

Rodent Host Abundance and Climate Variability as Predictors of Tickborne Disease Risk 1 Year in Advance

Emil Tkadlec, Tomáš Václavík, Pavel Šíroký

Using long-term data on incidences of Lyme disease and tickborne encephalitis, we showed that the dynamics of both diseases in central Europe are predictable from rodent host densities and climate indices. Our approach offers a simple and effective tool to predict a tickborne disease risk 1 year in advance.

In Europe, the generalist tick *Ixodes ricinus* is the principal vector transmitting tickborne pathogens to humans. It has 3 blood-feeding stages, depending on small rodents, such as voles and mice, as the chief reservoir hosts for larval ticks (1). The development from larva to nymph is a key aspect in pathogen transmission because the exposure to pathogens is most likely to happen at this stage and therefore directly influences the density of infected nymphs (2). Vole population densities change dramatically over time in intervals of 3–5 years (3), known as population cycles (4). As a result, the chances for questing larvae to encounter a host are expected to vary considerably over time, along with vole population numbers. Investigations of direct relationships between abundance of ticks, disease incidence, and host populations are rare, usually targeting large mammals that provide a blood meal for female adult ticks (5). Little is known about the effect of rodent population dynamics on abundance of nymphal ticks (6), and studies of the direct effects on disease risk are even rarer (7,8).

We studied interannual variation in incidences of 2 tickborne diseases (TBDs), Lyme disease (LD) and tick-borne encephalitis (TBE). We aimed to determine if, as suggested by a previous work in North America (8), disease risk is related to rodent abundance during

the previous year. We also tested the hypothesis that population outbreaks in the common vole (*Microtus arvalis*), along with favorable weather conditions, increase survival of larval ticks and the abundance of nymphal ticks in the following year, thereby resulting in higher disease incidence.

The Study

We analyzed periods of 17–18 years to assess TBD incidences in 7 countries in central Europe (Figure 1; Appendix Figure 1, <https://wwwnc.cdc.gov/EID/article/25/9/19-0684-App1.pdf>). First, we computed the cross-correlations between disease incidences, vole densities from the Czech Republic, and climate variables to examine the degree of synchrony among their dynamics. Second, we applied autoregressive linear models of order 0–2 to test whether the predictive abilities of vole abundance in year $t - 1$ are supported by data (Appendix). Finally, we tested the influence of climate indices that are known to affect tick ecology (9). We used Akaike information criterion for small samples to compare models. The effect included in the model was considered to be strongly supported by data if the model Akaike information criterion was reduced by >2 . We obtained data on annual TBD incidences, vole abundance (autumn counts of burrow entrances per hectare), and climate variability (North Atlantic oscillation [NAO] indices) from public databases (Appendix).

LD incidences for 3 countries in central Europe fluctuated over time (Figure 2). Cross-correlation analysis revealed strong positive correlations between incidences in the Czech Republic in year t and vole densities in $t - 1$ and negative correlations between the annual NAO index in $t - 1$ (Appendix Figures 2–4). By fitting autoregressive linear models, we found strong evidence that vole abundance in year $t - 1$ and the annual NAO index in $t - 1$ are key to predicting LD incidences during year t in the Czech Republic (Table 1); the final model predicted observed incidence with reasonable accuracy (Appendix Figure 5). LD incidence increased with vole densities and decreased with the annual NAO index (Appendix Figure 6).

TBE incidence from 7 countries fluctuated greatly from year to year (Figure 2). Cross-correlations showed that TBE incidence was strongly positively correlated with

Author affiliations: Palacký University Olomouc, Olomouc, Czech Republic (E. Tkadlec, T. Václavík); Institute of Vertebrate Biology, Brno, Czech Republic (E. Tkadlec), UFZ–Helmholtz Centre for Environmental Research, Leipzig, Germany (T. Václavík); University of Veterinary and Pharmaceutical Sciences Brno, Brno (P. Šíroký); Central European Institute of Technology, Brno (P. Šíroký)

DOI: <https://doi.org/10.3201/eid2509.190684>



Figure 1. Countries in central Europe where Lyme disease and tickborne encephalitis incidence were analyzed relative to the common vole abundance from the Czech Republic and climate indices, 2000–2017, and where we found evidence for these external predictors. LD, Lyme disease; TBE, tickborne encephalitis.

vole density with a lag of 1 year for the Czech Republic, Germany, and Slovenia (Appendix Figure 7). A lag of 1 year for the effect of the annual NAO index was negatively correlated with TBE incidence in the Czech Republic and Germany, whereas a 2-year lag was positively correlated with TBE incidence in Germany and Austria (Appendix Figure 8). Autoregressive linear models showed that including vole abundance from year $t - 1$ improved fit for the Czech Republic, Germany, and Slovenia (Table 2). Adding the effect of the annual NAO index in $t - 1$ to the model improved the fit in the Czech Republic and Germany. The effect of the annual NAO index in $t - 2$ produced better predictive power for Austria. As a result, the best models for TBE incidence in all 4 countries (Czech Republic, Germany, Slovenia, and Austria) included both host abundance and climate effect. Incidence of both diseases fluctuated over time in close synchrony, as revealed for the Czech Republic (correlation coefficient 0.71) and Poland (correlation coefficient 0.70) (Appendix Figure 9).

Conclusions

For 4 of the 7 countries in Europe we studied, our results show support for the hypothesis that incidence of 2 TBDs should lag 1 year behind the rodent host density because of the beneficial effect on survival of *I. ricinus* larvae (10). Our results agree with evidence from North America that the number of *I. scapularis* nymphs can be predicted by small rodent density from the preceding year (7,8). In addition, acorn abundance was demonstrated to predict the nymph densities equally well 2 years ahead (7,8). Hence,

results from North America indicated a complete causal mechanism for variation in LD incidences over time, starting with abundant acorns in year $t - 2$, which increased the population of rodents in year $t - 1$. High rodent density then led to the increased number of nymphs in year t , resulting in a greater disease incidence in humans. Our data support this mechanism and suggest that the LD system in North America based on *I. scapularis* and that in Europe based on *I. ricinus* might be functionally quite similar, differing primarily in the species involved, and that this mechanism also applies to other tickborne diseases, such as TBE.

Unlike bank voles (*Myodes glareolus*) and *Apodemus* mice (2), the common vole occupying open farmland habitats has never been regarded as the chief host for *Ixodes* larvae in central Europe, though it is well-known as a competent host for pathogens and larval ticks (11,12). We suggest 2 explanations for the role of this rodent in disease transmission. First, common voles can be encountered frequently in forests or wetlands in peak years (13), when their densities often exceed 2,000 voles/hectare. Thus, the common vole can act as an amplifying host and contribute substantially to the whole population of suitable hosts for larval ticks. The voles' irruptive population dynamics can readily explain the upsurge in TBE disease prevalence observed in the Czech Republic in 2006, which occurred after a massive population outbreak of voles during 2004–2005 (14). Second, population fluctuations of most rodent species are spatially synchronized across large geographic areas (15). Therefore, common vole abundance is a correlative measure for bank voles or mice.

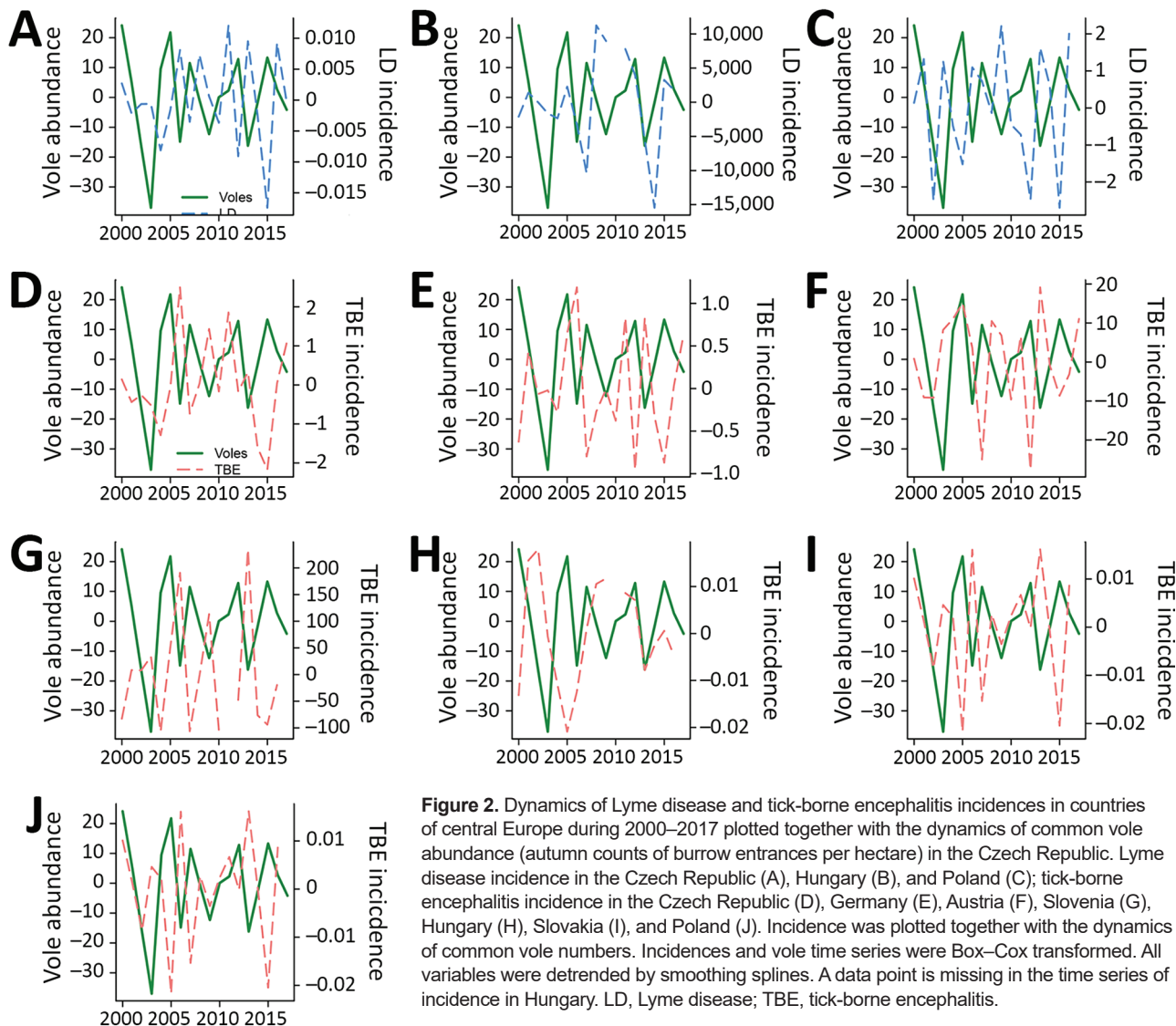


Figure 2. Dynamics of Lyme disease and tick-borne encephalitis incidences in countries of central Europe during 2000–2017 plotted together with the dynamics of common vole abundance (autumn counts of burrow entrances per hectare) in the Czech Republic. Lyme disease incidence in the Czech Republic (A), Hungary (B), and Poland (C); tick-borne encephalitis incidence in the Czech Republic (D), Germany (E), Austria (F), Slovenia (G), Hungary (H), Slovakia (I), and Poland (J). Incidence was plotted together with the dynamics of common vole numbers. Incidences and vole time series were Box–Cox transformed. All variables were detrended by smoothing splines. A data point is missing in the time series of incidence in Hungary. LD, Lyme disease; TBE, tick-borne encephalitis.

Our observation that the annual NAO index in $t - 1$ was able to improve model fit is in agreement with known tick ecology. A negative annual NAO index is generally associated with cold, snowy winters and moderate summers that are wetter, which can help larval ticks conserve body water and thus increase their survival to the nymphal stage (9). The positive effect of the annual NAO index in $t - 2$ might signify a generally warmer year that can be related to mast seeding of trees, triggering the growth of rodent populations.

Some countries in central Europe, such as the Czech Republic, Germany, and Poland, have built programs to monitor common vole densities. These data are stored in public electronic databases and thus can be used readily for predicting TBDs, using the methods we describe.

Acknowledgments

We thank Whalen W. Dillon and Monica A. Dorning for helpful comments that greatly improved the manuscript, the National Institute of Public Health for providing us with the data on TBD incidences, and the Central Institute for Supervising and Testing in Agriculture for the data on common vole abundance.

The work was supported by the Ministry of Health of the Czech Republic (grant no. AZV 16-33934A) and Palacký University Olomouc (grant no. IGA_PrF_2019_021).

Author contributions: E.T. and T.V. conceived the ideas; E.T. analyzed the data; and E.T., T.V., and P.Š. wrote the paper.

Table 1. Differences in AIC from the best model for Lyme disease incidences as modeled by AR linear models of order 0–2 with vole abundance and annual NAO index as external predictors, 3 countries in central Europe, 2000–2017*

Country and model structure	Order of AR model		
	0	1	2
Czech Republic			
Pure AR model	4.1	3.2	5.0
Voles _{t-1}	2.9	2.6	4.9
NAO annual index _{t-1}	2.8	3.2	3.7
Voles _{t-1} + NAO annual index _{t-1}	0.0	1.3	2.2
Hungary			
Pure AR model	0.0	3.2	4.6
Voles _{t-1}	0.0	2.1	5.6
NAO annual index _{t-1}	3.3	7.2	6.5
Voles _{t-1} + NAO annual index _{t-1}	4.1	7.0	12.0
Poland			
Pure AR model	0.4	0.0	1.6
Voles _{t-1}	3.1	3.5	4.8
NAO annual index _{t-2}	0.3	0.1	2.3
Voles _{t-1} + NAO annual index _{t-2}	3.9	4.5	6.5

*AIC, Akaike information criterion; AR, autoregressive; NAO, North Atlantic oscillation.

Table 2. Differences in AIC from the best model for tick-borne encephalitis as modeled by AR linear models of order 0–2 with vole abundance and annual NAO index as external predictors, 7 countries in central Europe, 2000–2017*

Country and model structure	Order of AR model		
	0	1	2
Czech Republic			
Pure AR model	4.5	7.4	10.6
Voles _{t-1}	2.8	6.0	10.1
NAO annual index _{t-1}	3.4	6.8	8.1
Voles _{t-1} + NAO annual index _{t-1}	0.0	3.5	7.5
Germany			
Pure AR model	6.0	7.2	9.2
Voles _{t-1}	3.6	6.4	10.1
NAO annual index _{t-1}	4.8	7.6	9.7
Voles _{t-1} + NAO annual index _{t-1}	0.0	3.8	7.1
Austria			
Pure AR model	5.3	6.5	9.1
Voles _{t-2}	5.8	7.3	9.3
NAO annual index _{t-2}	5.8	4.1	7.0
Voles _{t-2} + NAO annual index _{t-2}	0.0	3.5	5.7
Slovenia			
Pure AR model	3.8	5.2	5.7
Voles _{t-1}	0.2	3.3	5.8
NAO annual index _{t-1}	5.2	5.9	3.7
Voles _{t-1} + NAO annual index _{t-1}	0.0	3.2	4.2
Hungary			
Pure AR model	0.0	3.2	4.6
Voles _{t-2}	0.0	2.1	5.6
NAO annual index _{t-1}	3.3	7.2	6.5
Voles _{t-2} + NAO annual index _{t-1}	4.1	7.0	12.0
Slovakia			
Pure AR model	1.2	0.0	3.0
Voles _{t-1}	3.5	3.4	7.1
NAO annual index _{t-1}	3.3	1.3	3.0
Voles _{t-1} + NAO annual index _{t-1}	6.1	5.4	8.1
Poland			
Pure AR model	0.0	1.7	2.0
Voles _{t-1}	2.8	4.2	5.8
NAO annual index _{t-2}	2.3	4.2	6.3
Voles _{t-1} + NAO annual index _{t-2}	5.2	6.7	8.2

*AIC, Akaike information criterion; AR, autoregressive; NAO, North Atlantic oscillation.

About the Author

Dr. Tkadlec is a professor of ecology in the Department of Ecology and Environmental Sciences at Palacký University Olomouc, Czech Republic. His research interests include population ecology of vertebrates.

References

- Han BA, Schmidt JP, Bowden SE, Drake JM. Rodent reservoirs of future zoonotic diseases. *Proc Natl Acad Sci U S A*. 2015;112:7039–44. <http://dx.doi.org/10.1073/pnas.1501598112>
- van Duijvendijk G, Sprong H, Takken W. Multi-trophic interactions driving the transmission cycle of *Borrelia afzelii* between *Ixodes ricinus* and rodents: a review. *Parasit Vectors*. 2015;8:643. <http://dx.doi.org/10.1186/s13071-015-1257-8>
- Tkadlec E, Stenseth NC. A new geographical gradient in vole population dynamics. *Proc Biol Sci*. 2001;268:1547–52. <http://dx.doi.org/10.1098/rspb.2001.1694>
- Krebs CJ. Population fluctuations in rodents. Chicago: University of Chicago Press; 2013.
- Gilbert L, Maffey GL, Ramsay SL, Hester AJ. The effect of deer management on the abundance of *Ixodes ricinus* in Scotland. *Ecol Appl*. 2012;22:658–67. <http://dx.doi.org/10.1890/11-0458.1>
- Cayol C, Koskela E, Mappes T, Siukkola A, Kallio ER. Temporal dynamics of the tick *Ixodes ricinus* in northern Europe: epidemiological implications. *Parasit Vectors*. 2017;10:166. <http://dx.doi.org/10.1186/s13071-017-2112-x>
- Ostfeld RS, Schaubert EM, Canham CD, Keesing F, Jones CG, Wolff JO. Effects of acorn production and mouse abundance on abundance and *Borrelia burgdorferi* infection prevalence of nymphal *Ixodes scapularis* ticks. *Vector Borne Zoonotic Dis*. 2001;1:55–63. <http://dx.doi.org/10.1089/153036601750137688>
- Ostfeld RS, Levi T, Keesing F, Oggenfuss K, Canham CD. Tick-borne disease risk in a forest food web. *Ecology*. 2018;99:1562–73. <http://dx.doi.org/10.1002/ecy.2386>
- Sonenshine DE, Mather TN, editors. Ecological dynamics of tick-borne diseases. Oxford: Oxford University Press; 1994.
- Keesing F, Brunner J, Duerr S, Killilea M, Logiudice K, Schmidt K, et al. Hosts as ecological traps for the vector of Lyme disease. *Proc Biol Sci*. 2009;276:3911–9. <http://dx.doi.org/10.1098/rspb.2009.1159>
- Šumilo D, Bormane A, Asokliene L, Vasilenko V, Golovljova I, Avsic-Zupanc T, et al. Socio-economic factors in the differential upsurge of tick-borne encephalitis in Central and Eastern Europe. *Rev Med Virol*. 2008;18:81–95. <http://dx.doi.org/10.1002/rmv.566>
- Blaškovič D. The public health importance of tick-borne encephalitis in Europe. *Bull World Health Organ*. 1967;36(Suppl):5–13.
- Pelikan J. Stanoviště, sídliště a etologie. In: Kratochvíl J, Balát F, Folk Č, Grulich I, Havlín J, Holířová V, et al., editors. Hraňoš polní, *Microtus arvalis*. Prague: Nakladatelství ČSAV; 1959. p. 80–100.
- Daniel M, Kříž B, Danielová V, Beneš Č. Sudden increase in the tick-borne encephalitis cases in the Czech Republic, 2006. *Int J Med Microbiol*. 2008;298(S1):81–7. <http://dx.doi.org/10.1016/j.ijmm.2008.02.006>
- Carslake D, Cornulier T, Inchausti P, Bretagnolle V. Spatio-temporal covariation in abundance between the cyclic common vole *Microtus arvalis* and other small mammal prey species. *Ecography*. 2011;34:327–35. <http://dx.doi.org/10.1111/j.1600-0587.2010.06334.x>

Address for correspondence: Emil Tkadlec, Palacký University Olomouc, Department of Ecology and Environmental Sciences, Faculty of Science, Šlechtitelů 27, 783 71 Olomouc, Czech Republic; e-mail: emil.tkadlec@upol.cz

Rodent Host Abundance and Climate Variability as Predictors of Tickborne Disease Risk 1 Year in Advance

Appendix

Material and Methods

Tickborne disease data. Annual LD and TBE incidences in the Czech Republic between 2000 and 2017 were obtained from the Information System for Infectious Diseases (formerly Epidat) managed by the National Institute of Public Health. The data on annual incidences for the other six central European countries were obtained from the Global Infectious Diseases and Epidemiology Online Network (GIDEON, <https://www.gideononline.com/product-resources/?app>). As length of data is critical in time series analyses, we discarded time series shorter than 15 years. Consequently, we studied LD incidences for the Czech Republic, Slovakia and Poland, and the TBE incidences for the Czech Republic, Germany, Austria, Slovenia, Hungary, Slovakia and Poland (Figure 1, <https://wwwnc.cdc.gov/EID/article/25/9/19-0684-F1.htm>).

Vole data. Common vole abundances in the Czech Republic from 2000 to 2017 were obtained from the Central Institute for Supervising and Testing in Agriculture which estimates population densities twice a year during the spring (March–April) and autumn (October–November) by counting the number of active burrow entrances per hectare in crop fields. Active openings are indicated by the smooth margins of the entrances, fresh plants placed inside the burrow openings, fresh heaps of soil and/or fresh droppings. In each of the 77 districts, an administrative unit of on average 1000 km² in size, ≈10 sites are surveyed by counting burrow entrances while walking along four 100-m strips, each 2.5 m wide. The counts collected across a total area of 1000 m² are then multiplied by 10 to obtain the numbers per hectare. The indices for all districts were averaged to obtain the vole index for the whole country. We used the indices for autumn vole populations collected in fodder as a proxy for annual density estimates. Autumnal

densities exhibit much higher yearly variation than spring densities and are therefore commonly used in small rodent dynamics studies (1). This index of vole population density in the Czech Republic was used as a general predictor of disease incidences in all neighboring countries.

Climate data. We included two indices of large-scale climate variability, which are often more effective predictors of population behavior in animals than single weather variables (2). Specifically, we applied station-based Annual NAO index and station-based DJFM NAO index (also known as winter NAO index). Whereas the former simultaneously captures the effects of both temperature and precipitation throughout the year, the latter measures the prevailing character of winter, the harshest period of year for most organisms in the seasonal environment of central Europe. Because the annual NAO index outperformed the DJFM NAO index, we show results only for the former. The indices are available from <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>.

Statistical analysis. Most statistical tools for time series were specifically developed for description of time-varying processes. They assume constant mean and variance (stationarity). Though annually aggregated, the disease incidences are counts following Poisson distribution. Temporal trends in incidences are pervasive. Consequently, before performing time series analysis, we stabilized the variance of incidences and vole abundance by Box–Cox transformation (data transformation did not change the major results) with the transformation parameter lambda being also estimated from the data. Then we removed trends in all variables using smoothing splines (function `smooth.spline`), the common method used to smooth a volatile time series (Appendix Figure 1). The smoothness parameter is estimated directly from data using a generalized cross-validation method, preventing overfitting. We assessed the overall synchrony among dynamics by computing cross-correlations to get insight into the relationship between the incidences in different countries and external variables, such voles and climate variables. To account for the effect of serial autocorrelations among the adjacent incidence values, we applied autoregressive linear models of order 0 to 2 as implemented in R using the function `arima` (3) with vole abundances and climate variable as external predictors

$$X_t = a_0 + a_1X_{t-1} + a_2X_{t-2} + a_3V_{t-d} + a_4C_{t-d} + \varepsilon_t$$

where X_t are yearly disease incidences, a_0 is an intercept, a_1 to a_2 are autoregressive coefficients measuring the strength of dependence on the previous values, a_3 is a regression

coefficient measuring the strength of a vole effect, V_{t-d} is autumn Czech vole abundance in year $t - 1$ or $t - 2$, d is a delay of 1 to 2 years, a_4 is a regression coefficient measuring the strength of a climate effect, C_{t-d} is a climate variable in year $t - 1$ or $t - 2$, and ε_t is a Gaussian noise term quantifying the stochastic variation with a constant mean and variance. The delay $d = 2$ for vole abundances was chosen only for Austria and Hungary, i.e., that is countries with asynchronous incidence dynamics relative to the Czech ones. For climate variables, we were guided by cross-correlations. We avoided building models with more than one climate effect to maximize model parsimony. We used AIC_c for small samples to compare models. The effect included in the model was considered as strongly supported by data if the model AIC_c was reduced by more than 2 (4). Finally, we visualized vole and climate effects on disease incidences using generalized additive models which can accommodate nonlinearity in a relationship between two variables.

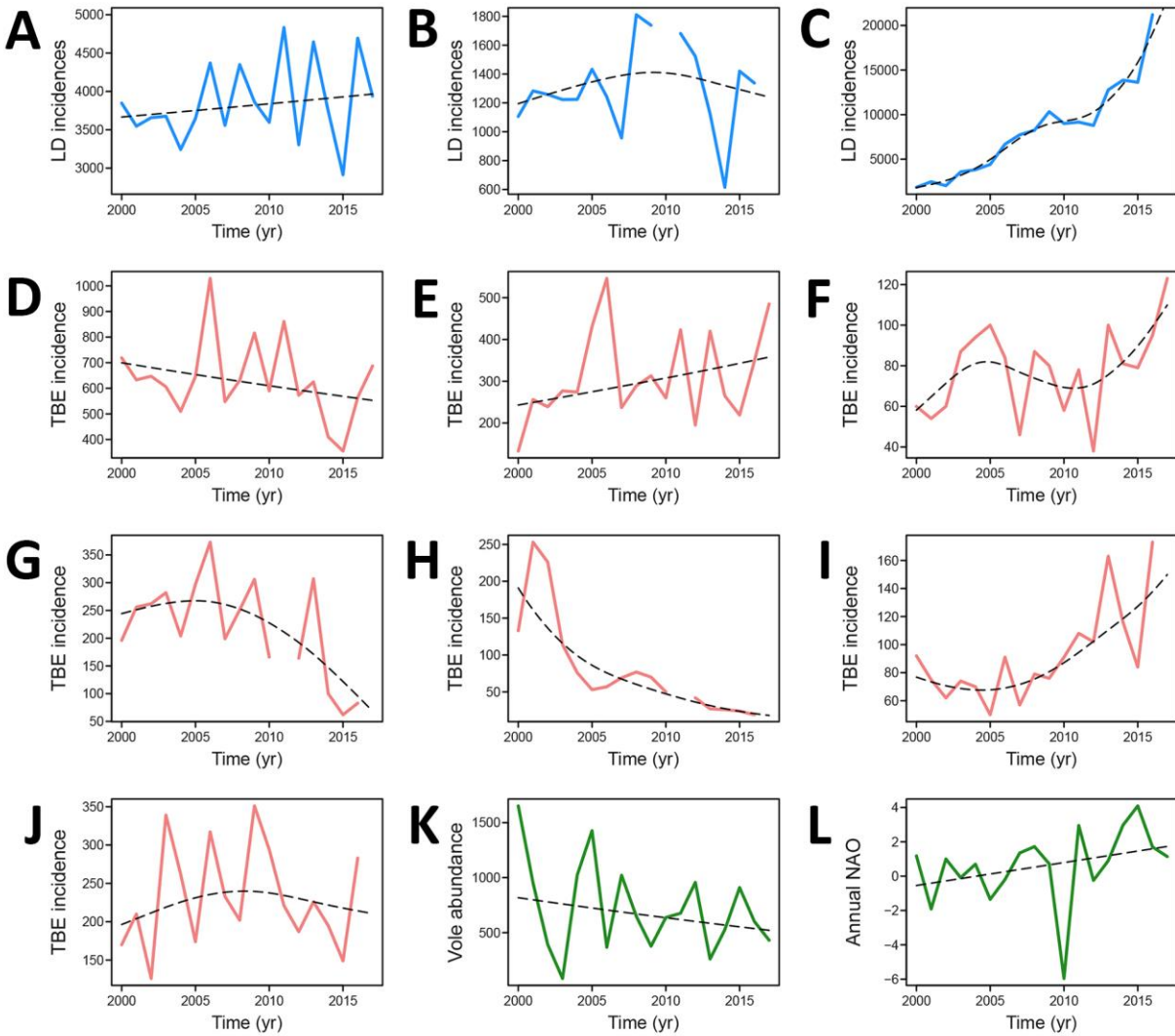
Results of time-series analysis. Cross-correlation analysis showed that Czech and Polish LD incidence dynamics were synchronous (Appendix Figure 2). A lag of 1 year was observed for the effect of vole densities on LD incidence in the Czech Republic while a lag of 2 years was indicated for Hungary (Appendix Figure 3). A 1-year lag was also identified for the annual NAO index in the Czech Republic, where it was negatively correlated with LD incidences, whereas no pattern or a lag of 2 years was observed for Hungary and Poland, respectively. In the Czech Republic, the negative annual NAO index is associated with a lower annual mean temperature and higher annual precipitation sum (Appendix Figure 4). By fitting autoregressive linear models of order 0–2, we found strong evidence that vole abundance in year $t - 1$ is key to predicting LD incidences during year t in the Czech Republic (Table 1). No effect of vole abundance was found for Hungary and Poland. Including the annual NAO index improved the model fit in the Czech Republic, with the final model predicting observed incidences with a reasonable accuracy (Appendix Figure 5). LD incidences increased with vole densities and decreased with annual NAO index (Appendix Figure 6).

TBE incidence dynamics were synchronous across countries, with the exception of Austria and Hungary (Appendix Figure 2). TBE incidences were strongly positively correlated with vole densities with a lag of 1 year for the Czech Republic, Germany and Slovenia (Appendix Figure 7). A 2-year lag was weakly indicated for Austria and Hungary. A lag of 1 year for the effect of annual NAO index was negatively correlated with TBE incidences in the Czech Republic and Germany, while a 2-year lag was positively correlated with TBE incidences

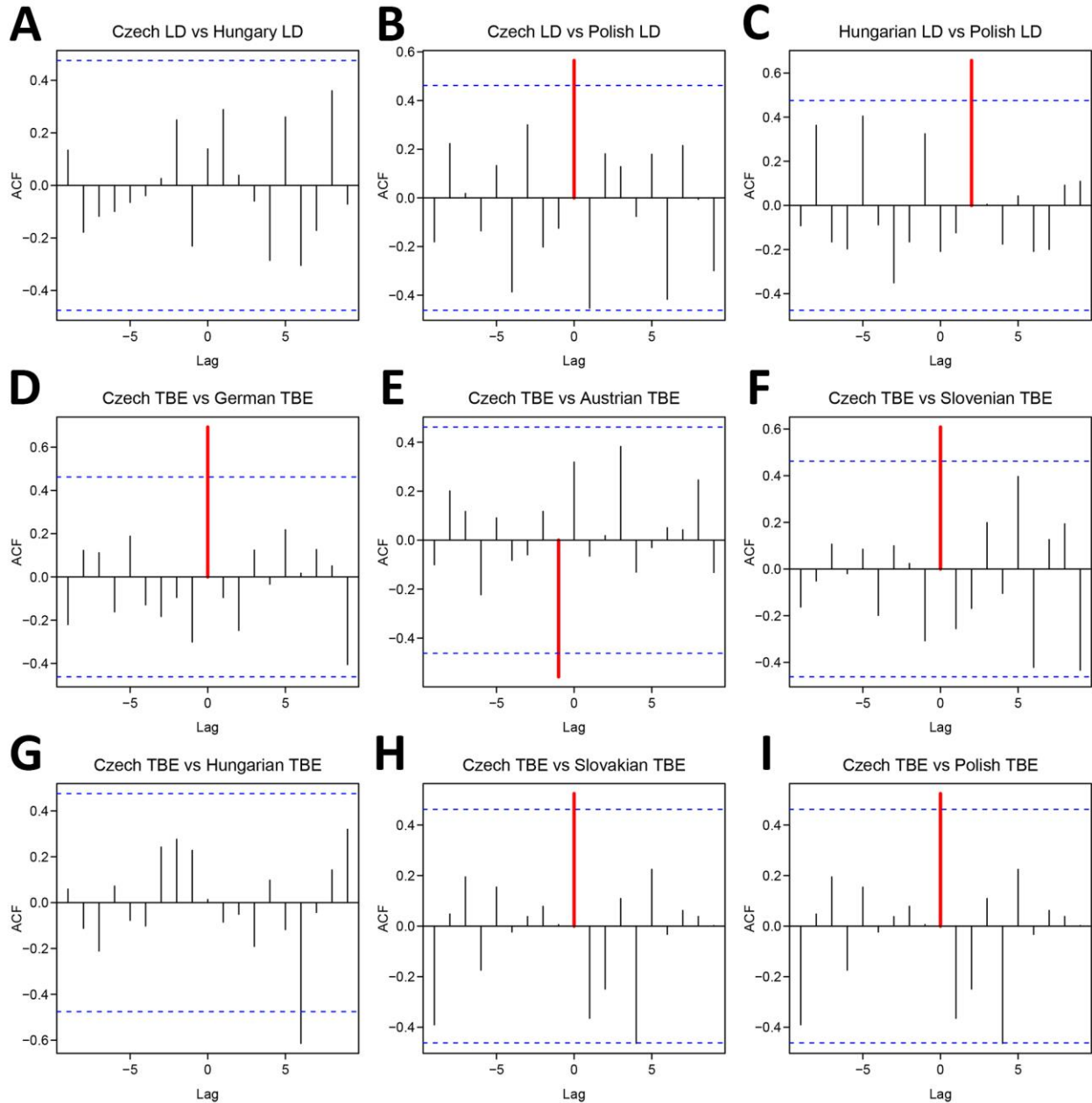
in Germany and Austria (Appendix Figure 8). Incidences of both diseases fluctuated over time in a great synchrony as revealed for the Czech Republic and Poland, with correlation coefficients of 0.71 and 0.70, respectively (Appendix Figure 9).

References

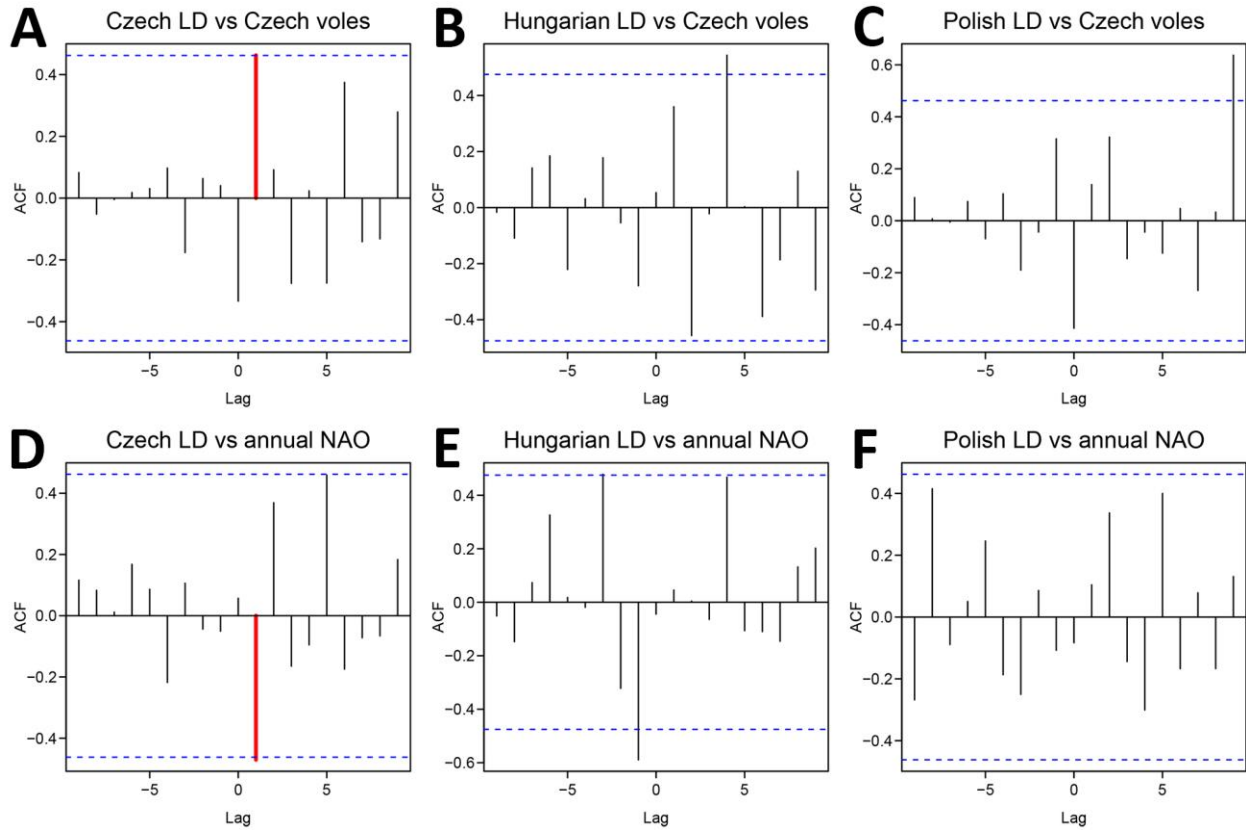
1. Tkadlec E, Stenseth NC. A new geographical gradient in vole population dynamics. *Proc Biol Sci.* 2001;268:1547–52. [PubMed http://dx.doi.org/10.1098/rspb.2001.1694](http://dx.doi.org/10.1098/rspb.2001.1694)
2. Stenseth NC, Mysterud A. Weather packages: finding the right scale and composition of climate in ecology. *J Anim Ecol.* 2005;74:1195–8. <http://dx.doi.org/10.1111/j.1365-2656.2005.01005.x>
3. R Core Team. *R: A language and environment for statistical computing.* Vienna: R Foundation for Statistical Computing; 2018.
4. Burnham KP, Anderson DR. *Model selection and multimodel inference: a practical information theoretic approach.* New York: Springer; 2002.



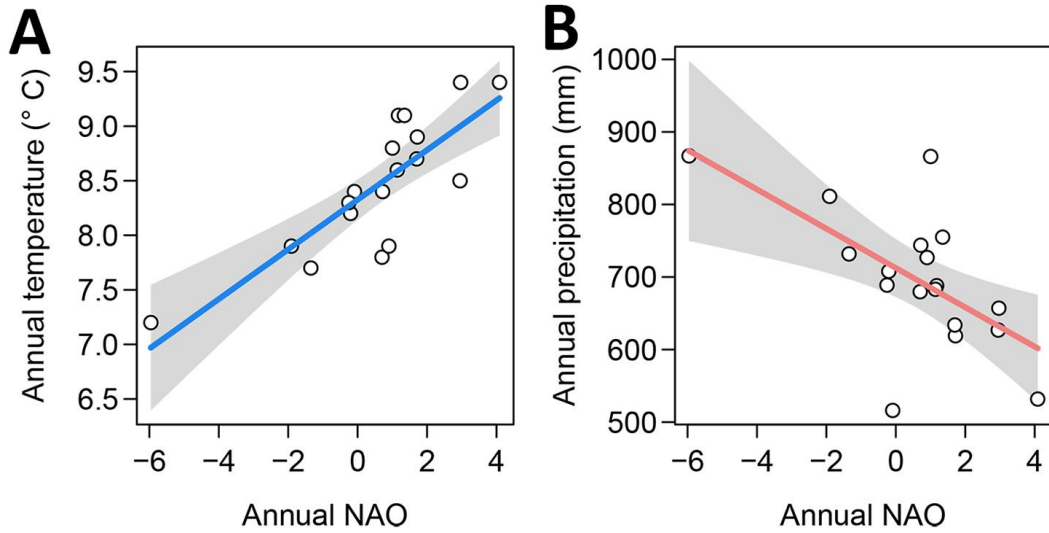
Appendix Figure 1. Trends in original time series (dashed line) of disease incidences (solid line), vole abundance and annual NAO index as modeled by smoothing splines (dashed line). The spar parameter controlling the degree of smoothness was set using a generalized cross-validation criterion. Lyme disease (LD) incidences (blue line) were available for the Czech Republic (A), Hungary (B) and Poland (C). Tickborne encephalitis (TBE) incidences (red line) were available for the Czech Republic (D), Germany (e), Austria (f), Slovenia (G), Hungary (H), Slovakia (I) and Poland (J). Lyme disease incidences in Poland exhibited a steep upward trend. Tickborne encephalitis incidences in Hungary exhibited a step downward trend. There is a missing data point in the Polish Lyme disease incidences and in the Slovenian and Hungarian tickborne encephalitis incidences.



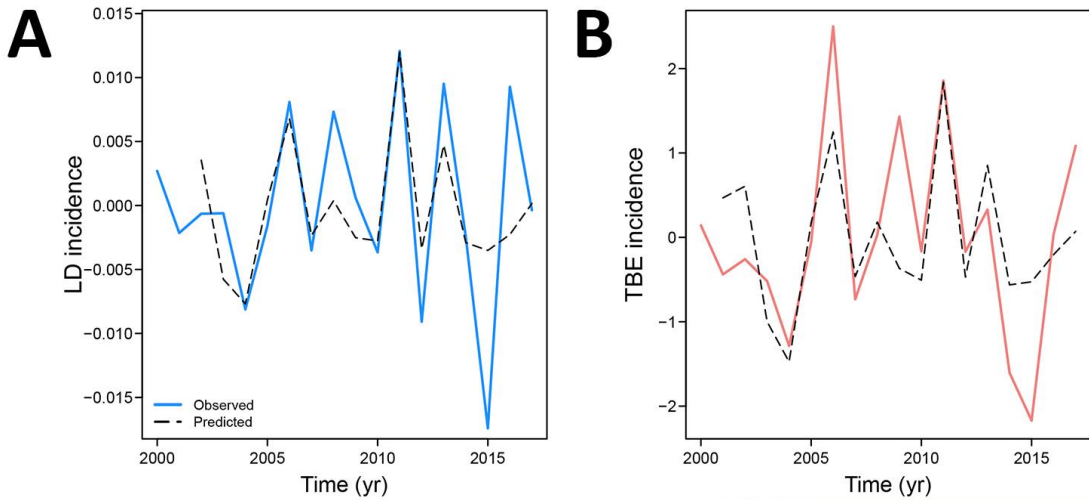
Appendix Figure 2. Cross-correlations showing the degree of temporal synchrony between the incidences from the Czech Republic and other European countries for Lyme disease (LD, A–C) and tickborne encephalitis (TBE, D–I). For Lyme disease, we found synchrony between Czech and Polish incidences. For tickborne encephalitis, Czech incidences fluctuated in synchrony with those from Germany, Slovenia, Slovakia and Poland. The dynamics of Austrian and Hungarian TBE incidences were asynchronous. The meaningful lags are in red.



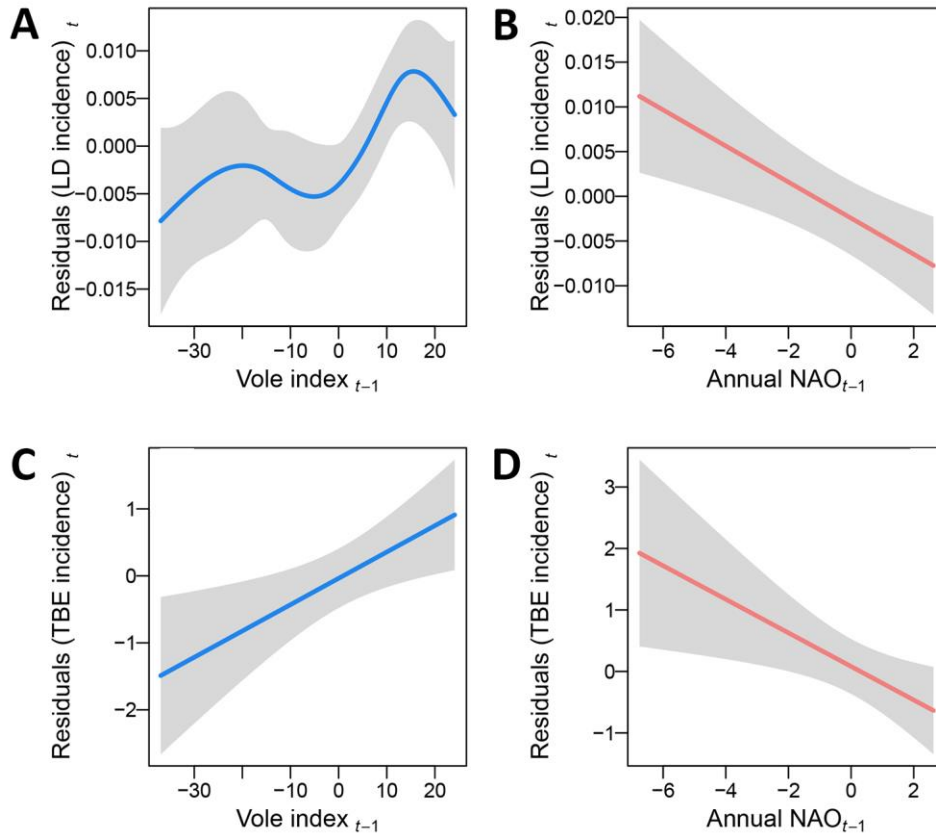
Appendix Figure 3. Cross-correlations between Lyme disease (LD) incidences and Czech voles (A–C) and between Lyme disease incidences and annual NAO index (D–F). The incidences lagged 1 year behind the vole densities in the Czech Republic whereas a lag of 2 years is indicated for Hungary and weakly for Poland. The incidences in the Czech Republic were either negatively correlated with the annual NAO index with a lag of 1 year or positively correlated with a lag of 2 years. A lag of 2 years weakly dominates in Poland. The meaningful lags are in red.



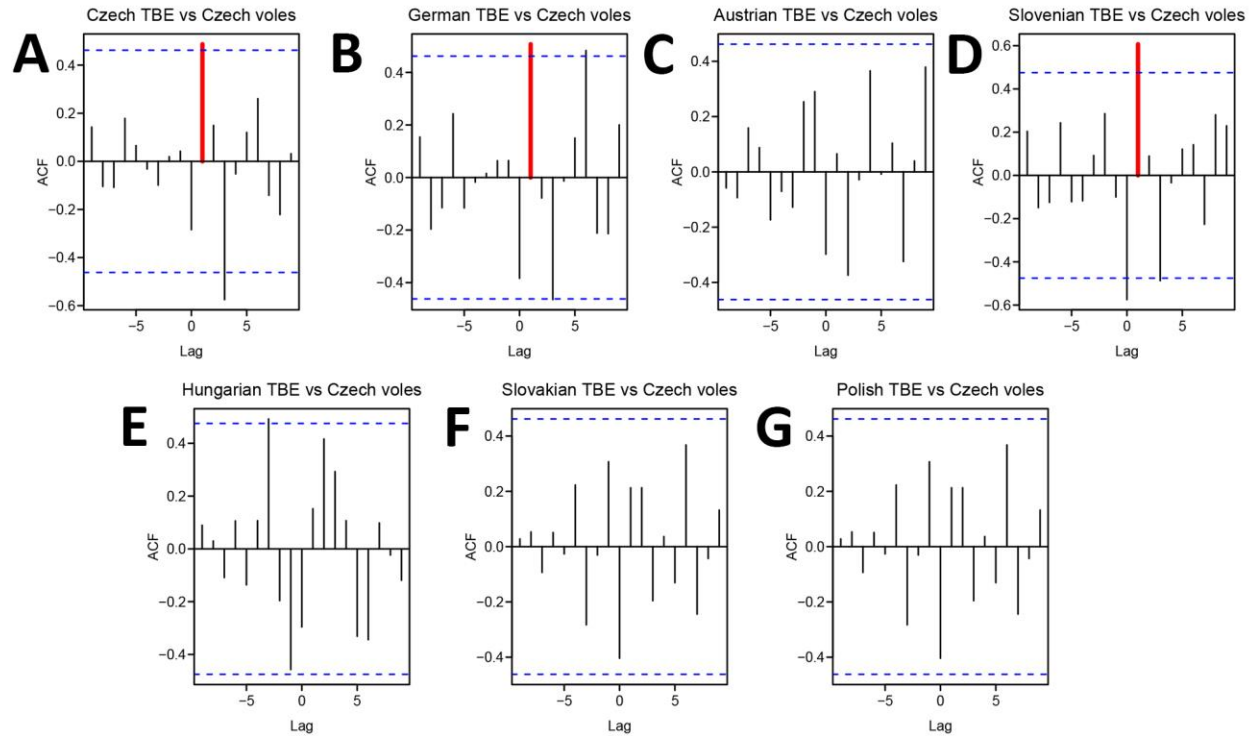
Appendix Figure 4. Annual NAO index in the Czech Republic is associated with a lower annual temperature mean (A) and higher annual sum of precipitation (B). The shaded areas indicated 95% confidence intervals.



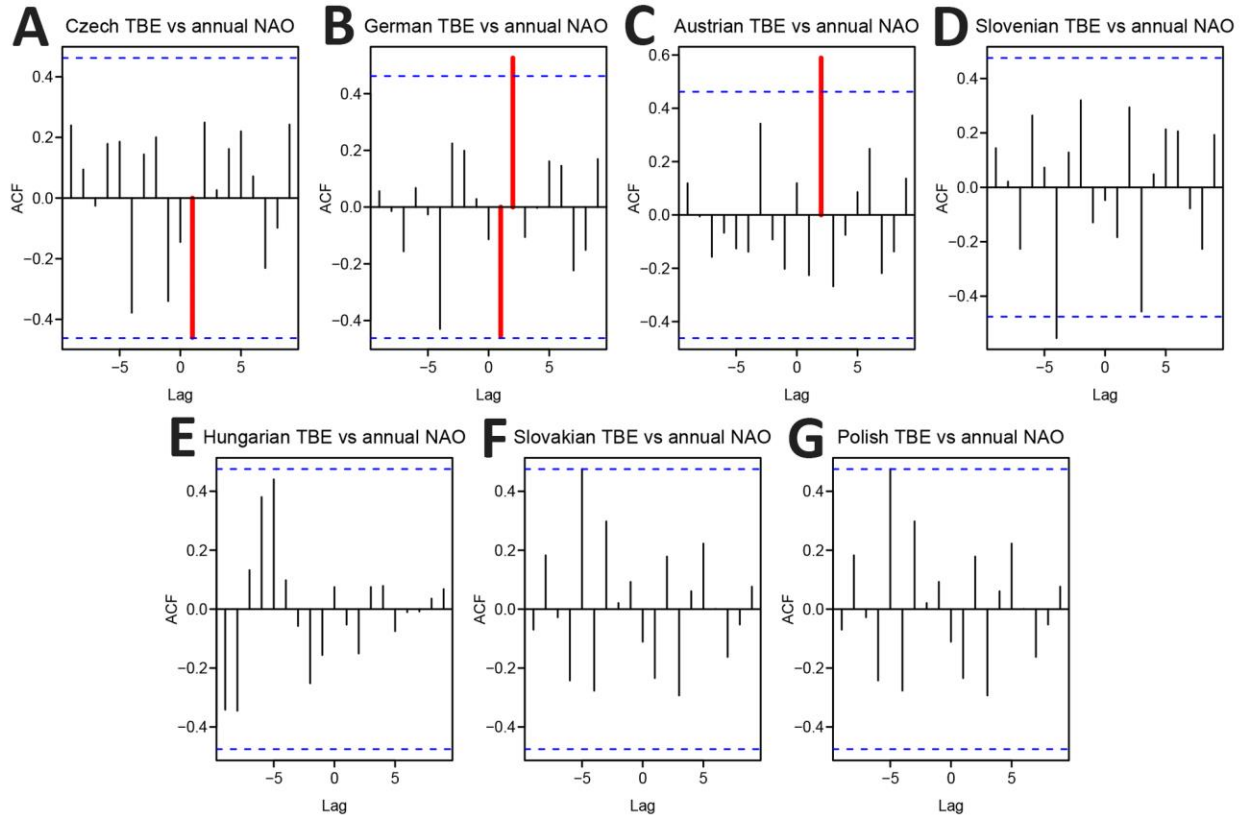
Appendix Figure 5. The observed (solid line) and predicted Lyme disease (LD) and tickborne encephalitis (TBE) incidences (dashed line) by best models with external predictors in the Czech Republic (A, B), Germany (C), Austria (D), and Slovenia (E). The fit is reasonably good even though the models are extremely simple containing just two predictors.



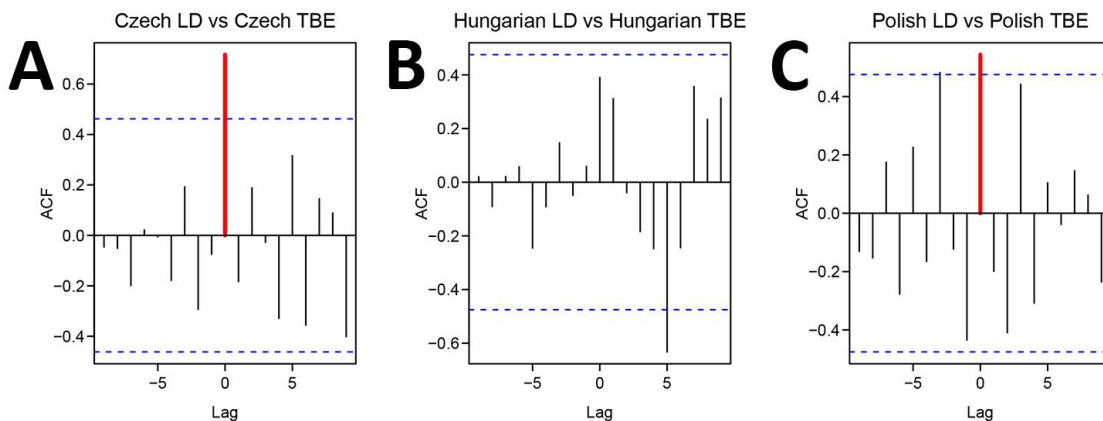
Appendix Figure 6. The effects of vole abundances (A, C) and annual NAO index (B, D) on Czech Lyme disease (LD) incidences (a, b) and Czech tickborne encephalitis (TBE) incidences (C, D) as visualized by generalized additive models (GAM) containing vole abundances and annual NAO index. GAM is a nonparametric regression which can accommodate nonlinearity in data. The y-axis shows the pure residual correlation after accounting for the variation caused by the second variable. The shaded areas show the 95% confidence intervals.



Appendix Figure 7. Cross-correlations between tickborne encephalitis (TBE) incidences from the Czech Republic (A), Germany (B), Austria (C), Slovenia (D), Hungary (E), Slovakia (F) and Poland (G) and Czech vole abundances. The dominant lag of 1 year is indicated in the Czech Republic (A), Germany (B) and Slovenia (C). A lag of 2 years is weakly indicated for Austria (C) and Hungary (E). In other countries, no clear pattern was observed. The meaningful lags are in red.



Appendix Figure 8. Cross-correlations between tickborne encephalitis (TBE) incidences from the Czech Republic (A), Germany (B), Austria (C), Slovenia (D), Hungary (E), Slovakia (F) and Poland (G) and annual NAO index. Time lag of 1 year is found for the Czech Republic (A), and Germany (B). A lag of 2 years strongly dominates in Germany (B), and Austria (C). The meaningful lags are in red.



Appendix Figure 9. Cross-correlations between incidences of Lyme disease (LD) and tickborne encephalitis (TBE) in the Czech Republic (A), Hungary (B) and Poland (C). No lag is found for the studied countries. The meaningful lags are in red.