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ORIGINAL ARTICLE

Small mammal community composition impacts bank vole (*Clethrionomys glareolus*) population dynamics and associated seroprevalence of *Puumala orthohantavirus*

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Abstract

Rodents are important reservoirs for zoonotic pathogens that cause diseases in humans. Biodiversity is hypothesized to be closely related to pathogen prevalence through multiple direct and indirect pathways. For example, the presence of non-host species can reduce contact rates of the main reservoir host and thus reduce the risk of transmission ("dilution effect"). In addition, an overlap in ecological niches between two species could lead to increased interspecific competition, potentially limiting host densities and reducing density-dependent pathogen transmission processes. In this study, we investigated the relative impact of population-level regulation of direct and indirect drivers of the prevalence of *Puumala orthohantavirus* (PUUV) in bank voles (*Clethrionomys glareolus*) during years with high abundance. We compiled data on small mammal community composition from four regions in Germany between 2010 and 2013. Structural equation modeling revealed a strong seasonality in PUUV control mechanisms in bank voles. The abundance of shrews tended to have a negative relationship with host abundance, and host abundance positively influenced PUUV seroprevalence, while at the same time increasing the abundance of competing non-hosts like the wood mouse (*Apodemus sylvaticus*) and the yellow-necked field mouse (*Apodemus flavicollis*) were associated with reduced PUUV seroprevalence in the host. These results indicate that for PUUV in bank voles, dilution is associated with increased interspecific competition. Anthropogenic pressures leading to the decline of *Apodemus* spp. in a specific habitat could lead to the amplification of mechanisms promoting PUUV transmission within the host populations.

Key words: bank vole, biodiversity, *Puumala orthohantavirus*, small mammals

INTRODUCTION

Anthropogenic alterations of ecosystems can cause major declines in biodiversity (Jones *et al.* 2008). Fragmentation of habitats for plant and animal populations as well as increasing agricultural land use is a driver of the loss of biodiversity (Pievani 2014) and alteration of

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species distribution (Boivin *et al.* 2016). Diverse ecosystems are characterized by multifaceted interactions between individuals, species, and communities to maintain vital ecosystem functions (Thompson *et al.* 2018). At the local level, the species composition of communities at a given site can affect processes in that ecosystem (Carrick & Forsythe 2020) and influence ecosystem stability (Loreau & De Mazancourt 2013). In addition, high biodiversity has been shown to mitigate potentially negative implications for humans, such as the spread of zoonotic pathogens (Schmidt & Ostfeld 2001).

In this respect, small mammals play ambivalent roles in ecosystems. Their reproductive potential and flexible social systems allow for high-amplitude eruptive population fluctuations (Andreassen *et al.* 2021). These are essential parts of many generalist rodent population dynamics and also lead to a multifaceted influence on ecosystem services, especially in agricultural landscapes. For example, small mammals are an integral part of terrestrial food webs, regulating larger predator species by bottom-up trophic processes through increasing availability of rodent prey (Hanski 1991). On the other hand, outbreaks of small mammals can cause great damage to agriculture and forestry with significant monetary losses (Jacob & Tkadlec 2010). In addition, rodents harbor the greatest diversity of zoonotic pathogens of any mammalian order (Johnson *et al.* 2020).

The bank vole [*Clethrionomys glareolus* (Schreber, 1780)] is a generalist rodent, distributed throughout much of Europe and parts of northern Asia. It prefers understory-rich forests and shrublands, where they feed on seeds, fruits, and leaves. During the reproductive period from about April to September, they give birth three to four times to about three to five young (Stenseth *et al.* 2002). As with other vole species in the northern hemisphere, marked population fluctuations are a key feature of bank vole population dynamics (Andreassen *et al.* 2021). During these outbreaks, the risk of transmission of associated zoonotic pathogens to humans increases (Haredasht *et al.* 2013; Reil *et al.* 2015). Most notably in Europe, this is the case for *Puumala orthohantavirus* (PUUV) (Reil *et al.* 2017).

These fluctuations reflect the net results of birth and death rates as well as migratory processes, which in turn can be influenced by biotic and abiotic factors. In Central Europe, increased food availability due to the masting of beech trees (*Fagus sylvatica* Linnaeus, 1753) promotes outbreaks in bank voles (Tersago *et al.* 2009; Reil *et al.* 2015). Other extrinsic factors, such as the presence and abundance of other small mammal species, can affect bank vole population size (Bujalska & Grüm 2008). An increase in small mammal biodiversity could suppress bank vole populations due to increased interspecific interactions with other small mammals for food and other resources, especially when species partly overlap in ecological niches (Leszek & Bujalska 2000). This includes carnivorous shrews, which have been hypothesized to be predators of bank vole pups (Liesenjohann *et al.* 2011; Khalil *et al.* 2016).

These interspecific interactions are of particular interest in the management of rodent-borne zoonotic diseases. It is speculated, that a diverse species community could control pathogen prevalence through different, not mutually exclusive pathways (Khalil *et al.* 2014). For example, the presence of non-host species can reduce contact rates of the main reservoir host (i.e. hosts most competent to propagate and transmit a pathogen) and thus reduce the risk of transmission within the reservoir population. This phenomenon has been branded the dilution effect (DE) hypothesis (Schmidt & Ostfeld 2001). In addition, an overlap in ecological niches between two species could lead to increased interspecific competition, potentially limiting host densities and reducing density-dependent pathogen transmission processes. The relative strength of these direct and indirect pathways remains poorly understood and may depend on small mammal community composition. Although there is a debate about the generality of DE (Randolph & Dobson 2012), there is evidence in multiple host–pathogen systems where the net effect of DE leads to a decrease in host infection incidence (Magnusson *et al.* 2020; Morand 2020; Keesing & Ostfeld 2021).

In this study, we investigated the relative impact of population-level regulations of bank vole abundance in years with generally high abundance (outbreak years), in years with generally low abundance (non-outbreak years), and the direct and indirect drivers of PUUV seroprevalence in bank voles during years with high abundance. Our hypotheses were that: (i) small mammal diversity has a stabilizing effect on bank vole abundance and PUUV seroprevalences, and that (ii) drivers of population abundance act more pronounced during outbreak years compared to non-outbreak years.

MATERIALS AND METHODS

Rodent trapping

We used data from previously published studies that utilized some of the information presented here for an assessment of the ecology of PUUV (Reil *et al.* 2017; Fischer *et al.* 2018; Binder *et al.* 2020).

Figure 1 Map of the four study locations (a) and their respective federal state (highlighted in gray) in a European context (b). Within each location, three replicate forest sites were sampled.

Live-trapping and snap-trapping were conducted from 2010 to 2013 in Weissach (Baden-Wuerttemberg 48°49.88′N, 8°57.71′E), Jeeser (Mecklenburg-Western Pomerania 54°9.75′N, 13°15.55′E), Billerbeck (North Rhine-Westphalia 51°59.63′N, 7°18.99′E), and Gotha (Thuringia 50°57.38′N, 10°39.13′E) (Fig. 1). Habitat consisted mainly of broadleaved forest, dominated by beech (*Fagus sylvatica*). There were no forest management activities ongoing during the study period.

Briefly, trapping was conducted in three forest sites (each >2 km apart) in each federal state. Snap-trapping (FOX mouse trap, No. 901006, DEUFA) and live-trapping with Ugglan traps (Ugglan No.1, Grahnab, Sweden) were carried out per site at least 200 m apart with 49 traps per trapping methodology in a 7×7 grid with 10-m trap spacing. In live-trapping, a mixture of food pellets, apple pieces, and rolled oats was used as bait and wood wool as nesting material. Traps were checked at sunrise and sunset for 2–3 consecutive days. Animals caught for the first time were marked with a PIT tag (LUX-IDent, Lanškroun, Czech Republic). Snap traps were baited with a sultana and checked every 24 h for 2–3 days. All small mammals were identified to species based either on external morphology or established molecular confirmation (Schlegel *et al.* 2012). A relative abundance index (trap success as individuals/100 trap nights) for each site was calculated as a combined value for both trapping methodologies. If fewer than five bank voles were caught in a particular forest per season, the data were not included in the calculation of PUUV seroprevalences.

PUUV seroprevalences

Blood (diluted 1:200) or chest cavity fluid (diluted 1:10) was analyzed in an immunoglobulin G (IgG) enzyme-linked immunosorbent assay (ELISA), which uses a yeast-expressed PUUV nucleocapsid protein to test for anti-PUUV antibody presence in the sample (Essbauer *et al.* 2006; Mertens *et al.* 2011). Scoring of reactivities (positive, equivocal, negative) followed a previously described decision tree (Mertens *et al.* 2009). In further analyses, explicitly positive or negative results were required; hence, equivocal test results were classified as negative. For each federal state and season, mean seroprevalences ± standard deviation were calculated from plots where >5 samples were obtained. Further statistical analysis focused only on data from sites in two federal states (Baden-Wuerttemberg; North Rhine-Westphalia) as it has been previously established that PUUV is only present in the aforementioned regions (Drewes *et al.* 2017). We acknowledge that seropositivity does not imply acute infection at the time of sampling and that other factors could impact seropositivity over time (Kallio *et al.* 2006). For example, juvenile individuals may carry maternal antibodies, which do not reflect processes under investigation in this study (Kallio *et al.* 2010). As proposed by Kallio *et al.* (2010), we used a generalized additive mixed model between the individual infection status and the individual weight (see Supporting Information) to identify a threshold, below which we can define seropositive individuals as potentially carrying maternal antibodies. Random factors for sites nested within the respective federal states were used to account for the spatial design of the study. As a result, we excluded all bank voles with body mass <15 g ($N = 269$) (see Fig. S1, Supporting Information) from the analysis on PUUV seroprevalence, as their status potentially does not reflect genuine infection (Khalil *et al.* 2016).

Statistical analysis

The Shannon index was used as a measure of small mammal biodiversity. Calculations were done using R software (version 4.3.1, R Core Team 2023) and the *vegan: community ecology*-package (Oksanen *et al.* 2013) based on the relative abundance index.

We used structural equation models (SEM) that allow for a multivariate analysis of external factors in relation to bank vole abundance. SEMs can incorporate hypothesis-driven interrelations between multiple variables, and each variable can act as a predictor and response variable at the same time (Boch *et al.* 2021). Two SEMs were constructed both for outbreak years (2010, 2012) and non-outbreak years (2011, 2013). External factors included the non-target biodiversity (Shannon index; excluding bank voles) as well as the abundance of two dominant genera of small mammals, *Apodemus* spp. (here: wood mouse [*Apodemus sylvaticus* (Linnaeus, 1758)], yellow-necked field mouse [*Apodemus flavicollis* (Melchior, 1834)], and striped field mouse [*Apodemus agrarius* (Pallas, 1771)] and *Sorex* spp. (here: common shrew (*Sorex araneus* Linnaeus, 1978), crowned shrew (*Sorex coronatus* Millet, 1828), and Eurasian pygmy shrew (*Sorex minutus* Linnaeus, 1766)). All three factors interacted with bank vole abundance and with each other. We also allowed bank vole abundance to influence *Apodemus* spp. and *Sorex* spp. by assuming a covariance structure. These analyses included sites in all four federal states. Additional seasonal SEMs were constructed to investigate the relationship between external drivers and the prevalence of PUUV in bank vole populations during outbreak years, as these are typically associated with the highest infection probabilities (Olsson *et al.* 2002). Seasonal SEMs were only conducted for the federal states of Baden-Wuerttemberg and North Rhine-Westphalia. In these SEMs, we included the influence of host abundance on PUUV prevalence as well as non-host biodiversity and non-host abundances of the two main additional species groups, *Apodemus* spp. (Nyholm & Meurling 1979) and *Sorex* spp. (Khalil *et al.* 2016) that are hypothesized to influence bank vole dynamics and potentially PUUV seroprevalences. For non-host abundances, we considered direct and indirect effects, where non-host species can have a direct effect on PUUV seroprevalences in bank voles or indirect effects through either their influence on non-host biodiversity or host abundance. To meet normality assumptions, all variables were z-scaled prior to analysis. Individual, significant associations were additionally analyzed using linear mixed-effect models based on seasonal data with the site as a random factor. All SEMs were generated using the *lavaan*-package in R (Rosseel 2012).

RESULTS

During the study period, 12 species of small mammals were trapped, with a total of 7194 individuals captured in live- and snap-trapping. 70% (5042) of those were bank voles and 30% belonged to other species (Table 1). Apart from bank voles, yellow-necked field mice and common shrews were the most common species.

Mean abundances of dominant species groups (bank voles, *Apodemus* spp. and *Sorex* spp.) and associated

Table 1 Small mammals captured in live- and snap-trapping in the four German federal states Baden-Wuerttemberg (BW), Mecklenburg-Western Pomerania (MWP), North Rhine-Westphalia (NW), and Thuringia (THR)

		Federal state				
Species	Common names	BW	NW	MWP	THR	Total
Clethrionomys glareolus	Bank vole	1607	1090	1078	1267	5042
Apodemus flavicollis	Yellow-necked field mouse	540	310	237	432	1519
Apodemus sylvaticus	Wood mouse	44	0	97	17	158
Apodemus agrarius	Striped field mouse	0	0	46	4	50
Arvicola amphibius	Water vole	0	0	0	3	3
Microtus arvalis	Common vole	3	1	0	4	8
Microtus agrestis	Field vole	8	15	0	8	31
Micromys minutus	Eurasian harvest mouse	0	1	6	1	8
Neomys fodiens	Eurasian water shrew	0	4	1	0	5
Sorex araneus	Common shrew	23	142	20	45	230
Sorex coronatus	Crowned shrew	58	5	26	0	89
Sorex minutus	Eurasian pygmy shrew	29	9	8	5	51
Total		2312	1577	1519	1786	7194

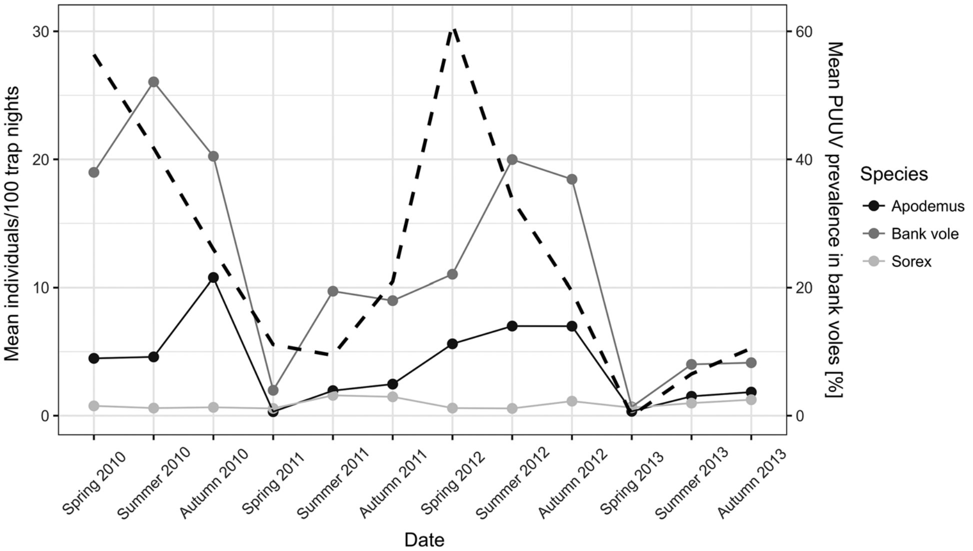

Figure 2 Overview of temporal changes within the study period for *Apodemus* spp. and *Sorex* spp. and bank voles. In addition, *Puumala orthohantavirus* (PUUV) seroprevalences are shown (black dashed line).

host PUUV seroprevalences can be found in Fig. 2. Bank vole dynamics indicate high abundances in the years 2010 and 2012 with lower abundances in 2011 and 2013. *Apodemus* spp. abundances seemed to follow that trend, though the amplitude of fluctuations was lower compared to the bank vole. For *Sorex* spp., no clear temporal trend was observed. Site-specific and seasonal abundances for bank voles, *Apodemus* spp. and *Sorex* spp., can be found in Table S1, Supporting Information. Host abundances ranged from 0 to 53 individuals per 100 trap nights with PUUV seroprevalences ranging from 0.0% to 89.6%.

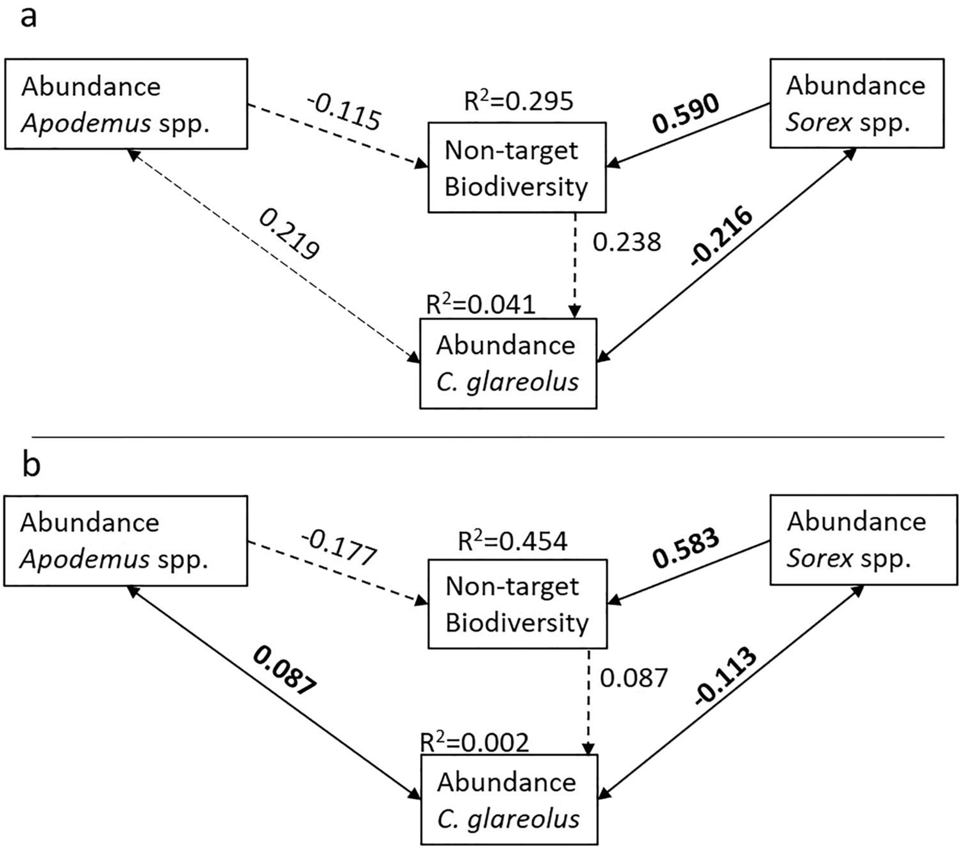

Figure 3 Results of structural equation model showing the impact of external drivers of bank vole abundance in the outbreak (a) and non-outbreak (b) years. Correlation coefficient estimates of significant (continuous lines) and not significant (dashed lines) relationships are displayed. Single-headed arrows indicate a regression and double-headed arrows indicate a covariance in the error structure. Goodness of fit statistics: (a) Fishers C = 0.015, df = 1, and *P*-value = 0.901; (b) Fishers C = 5.414, df = 1, and *P*-value = 0.02.

All relationships of drivers of bank vole abundance in outbreak and non-outbreak years are shown in Fig. 3 (see Table S2, Supporting Information, for SEM details; goodness of fit statistics indicated that only in outbreak years the SEM model fitted the observed data very well (Fig. 3)). In both scenarios, non-target biodiversity never had a direct impact on bank vole abundance. In turn, non-target biodiversity itself was negatively associated with increasing *Apodemus* spp. abundance and positively associated with increasing *Sorex* spp. abundance. Interspecific interaction suggests a slight difference between outbreak and non-outbreak years. In both scenarios, an increase in *Sorex* spp. abundance was significantly negatively associated with bank vole abundances. In contrast, an increase in *Apodemus* spp. abundances was positively correlated with bank vole abundance, though only significant in non-outbreak years.

Population-level drivers of PUUV seroprevalence in bank voles differed markedly between seasons (Figs 4,5; see Table S3, Supporting Information, for SEM details; goodness of fit statistics indicated that in summer and autumn, the SEM model fitted the observed data very well (Fig. 4)). The greatest number of significant interactions was observed in summer while only one of the interactions was significant in autumn. Non-target biodiversity did not have a significant direct impact on PUUV seroprevalences, though estimates remain always negative. In contrast to biodiversity, host abundance only has a significant positive impact on PUUV seroprevalence during summer. Interspecific relationships were only significant during summer when an increase in *Apodemus* spp. abundances significantly decreased PUUV seroprevalences in bank voles. An additional linear mixed-effect model confirmed the

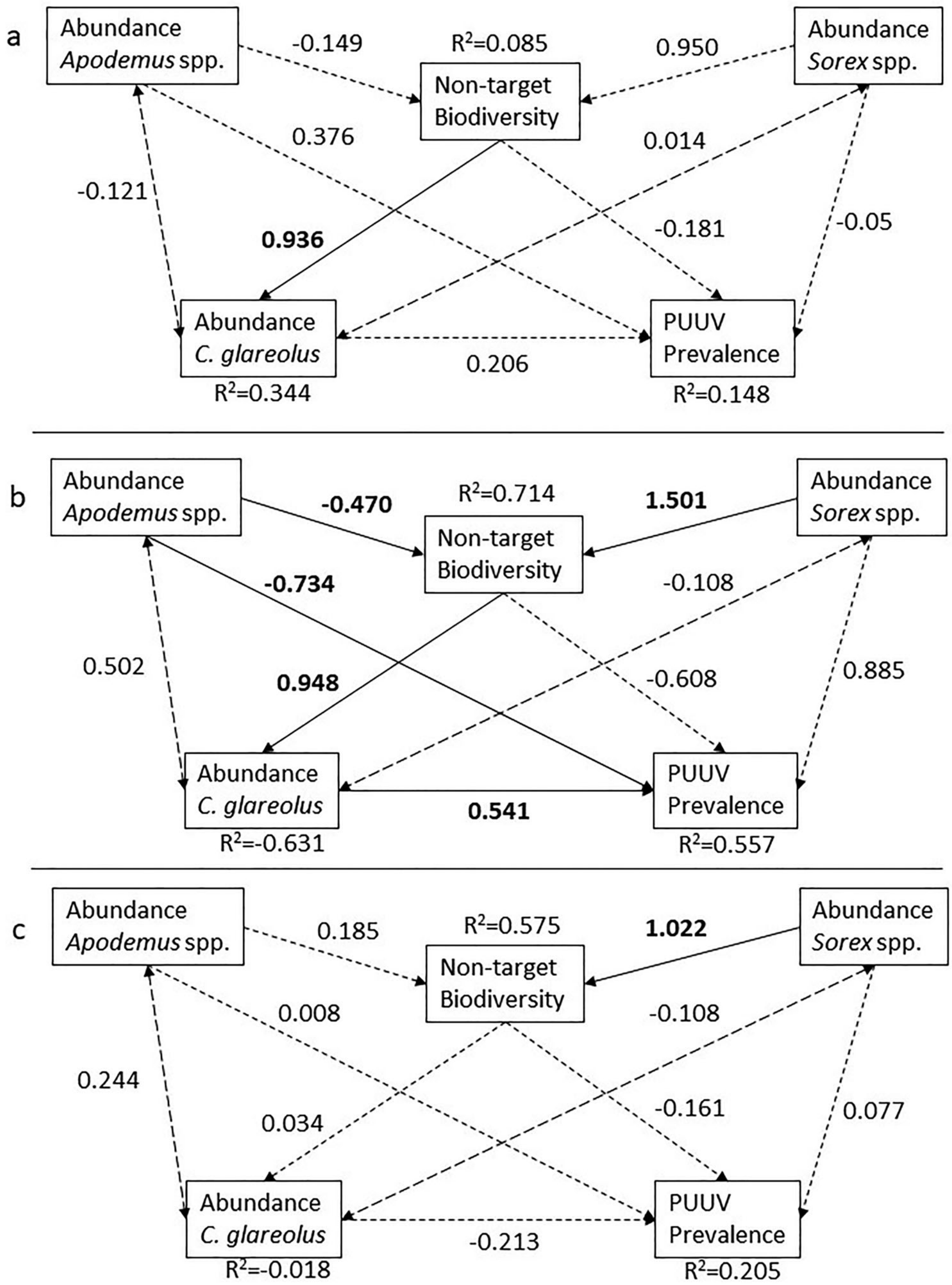

Figure 4 Structural equation models (SEMs) showing the impact of external factors on seasonal *Puumala orthohantavirus* (PUUV) seroprevalence in spring (a), summer (b), and autumn (c). Correlation coefficient estimates of significant (continuous lines) and not significant (dashed lines) relationships are displayed. Single-headed arrows indicate a regression and double-headed arrows indicate a covariance in the error structure. Goodness of fit statistics: (a) Fishers C = 7.778, df = 1, and *P*-value = 0.005; (b) Fishers C = 0.05, df = 1, and *P*-value = 0.824; (C) Fishers C = 1.291, df = 1, and *P*-value = 0.256.

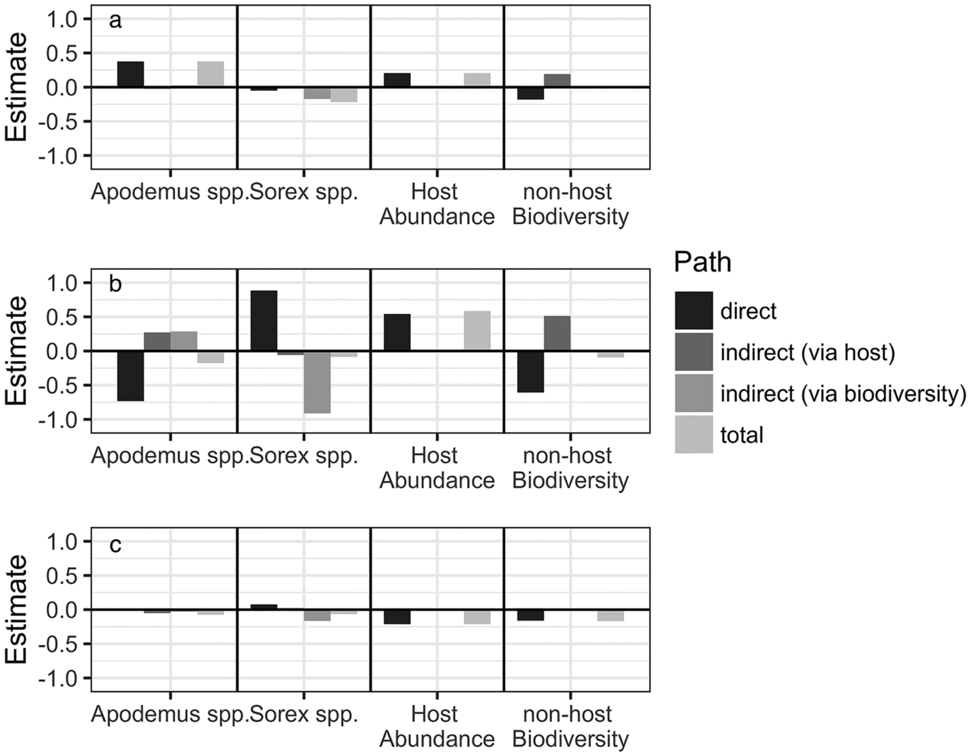

Figure 5 Summary of direct, indirect, and total (cumulative) effects of predictors (*x*-axis) on *Puumala orthohantavirus* (PUUV) seroprevalence for each season (spring (a); summer (b); autumn (c)), based on the structural equation model (SEM) presented in Fig. 3. Indirect effects on PUUV seroprevalence occurred from the effects of *Apodemus* spp. and *Sorex* spp. abundance either through host abundance or their impact on non-host biodiversity. Indirect effects = effect 1 × effect 2; total effect = direct + indirect (via host) + indirect (via biodiversity).

seasonality and magnitude of this particular effect (Table 2; Fig. 6).

DISCUSSION

This study highlights that factors driving bank vole populations and associated pathogens can vary between years as well as within years. Especially, the direct and indirect controls of PUUV seroprevalence in bank voles reveal a strong seasonal component. During non-reproductive periods of spring and autumn, there is very little influence of host abundance and small mammal community composition, while these factors are involved in regulating PUUV seroprevalence during summer. During bank vole outbreaks, there are mainly two significant competing factors directly determining PUUV seroprevalence. The first is positive direct density dependence, where an increase in host abundance also increases PUUV seroprevalence. Density-dependent transmission of pathogens is a common feature in many orthohantaviruses worldwide. Khalil *et al.* (2014) showed that density dependence was found in 59% of studies that were considered in their review of different hantaviruses. Similar to Reil *et al.* (2017), using only the live-trapping data of the current study, we confirm that there appears to be a strong seasonality in the influence of host abundance on PUUV prevalence and that a positive correlation between the two is most pronounced during the summer. Second, the increasing abundance of *Apodemus* spp. (here yellow-necked field mouse and wood mouse) during summer leads to a decrease in PUUV seroprevalence in the host. Our results indicate that this is a direct effect of increased *Apodemus* spp. presence in the same habitat that is not mediated by host abundance or non-host biodiversity (Fig. 5). This finding is consistent with the dilution effect hypothesis (Keesing *et al.* 2006) where increased numbers of non-competent species can limit pathogen transmission within the host species. Our results also highlight that driving PUUV seroprevalence is not exerted by biodiversity *per se* but rather

Table 2 Results of a linear mixed effect model to estimate the relationship between *Puumala orthohantavirus* (PUUV) seroprevalence and the ratio of *Apodemus* spp. and bank voles (*C. glareolus*) within the community for spring, summer, and autumn in outbreak years (2010, 2012)

						Random effect (Site)	
Factor	Estimate	SE	df	*t*-Value	*P*-value	Variance	SD
Spring							
Intercept	63.730	15.253	10	4.178	0.002	65.350	8.084
Ratio *Apodemus* spp. vs *C. glareolus*	−15.311	43.478	8	−0.352	0.733		
Summer							
Intercept	54.691	7.159	10	7.640	<0.001	0	0
Ratio *Apodemus* spp. vs *C. glareolus*	−88.271	32.285	10	−2.734	0.021		
Autumn							
Intercept	23.761	6.184	7	3.842	0.006	0	0
Ratio *Apodemus* spp. vs *C. glareolus*	−2.165	20.006	7	−0.108	0.917		

SE, standard error; df, degrees of freedom; SD, standard deviation.

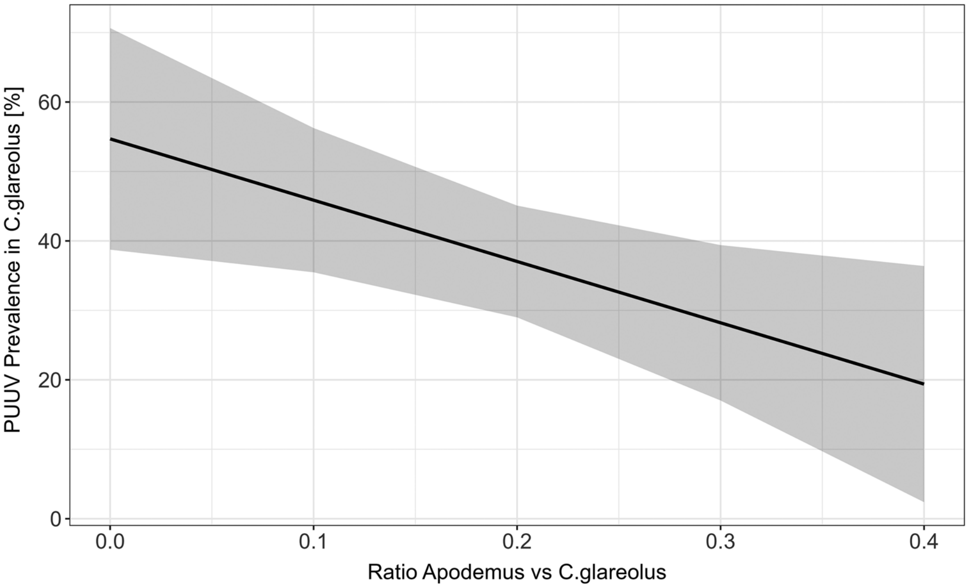

Figure 6 Graphical representation of the relationship between the ratio of *Apodemus* spp. and bank voles and the *Puumala orthohantavirus* (PUUV) seroprevalence in bank voles during the summer (see Table 2). The ratio is expressed between 0 and 1 with 0 being dominated by the bank vole and 1 dominated by *Apodemus* spp. Solid lines represent the mean effect and the gray area represents the upper and lower 95% confidence interval.

interspecific competition between two generalist species/species groups with partly overlapping ecological niches. Rohr *et al.* (2020) highlighted that the dilution capacity of a non-competent species is best observed at a small scale, where direct observations of interactions can be directly linked to changes in host prevalences, which might be a process explanation for the observed results in this study.

Apodemus spp. and bank voles are both widely distributed throughout continental Europe, preferring mostly deciduous and mixed forests (Döhle *et al.* 1984), where they represent the two most abundant taxa (Hotopp *et al.* 2022). There is considerable overlap in food preferences with both species being considered largely granivorous (Hansson 1985). In northern Italy, Canova (1993) found no significant differences in food preferences between the bank vole and the wood mouse.

Given the overlap in ecological niches, frequent and asymmetric interspecific interactions have been reported. Fasola and Canova (2000) reported a dominance of wood mice over bank voles in Italian small mammal populations, while a similar asymmetry was found for yellow-necked field mice in Polish populations (Andrzejewski & Olszewski 1963). When co-occurring in the same habitat, interactions can be minimized through behavioral adaptations like food partitioning through temporal separation of daily activity (Viviano *et al.* 2022). Although we can assume interspecific competition between the two species groups, the evidence for a direct interspecific influence on host abundance is less convincing. Marsh *et al.* (2001) noted that in British populations, when ranges overlapped, bank voles were less abundant, while Casula *et al.* (2019) showed that interspecific competition does not lead to adjustments in home ranges and that coexistence is possible, for example, when microhabitat can be partitioned (Hille & Mortelliti 2011). Our results show a similar trend, as abundances of *Apodemus* spp. and bank voles showed slightly positive covariance (Fig. 3). This highlights that the main effect of increasing *Apodemus* spp. abundance on PUUV is likely not through regulation of host densities, but rather amplifying behavioral responses to avoid competition (i.e. activity pattern, habitat use) and in the process limiting pathogen transmission within the host population.

In addition to direct interspecific interference in within-host transmission, pathogen spillover events to dead-end hosts might lead to termination of the transmission cycle and act as viral sinks (Khalil *et al.* 2014). For this dataset, Binder *et al.* (2020) tested a subset of yellow-necked field mice and wood mice from BW and NW with serological assays (ELISA; total $N = 444$) and real-time PCR (PUUV RNA detection; total $N = 187$). None of the tested individuals were PUUV-positive, so we can assume that PUUV spillover events are rare in these regions.

The influence of *Sorex* shrews is less clear. Our results indicate a significantly negative covariance structure between *Sorex* spp. and bank voles (Fig. 3a,b). This indicates that increasing *Sorex* spp. abundances are associated with decreasing bank vole abundances although we cannot draw any conclusion on the underlying causal mechanisms. In turn, there was no significant direct effect on host PUUV seroprevalence (Fig. 5a–c). While indirect effects via non-host biodiversity and host abundance were both negative in summer, the overall effect remained negligible. Only a few studies have investigated similar interactions. Khalil *et al.* (2016) found that for Fennoscandian populations, where *Apodemus* species are mostly absent, increasing abundances of common shrews (*Sorex araneus*) can decrease PUUV seroprevalence in bank voles, similar to the observed effect for *Apodemus* species in this study. It is speculated that this might be due to predation on bank vole offspring by *S. araneus* as demonstrated by (Liesenjohann *et al.* 2011), which is then countered by bank voles through reduced home ranges to guard offspring. This mechanism might still be present in our populations but is likely dwarfed by the effect of the ratio between *Apodemus* species and bank voles (Fig. 6). Ecke *et al.* (2017) were able to show that the proportion of bank voles within the small mammal community has a positive impact on PUUV prevalence, highlighting the importance of the community composition in relation to host species and dominant non-competent species.

In small mammal forest communities of central Europe, the effect of *Apodemus* spp. on PUUV circulation in bank voles has been studied, but with varying results. In Belgium, Tersago *et al.* (2011) found no relationship between the relative proportions of *Apodemus* spp. on PUUV seroprevalence in one part of the country, while it did have an effect in another part of the country (Tersago *et al.* 2008). Our results show a clear dilution effect in at least two regions in Germany based on the community composition rather than biodiversity *per se*. Rohr *et al.* (2020) highlighted that for some diseases a targeted approach in species management might outweigh the benefits of biodiversity management as a tool for disease control. Although the two main dominant species groups discussed here have overlapping ecological niches, *Apodemus* spp. are generally associated with less deteriorated habitat compared to the bank vole (Heyman *et al.* 2009). From this, it could be speculated that in highly managed forest habitats, less competition by *Apodemus* spp. might amplify mechanisms leading to higher PUUV seroprevalence (i.e. density dependence). In disturbed landscapes, communities of reduced biodiversity are mainly dominated by more generalist species (McFarlane *et al.* 2012), which are characterized by high densities and carry a higher proportion of zoonotic pathogens (Palma *et al.* 2012). In their review, Jones *et al.* (2013) concluded that the research on land use and farming practices is insufficient so far, and local interdisciplinary research is needed, that provides a locally relevant, holistic perspective on the wildlife/human interface. If indeed the ratio between the two main species groups in German forests is a key driver in PUUV dynamics, then implementing forest management practices aiming for a more balanced small mammal community structure could be part of an integrated approach to managing zoonoses. In Scandinavia, forest management practices have been identified as one of the dominant drivers of PUUV host prevalence (Magnusson *et al.* 2015). To derive meaningful recommendations, detailed knowledge of forest management intensity is required to link forest structure (tree density, age structure, species diversity) or practices (harvesting, reforestation) to small mammal community structure and associated zoonoses.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Seasonal abundances (combined live- and snap-trapping; as individuals per 100 trap nights) of *Puumala orthohantavirus* (PUUV) host (*Clethrionomys glareolus*), *Apodemus* spp. (*Apodemus agrarius*, *A. flavicollis*, *A. sylvaticus*) and *Sorex* spp. (*Sorex araneus*, *S. coronatus*, *S. minutus*) and seroprevalences (in %) of PUUV in *C. glareolus*

Table S2 Estimates (*z*-scaled) and their respective standard errors (Std. Error) *z* values and *P* values of all relations included in the external driver of bank vole abundances in years with generally high abundance (outbreak years) and years with generally low abundance (non-outbreak years)

Table S3 Estimates (*z*-scaled) and their respective standard errors (Std. Error) *z* values and *P* values of all relations included in the external driver of bank vole abundances und *Puumala orthohantavirus* (PUUV) seroprevalence (in outbreak years; Fig. 3 in the main manuscript). Numbers in bold indicate a significant relationship ($P < 0.05$) between response and predictor variable

Figure S1 Results from generalized additive mixed models to establish predicted probability (solid line) with 95% confidence interval (dashed line).

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