased fallow deer densities followed by strongly declining roe deer densities (FBE Noord-Holland, 2020; Huysentruyt and Casaer, 2015).

Deer species, including roe and fallow deer, play a major role in the life cycle of the tick species *Ixodes ricinus* and the circulation of tick-borne zoonotic pathogens, such as *Anaplasma phagocytophilum* and *Borrelia burgdorferi* s.l. (Fabri et al., 2022; Hofmeester et al., 2016). However, we recently showed that the size and nature of this role varies among deer species (Fabri et al., 2021), and the overall effect of deer on these pathogens consequently depends on the composition of the deer host community. Bird and small mammal communities are also important for the maintenance of certain tick-borne pathogens. For example, birds are associated with *Borrelia garinii* and small mammals with *Borrelia afzelii* (Hanincová et al., 2003; Taragel'ová et al., 2008). In the USA, Vuong et al. (2017) concluded that the composition of the small mammal host community was associated with the number of *Ixodes scapularis* nymphs infected with *B. burgdorferi* s.l.

In this study, we explored how the composition of the host community affects the transmission potential of four tick-borne pathogens: *A. phagocytophilum* ecotype 1, *A. phagocytophilum* ecotype 2, *B. afzelii* and *B. garinii*. We did this by calculating the basic reproduction number (R_0), a key measure in epidemiology. R_0 is defined as the average number of cases caused by a single infected individual, and it represents a measure for the risk that a pathogen once introduced will cause an outbreak. The R_0 quantifies the early potential for transmission, and hence growth of infections, in a population where all species and their life stages are in a pathogen-free steady state. If $R_0 > 1$, the pathogen can initially spread successfully when introduced into this population. Quantifying R_0 for scenarios with different host compositions, required that we adapted the matrix model approach developed in Hartemink et al. (2008) and in Matser et al. (2009) by including different host types, rather than a single host species. We used published data on co-varying roe deer and fallow deer densities following a hunting ban, to explore how the R_0 of the four pathogens is affected by the host composition. Furthermore, we quantified the contribution of each species in the transmission.

2. Materials and methods

2.1. Construction of next-generation matrix

To characterize R_0, we applied a next-generation matrix (NGM) approach based on the NGM for tick-borne pathogens developed in Hartemink et al. (2008). In the NGM approach, the first step consists of identifying the different types of individuals involved in the transmission (the types-at-infection). For a system with n types-at-infection, the NGM is an $n \times n$ matrix, where every element k_{ij} of the matrix indicates how many cases of type i are on average caused by a typical infectious individual of type j; R_0 is the dominant eigenvalue of the NGM (Diekmann et al., 2010). Hartemink et al. (2008) developed an NGM to calculate R_0 for infections transmitted by ticks that take three bloodmeals during their lifetime: as larva, as nymph and as (female) adult. In this NGM, the fact that ticks that became infected as (feeding) larva have a different epidemiological potential (here: more opportunities to infect individuals) than ticks that became infected as (feeding) nymphs, is taken into account by characterizing the types-at-infection for ticks by the life stage at which they become infected.

In Hartemink et al. (2008), a single type of infectious host was considered. In this study, we expanded the NGM by distinguishing four types of hosts (fallow deer, roe deer, small mammals and birds) instead of a single host type. Small mammals here refers to mice, voles and shrews. In total, we distinguished six states-at-infection: ticks infected as larvae (L), ticks infected as nymphs (N), fallow deer (F), roe deer (R), small mammals (S) and birds (B). This led to a 6 × 6 matrix $\boldsymbol{K}$ (see Fig. 1 and Appendix A, Text A.1). In this matrix, the non-zero elements in the first row (k_{13}, k_{14}, k_{15} and k_{16}) represent the expected number of larvae infected by a typical infected fallow deer, roe deer, small mammal and bird, respectively. Similarly, elements k_{23}, k_{24}, k_{25} and k_{26} represent the average number of nymphs infected by a typical infected individual of each of the host species. Elements in the first two columns give the expected number of hosts of each type infected by a tick that was infected as a larva (first column) or as a nymph (second column). We only included systemic infection (from tick to host and vice versa) as transmission route, as non-systemic transmission routes are not considered to be relevant for *A. phagocytophilum* and *B. burgdorferi* s.l. (Hartemink et al., 2008; Hauck et al., 2020; Richter et al., 2011).

2.2. Host densities

We parameterized the NGM for the two ecotypes of *A. phagocytophilum, B. afzelii* and *B. garinii* (details can be found in Appendix A, Text A.2). We constructed several scenarios with different densities of the respective hosts, representing different host community compositions. Some of the parameters in the NGM, e.g., the probability

$$\boldsymbol{K} = \begin{array}{c|cccccc|}
 & L & N & F & R & S & B \\
L & k_{11} & k_{12} & k_{13} & k_{14} & k_{15} & k_{16} \\
N & k_{21} & k_{22} & k_{23} & k_{24} & k_{25} & k_{26} \\
F & k_{31} & k_{32} & k_{33} & k_{34} & k_{35} & k_{36} \\
R & k_{41} & k_{42} & k_{43} & k_{44} & k_{45} & k_{46} \\
S & k_{51} & k_{52} & k_{53} & k_{54} & k_{55} & k_{56} \\
B & k_{61} & k_{62} & k_{63} & k_{64} & k_{65} & k_{66}
\end{array}$$

Fig. 1. The 6 × 6 next generation matrix used in our study to model the basic reproduction number R_0 for each of the four pathogens in the different scenarios. L = ticks infected as larvae, N = ticks infected as nymphs, F = fallow deer, R = roe deer, S = small mammals, B = birds.

that a tick will take a blood meal on a certain host type, are a function of the (relative) host densities (see for details Appendix A2). This allows us to study the effect of the community composition on the value of R_0. Our overall approach consists of modelling a continuous scale of co-varying densities of fallow deer and roe deer, based on published population trend data from Amsterdamse waterleidingduinen (AWD) (FBE Noord-Holland, 2020). This area is a Natura2000 protected dune area on the west coast of the Netherlands. Roe deer have always been present and common in AWD, until fallow deer escaped from a local animal park into the area and established a population in the mid-1990s. From that time, and until very recently, hunting in AWD was banned, which led to an exponential increase in fallow deer and, subsequently, a drastic decline in roe deer (Fig. 2). This population development of both deer has been closely monitored by FBE Noord-Holland through yearly counts (FBE Noord-Holland, 2020). We used this monitoring data to model the co-varying densities of both species in our models.

As small mammals and birds are important feeding hosts of ticks and tick-borne pathogens, we used four different scenarios, per pathogen, for their densities (Table 1): low densities of both small mammals and birds (scenario A), high bird density and low density of small mammals (scenario B), high density of small mammals and low bird density (scenario C), and high densities for both small mammals and birds (scenario D). These densities are based on a weighted average of densities of dominant small mammal and bird species in Europe (Bjärvall and Ullström, 1995; Cramp and Perrins, 1994; Ecke and Hörnfeldt, 2021; Hörnberg, 2001; Niethammer and Krapp, 1978). We varied small mammal density with a ten-fold difference, reflecting the contrasting densities that these small mammal species undergo as part of their population cyclicity in large parts of Europe (Andreassen et al., 2021). Such a cyclicity does not occur in birds. However, it is shown that the abundance of birds can change strongly over the years (Udo de Haes et al., 2020) and therefore, we varied the bird density with a five-fold difference.

2.3. Parameter estimates

In Appendix A (Text A.2), we provide a detailed description on how we obtained the values for the parameters in the NGM (Table 2). Here, we give a summary for the important parameters. We based the *transmission efficiency from tick to host species* on the infection prevalence in hosts and their tick burden of the different life stages. We obtained these parameters from the meta-analyses by Hofmeester et al. (2016) and Fabri et al. (2022), after supplementing their datasets with recently published (January 2014–August 2021) data on *B. burgdorferi* s.l. infection prevalence of vertebrate species and with recently published (January 2019–August 2021) data on the *I. ricinus* burdens of vertebrate species, as described in Appendix B. This led to an updated database on infection prevalence of *A. phagocytophilum* and *B. burgdorferi* s.l. and tick burdens of hosts (see Appendix C for the database and Appendix B for a more detailed description of how we constructed this database). Furthermore, we also included data from Fabri et al. (2021). We used the same dataset to obtain the *transmission efficiency from host species to ticks*, based on the infection prevalence of feeding larvae and nymphs. *Days of attachment* is life-stage dependent, with nymphs feeding longer than larvae. We obtained the values for this parameter from Militzer et al. (2021). Under the assumption that the *mean number of ticks on host species* does not change with changing densities of the host species, due to the heterogenous distribution of both hosts and ticks, we obtained the mean number of ticks, per life stage, from our dataset (Appendix C). The maximum *period of infectivity* was calculated based on the life expectancy of the host species, using a method described by Wedekind-Grunert et al. (2019). The *survival probability* from feeding nymph to feeding adult was the same as in Hartemink et al. (2008). Whether or not a tick survives to a next stage largely depends on whether it finds a host, and we therefore made the survival probability from a feeding larvae to a feeding nymphs dependent on the density of small mammals and birds. We increased this value with an increasing density of small mammals and birds. The *probability that a tick will take a blood meal on a certain host species* (h_{Ni} or h_{Ai}) was calculated as the proportion of the ticks feeding on that particular host species (tick burden times the relevant host density) out of all the feeding ticks.

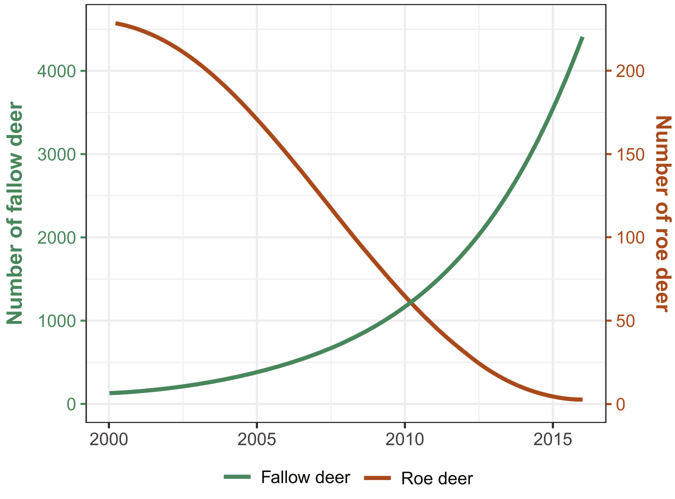

Fig. 2. The number of fallow deer (green) and roe deer (orange) in Amsterdamse waterleidingduinen after the establishment of fallow deer in the early 2000s (FBE Noord-Holland, 2020).

Table 1
The four scenarios and the correspondent densities of small mammals and birds in these scenarios.

	Scenario A	Scenario B	Scenario C	Scenario D
Density of small mammals (km^{-2})	400	400	4000	4000
Density of birds (km^{-2})	250	1250	250	1250

2.4. R_0 computation

We explored how the co-varying densities of the two considered deer species affected the R_0 of the four different pathogens, in four scenarios differing in densities of the small mammal and bird species. For each pathogen, we plotted the value of R_0 against the fallow deer density for each of the four scenarios. With increasing fallow deer density, the roe deer density decreased. We also established the contribution of each species group to R_0 as the elasticity of each species in the NGM, as described by Hartemink et al. (2008) and Matser et al. (2009). We performed all analyses and visualisations in RStudio version 3.6.0 (R Core Team, 2019) using the packages *popbio, doParallel, foreach, ggpubr* and *tidyverse* (Kassambara, 2020; Stubben et al., 2020; Walling et al., 2020a, 2020b; Wickham and RStudio, 2021).

3. Results

The value of R_0 for *A. phagocytophilum* changed strongly along the co-varying densities of fallow deer and roe deer, and in different ways for ecotype 1 and 2. The value of R_0 for the zoonotic *A. phagocytophilum* ecotype 1 was higher at high fallow deer densities (and consequently low roe deer densities) (Fig. 3). In contrast, the value of R_0 for the non-zoonotic *A. phagocytophilum* ecotype 2 was lower at high fallow deer and low roe deer densities (Fig. 4). The value of R_0 for ecotype 1 was dominated by fallow deer; only at very low fallow deer densities, did other species groups have a noticeable contribution (Fig. 5). For ecotype 2, at relatively low fallow deer densities roe deer contributed the most to

Table 2

Parameters of the next-generation matrix: A) non-density dependent, pathogen-related parameters, B) non-density dependent, tick-related parameters and C) density dependent parameters. How the values of these parameters were obtained can be found in Appendix A: Text A.2.

A)

Parameter	Definition	Pathogen	Fallow deer	Roe deer	Small mammals	Birds
p_L	Transmission efficiency from host species to larva*	*AP* e1	0.92	0.90	0.007	0.001
		AP e2	0.92	0.90	0.007	0.001
		Ba	NA	NA	0.178	0.005
		Bg	NA	NA	0.001	0.177
p_N	Transmission efficiency from host species to nymph*	*AP* e1	0.92	0.90	0.007	0.001
		AP e2	0.92	0.90	0.007	0.001
		Ba	NA	NA	0.178	0.005
		Bg	NA	NA	0.001	0.177
q_N	Transmission efficiency from nymph to host species*	*AP* e1	0.8–1.0	0.01–0.1	0.0–1.0	0.0–1.0
		AP e2	0.01–0.1	0.8–1.0	0.0–1.0	0.0–1.0
		Ba	0.0	0.0	0.8–1.0	0.01–0.1
		Bg	0.0	0.0	0.01–0.1	0.8–1.0
q_A	Transmission efficiency from adult to host species*	*AP* e1	0.8–1.0	0.01–0.1	0.0–1.0	0.0–1.0
		AP e2	0.01–0.1	0.8–1.0	0.0–1.0	0.0–1.0
		Ba	0.0	0.0	0.8–1.0	0.01–0.1
		Bg	0.0	0.0	0.01–0.1	0.8–1.0

B)

Parameter	Definition	Fallow deer	Roe deer	Small mammals	Birds
D_L	Days of attachment of larva	3.8	3.8	3.8	3.8
D_N	Days of attachment of nymphs	5.3	5.3	5.3	5.3
N_L	Mean number of larvae on host species	0.45	0.11	2.25	0.51
N_N	Mean number of nymphs on host species	10.92	5.04	0.08	0.6
N_A	Mean number of adults on host species	5	9.02	0	0
I	Period of infectivity of host species	825	825	191	647
S_A	Survival probability from feeding nymph to feeding adult	0.1	0.1	0.1	0.1

C)

Parameter	Definition	Scenario	Fallow deer	Roe deer	Small mammals	Birds
S_N	Survival probability from feeding larva to feeding nymph	A	0.1	0.1	0.1	0.1
		B	0.125	0.125	0.125	0.125
		C	0.15	0.15	0.15	0.15
		D	0.2	0.2	0.2	0.2
h_{Ni}	Fraction of blood meals taken on host species i by nymphs	$\frac{N_{Ni}D_i}{N_{NF}D_F + N_{NR}D_R + N_{NS}D_S + N_{NB}D_B}$				
h_{Ai}	Fraction of blood meals taken on host species i by adults	$\frac{N_{Ai}D_i}{N_{AF}D_F + N_{AR}D_R + N_{AS}D_S + N_{AB}D_B}$				

AP e1 = *Anaplasma phagocytophilum* ecotype 1, AP e2 = *A. phagocytophilum* ecotype 2, Ba = *Borrelia afzelii*, Bg = *B. garinii.*

* Transmission efficiency is the probability that a bite of an infected tick leads to a systemic infection in the host, or vice versa, that a bite on an infected host, leads to infection of a tick.

D = density of the host species in the different scenarios, N_N = mean number of nymphs on host species, N_A = mean number of adults on host species.

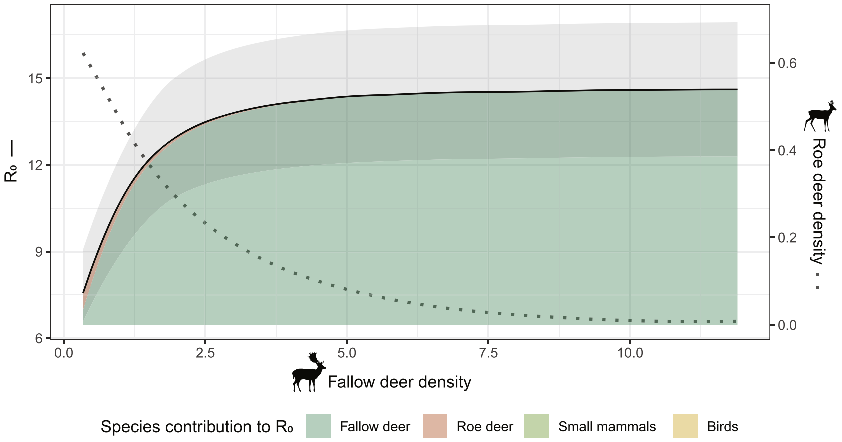

Fig. 3. Basic reproduction number R_0 (solid line) of *Anaplasma phagocytophilum* ecotype 1 with the standard deviation (grey shaded), for co-varying densities (km^{-2}) of fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*) (dotted line) as observed in Amsterdamse waterleidingduinen (FBE Noord-Holland, 2020). The coloured area under the R_0-curve represents the contribution of the different host species groups to the value of R_0. The graphs for each of the scenarios with different small mammal and bird densities are very similar, and therefore only the graph for scenario A is shown. The other graphs can be found in Appendix D: Fig. D.1. At low fallow deer densities there is a small difference in the contribution of the host species groups among the scenarios, which is shown in Fig. 5.

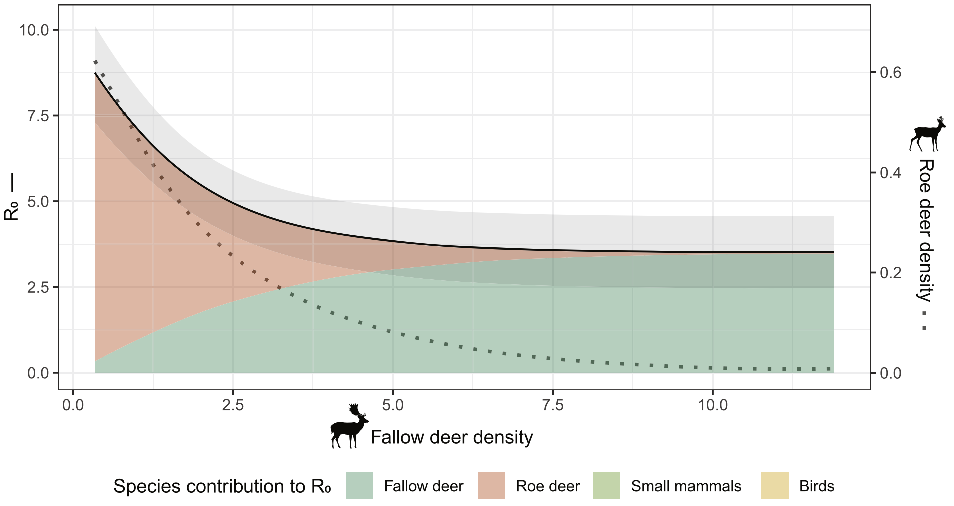

Fig. 4. Basic reproduction number R_0 (solid line) of *Anaplasma phagocytophilum* ecotype 2 with the standard deviation (grey shaded), for co-varying densities (km^{-2}) of fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*) (dotted line) as observed in Amsterdamse waterleidingduinen (FBE Noord-Holland, 2020). The coloured area under the R_0-curve represents the contribution of the different host species groups to the value of R_0. The graphs for each of the scenarios with different small mammal and bird densities are very similar, and therefore only the graph for scenario A is shown. The other graphs can be found in Appendix D: Fig. D.2.

the R_0, while fallow deer contributed the most when fallow deer densities were intermediate to high (Fig. 4). For both *A. phagocytophilum* ecotype 1 and 2, we did not detect major differences in the value of R_0 under the four scenarios of different small mammal and bird densities (Appendix D, Figs. D.1 and D.2). Although, for ecotype 1 we saw small differences in the contribution of small mammals and birds to R_0, when fallow deer density was low (Fig. 5).

The co-varying densities of fallow deer and roe deer hardly influenced the R_0 for *B. afzelii* and *B. garinii* (Figs. 6 and 7) and the value only slightly decreased towards very high fallow deer densities. Small mammals made up near 100 % of the contribution to the value of R_0 for *B. afzelii* while birds did so for *B. garinii*. The contribution of the other mammal taxa was negligible (Figs. 6 and 7). The value of R_0 for *B. afzelii* increased when small mammals occurred at high densities, while it decreased when birds occurred at high densities (Fig. 6). The highest value of R_0 for *B. garinii* was found when both birds and small mammals occurred at high densities (Fig. 7, panel D).

4. Discussion

In this theoretical study, we showed that the composition of host communities influences the outbreak potential of four tick-borne pathogens. We used data from a real-life situation with a hunting ban. In this area all four investigated pathogens have been found in recent studies (Köhler et al., 2023; Takumi et al., 2019, 2021). The influence was expressed as the relative differences in the values of R_0. We found that for each of the pathogens, the relative differences in the values of R_0 can be explained by regarding the differences in host species composition of the model community.

The values of R_0 for both ecotypes of *A. phagocytophilum* were mainly driven by the two deer species in our model: fallow and roe deer. Deer species are main reservoir hosts for *A. phagocytophilum* (Stuen et al., 2013), and previous work already suggested that the different ecotypes are mainly associated with different species (Jaarsma et al., 2019; Jahfari et al., 2014). Our model showed that changes in fallow deer density drive changes in the R_0 for ecotype 1, which corresponds with the fact that the transmission efficiency from ticks to fallow deer is higher than to roe deer (Table 2). Across the full fallow deer density range used in our model they make up near 100 % of the host community to R_0 for this ecotype (Fig. 3). At low densities, however, we see that the other species groups also contribute slightly to R_0 for ecotype 1 (Fig. 5). This is in line with the hypothesis that this ecotype is a more generalized pathogen than ecotype 2 (Jahfari et al., 2014). The patterns of the relation of host density and R_0 for *A. phagocytophilum* ecotype 2 were rather different. Here, roe deer, not fallow deer, contributed most strongly and the value of R_0 was lower at low roe deer densities. Fallow deer, however, can become infected with ecotype 2, and can transmit this pathogen to ticks, with low efficiency (Table 2 and Jaarsma et al., 2019). This explains why the value of R_0 did not drop any further after a certain (high) density of fallow deer had been reached (Fig. 4).

For both ecotype 1 and ecotype 2 of *A. phagocytophilum*, the value of R_0 reached a plateau as a function of fallow deer density in our system (Figs. 3 and 4). In our model, we assumed that the tick survival rates and mean tick burden per host are not affected by the density of deer (in contrast to the assumption for small mammal and bird densities, where higher densities do increase the survival rates). This is in line with a study indicating that deer presence rather than deer density determines the tick density (Hofmeester et al., 2017). Still, it is a very strong assumption, and the implication is that for the effect of the varying densities of the two deer species on R_0, we are actually looking at the effect of the proportion of bites taken on either species. This explains why, in our model, the value of R_0 reaches a plateau at higher densities of fallow deer, because the proportion of adults feeding on fallow deer approaches 100 % (Appendix A: Fig. A.2), and therefore R_0 cannot increase anymore.

The pattern for the two considered genospecies in the *B. burgdorferi* s. l. complex was quite different from what we observed for *A. phagocytophilum*. The former is driven by the bird and small mammal communities, with no visible contribution of the two deer species. *Borrelia afzelii* is commonly associated with small mammals (Hanincova et al., 2003). In an earlier study by Wedekind-Grunert et al. (2019), the value of R_0 for *B. afzelii* was above 1 for small mammals, while it was below 1 for lizards and birds. Our results are in line with this and show that R_0 for *B. afzelii* is strongly driven by small mammals. R_0 values for *B. afzelii* were lower in scenarios with low densities of small mammals (Fig. 6). Even though birds were not clearly associated with *B. afzelii* in our elasticity analyses, the scenarios with a high bird density had a lower R_0 for *B. afzelii* compared to the scenario with the same small mammal density and a low bird density. This pattern might be explained by a dilution effect of birds: when bird density was higher, relatively more nymphs fed on birds than when bird density was lower (Appendix A: Fig. A.1). Since the fraction of bloodmeals taken by nymphs was a parameter for the matrix elements in our next generation matrix (Table 2), a high density of birds lowered the value of R_0 for *B. afzelii*. In a similar way,

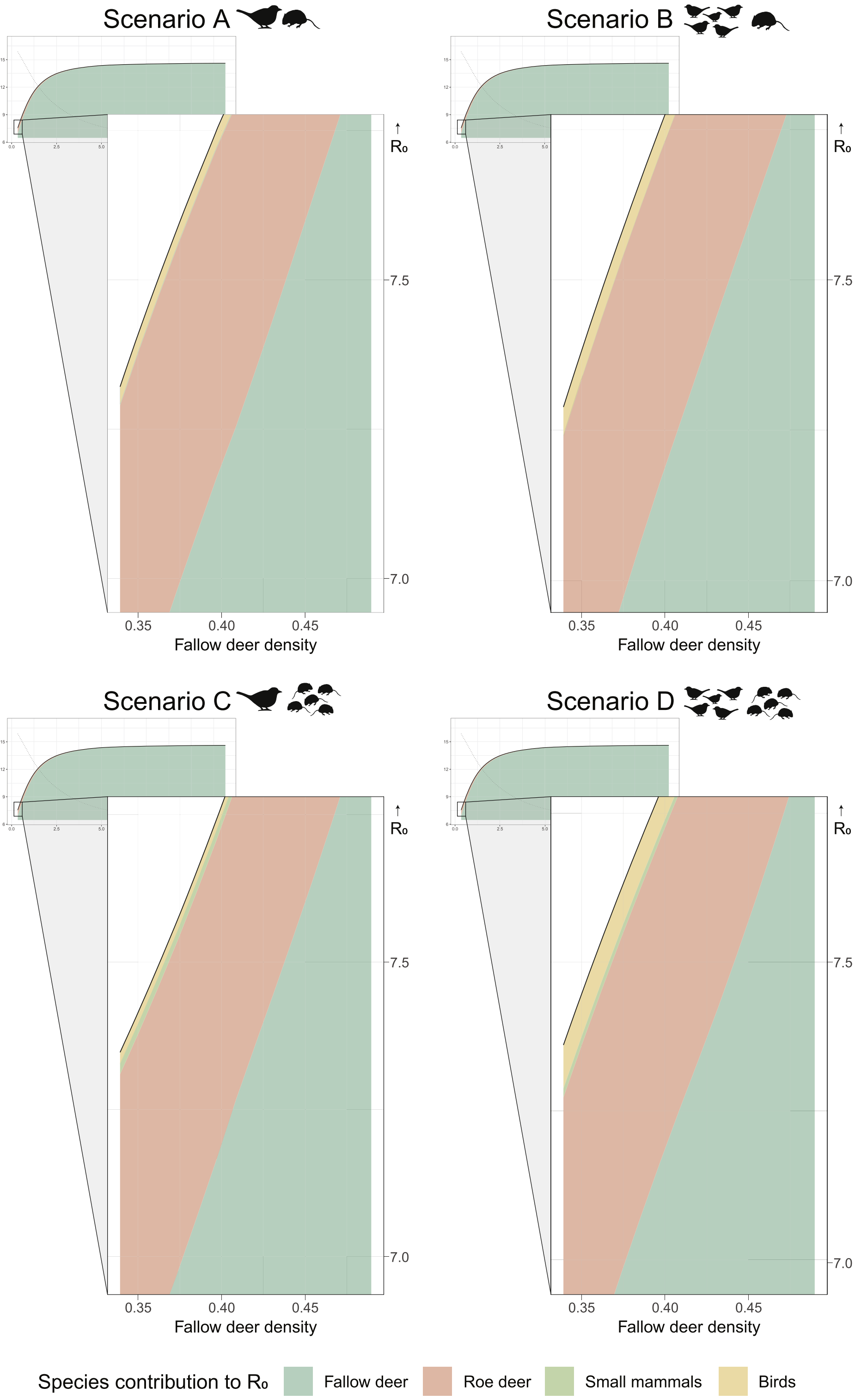

Fig. 5. Enlargement of the basic reproduction number R_0 of *Anaplasma phagocytophilum* ecotype 1 for low fallow deer (*Dama dama*) densities (km^{-2}). It is plotted against the fallow deer density for different scenarios with different densities of small mammals and birds (Table 1). The coloured area under the R_0-curve represents the contribution of the different host species to the value of R_0. The unenlarged graphs per scenario can be found in Appendix D: Fig. D.1.

infectious bites are wasted on incompetent hosts as fallow deer, which dilutes the transmission opportunities (Telford et al., 1988). With higher densities of fallow deer, we assume that nymphs take a relatively large fraction of their bloodmeals on deer, leading to a relatively lower fraction of bloodmeals taken by nymphs on small mammals (Appendix A: Fig. A.1).

The value of R_0 for *B. garinii* was driven by birds, in line with previous work that argued that *B. garinii* is a bird-associated species of the *B. burgdorferi* s.l. complex (e.g., Taragel'ová et al., 2008). In the scenarios with high bird density (scenarios B and D), the R_0 for *B. garinii* was higher compared to the other scenarios. In scenario D we expected that the higher density of small mammals would have led to relatively fewer nymphs feeding on birds (Appendix A: Fig. A.1), and hence lower the transmission of *B. garinii*. This was not the case, and it is possible that the expected effect has been counteracted by the increased survival of nymphs in the scenarios with high densities of birds and small mammals

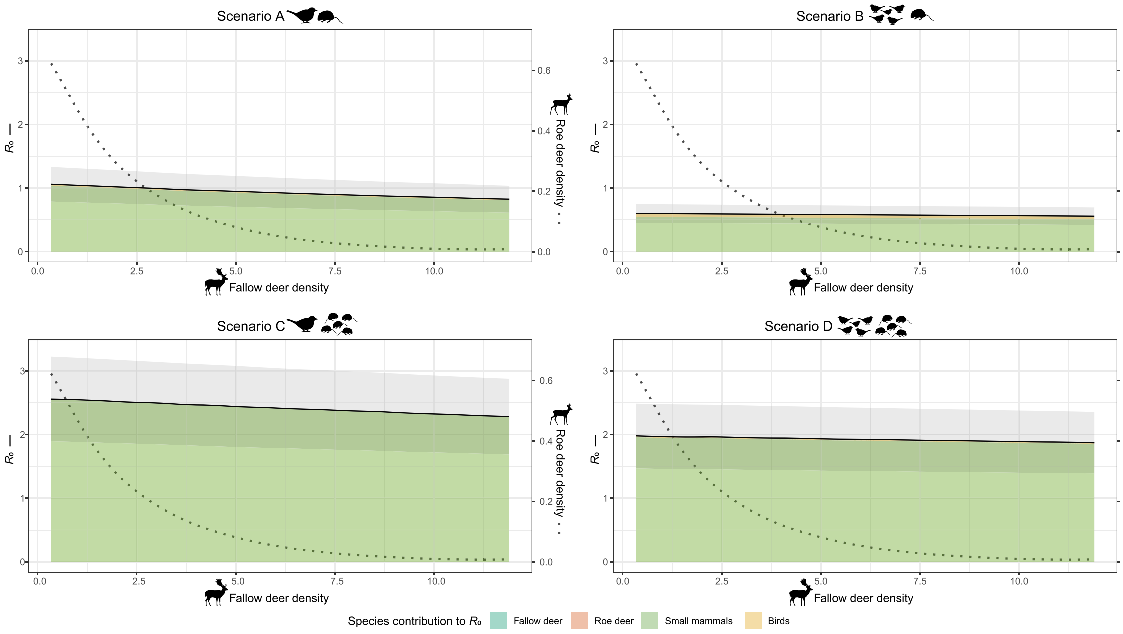

Fig. 6. Basic reproduction number R_0 (solid line) of *Borrelia afzelii* with the standard deviation (grey shaded), for co-varying densities (km^{-2}) of fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*) (dotted line) as observed in Amsterdamse waterleidingduinen (FBE Noord-Holland, 2020). Four scenarios (A–D) are depicted with different densities of small mammals and birds (Table 1). The coloured area under the R_0-curve represents the contribution of the different host species groups to the value of R_0.

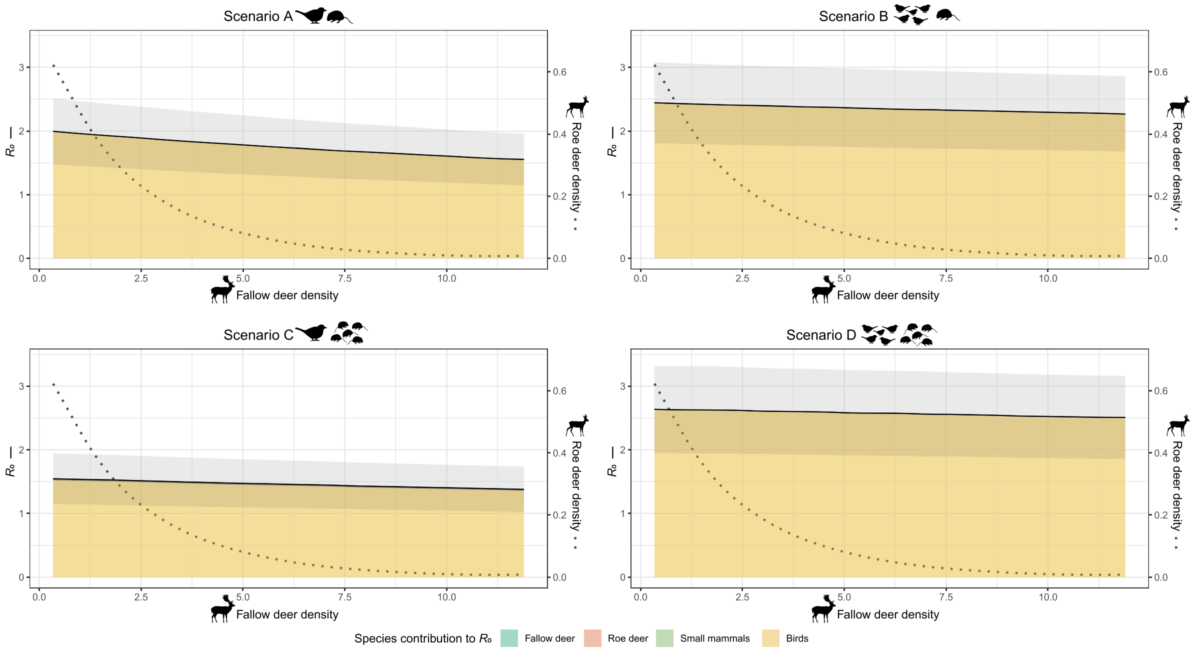

Fig. 7. Basic reproduction number R_0 (solid line) of *Borrelia garinii* with the standard deviation (grey shaded), for co-varying densities (km^{-2}) of fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*) (dotted line) as observed in Amsterdamse waterleidingduinen (FBE Noord-Holland, 2020). Four scenarios (A–D) are depicted with different densities of small mammals and birds (Table 1). The coloured area under the R_0-curve represents the contribution of the different host species groups to the value of R_0.

(Table 2). We have repeated the analyses, but with the assumption that the survival of nymphs does not depend on the densities of small mammals and hosts, and we found that in this case, the expected effect was visible (Appendix D: Fig. D.3). This is a reminder that increasing densities of incompetent or less competent hosts can have two counteracting effects: it may lower the proportion of bites taken on competent hosts and it will increase the total availability of blood meals, which may increase the survival and the population size of ticks (Levi et al., 2016; Ogden and Tsao, 2009).

In our model we see that, for all four pathogens, there are different contributions of the species groups. This is an important observation for mitigating public health risk, especially when comparing a zoonotic pathogen (*A. phagocytophilum* ecotype 1, *B. afzelii* or *B. garinii*) with a non-zoonotic pathogen (*A. phagocytophilum* ecotype 2). This could implicate that a management that, for example, promotes animals with a higher contribution to a non-zoonotic pathogen compared to animals with a higher contribution to a zoonotic pathogen, could help mitigate public health risk. However, even though we used real-life data of co-varying densities of fallow and roe deer, densities of other species in the same area were not available during the experiment. Therefore, we could not include several ecological dynamics in our model. These dynamics include, but are not limited by, the effects of co-varying deer densities on the populations of ticks, small mammals and/or birds. Furthermore, the densities of deer in all our models were intermediate to high, with the assumption that the density of deer is not limiting the tick densities. To be able to include limiting densities of deer, and ecological dynamics in our model, insight is needed of the effect of deer densities on the tick, bird and small mammal populations. These effects are not sufficiently investigated yet to be included in our models. Few studies have investigated the effect of deer density on the community composition and densities of small mammals, birds and *I. ricinus*, and among these studies no consensus has been reached (e.g., Buesching et al., 2011; Gilbert et al., 2012; Hofmeester et al., 2017; Palmer et al., 2015). To explore realistic management options, such information could be important. We did not include these relevant aspects of ecological dynamics, and neither did we include other important aspects such as human-wildlife interaction. Our current model is therefore not intended to predict how deer management scenarios will affect tick populations and human health risk of tick-borne pathogens.

In this study we showed that changes in the host community can strongly affect the value of R_0 for several common tick-borne zoonotic pathogens. For *A. phagocytophilum*, changes in the relative abundance of fallow versus roe deer influenced R_0 for the zoonotic ecotype 1 and the non-zoonotic ecotype 2 in contrasting ways. Management actions, such as the ban of hunting in areas where both deer species occur, may thus affect the circulation of these two ecotypes: management actions promoting fallow deer seem to promote the zoonotic ecotype over the non-zoonotic ecotype, while the opposite is true for management aimed at promoting roe deer. However, our results also clearly show that one must be extremely careful with such simple conclusions. Exact effects of changes in the host community are complex and depend on the pathogen and the target species of the management action. This is clearly shown by the different responses of R_0 for *A. phagocytophilum* and *B. burgdorferi* s.l. to changes in their host communities. There are many other zoonotic, tick-borne and differently spread, pathogens out there, with a wide variety of host ranges and host communities. Moreover, we did not explore dynamic ecological interactions in the host communities or the fuller complexity of the ecosystem that includes non-host species at all trophic levels. Such interactions have been shown to influence emergence and pathogen dynamics (Roberts and Heesterbeek, 2020, 2021). Promoting roe deer over fallow deer to manage the zoonotic *A. phagocytophilum* ecotype 1 may thus have unexpected consequences for pathogens that we did not include in our analyses. Our study does show the importance of taking a fuller community and ecosystem view, when contemplating management actions aimed at host species of tick-borne pathogens or aimed at mediating risk of these pathogens to humans, and that such a view needs substantially more attention in future research, combining field work with modelling.

Finally, it is important to emphasize that we did not aim to obtain precise absolute estimates of R_0 for the pathogens we included. In our model, we worked with a theoretical host assemblage where ticks can feed and have no limitations, and therefore our results should be interpreted as relative effects on the value of R_0. Our study therefore does not show how management actions could be used to lower the value of R_0 below the threshold of 1. To be able to make such predictions, we first need more knowledge on the biology of *I. ricinus* and the pathogens in question and the interactions in the ecosystem they inhabit.

5. Conclusions

Our results show that the effect of species composition is substantial in the circulation of tick-borne pathogens with different transmission cycles. This effect is already different for the four pathogens we investigated, and there may well be a wider range of outcomes for other pathogens and situations. This means that management actions affecting this species composition, could very well have an unintended effect on the circulation of tick-borne pathogens. A different species composition could have unintended side effects on the transmission of other pathogens, or even ecotypes of pathogens. Both the direct effects, as shown here, as also the effects through the ecological dynamics, which are vastly understudied.

Appendices

Appendix A: Description of the next generation matrix. Text A.1: Description of the elements of the next generation matrix. Text A.2: Description of the parameters of the elements of the next generation matrix.

Appendix B: Description of the additional systematic literature search.

Appendix C: Dataset for parameters. The combined dataset of the data collected by Hofmeester et al. (2016), Fabri et al. (Unpublished data) and our own meta-analysis as described in detail in Appendix B.

Appendix D: Additional figures. Figure D.1: Basic reproduction number R_0 (solid line) of Anaplasma phagocytophilum ecotype 1 with the standard deviation (grey shaded), for co-varying densities (km−2) of fallow deer (Dama dama) and roe deer (Capreolus capreolus) (dotted line) as observed in Amsterdamse waterleidingduinen (FBE Noord-Holland, 2020). Four scenarios (A-D) are depicted with different densities of small mammals and birds. The coloured area under the R_0-curve represents the contribution of the different host species groups to the value of R_0. Figure D.2: Basic reproduction number R_0 (solid line) of Anaplasma phagocytophilum ecotype 2 with the standard deviation (grey shaded), for co-varying densities (km^{-2}) of fallow deer (Dama dama) and roe deer (Capreolus capreolus) (dotted line) as observed in Amsterdamse waterleidingduinen (FBE Noord-Holland, 2020). Four scenarios (A–D) are depicted with different densities of small mammals and birds. The coloured area under the R_0-curve represents the contribution of the different host species groups to the value of R_0. Figure D.3: Basic reproduction number R_0 (solid line) of Borrelia garinii in an approach where the survival probability from feeding larva to feeding nymph is equal to 0.1 for all the scenarios, with the standard deviation (grey shaded), for co-varying densities (km^{-2}) of fallow deer (Dama dama) and roe deer (Capreolus capreolus) (dotted line) as observed in Amsterdamse waterleidingduinen (FBE Noord-Holland, 2020). Four scenarios (A–D) are depicted with different densities of small mammals and birds. The coloured area under the R_0-curve represents the contribution of the different host species groups to the value of R_0.

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CRediT authorship contribution statement

Nannet D. Fabri: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Funding acquisition. **Hans Heesterbeek:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Joris P.G.M. Cromsigt:** Conceptualization, Writing – original draft, Writing – review & editing, Funding acquisition. **Frauke Ecke:** Writing – review & editing. **Hein Sprong:** Writing – review & editing, Funding acquisition. **Lonneke Nijhuis:** Investigation, Writing – review & editing. **Tim R. Hofmeester:** Writing – review & editing. **Nienke Hartemink:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

Data availability

Data are in Supplementary Information.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ttbdis.2023.102275.

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