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Research article

Biodiversity and pathogen dynamics in traditionally managed livestock systems

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ABSTRACT

The dynamics of generalist pathogens in complex host communities, such as those in grassland ecosystems, constitutes a frontier of knowledge in ecology and epidemiology. Globally, the increase in ruminant livestock has been associated with outbreaks of infectious diseases and a rise in the number of threatened species, leading to challenges for public health and biodiversity conservation by linking livestock, pathogens, and wildlife. However, the traditionally managed European grasslands and unfertilized open areas represent a kind of regenerative grazing characterized by high biodiversity and additional socio-ecological benefits, including enhanced ecosystem resilience and adaptive capacity.

With the aim to assess the relationship among traditional livestock grazing, biodiversity, and pathogen circulation, we analysed the mammal community biodiversity and interactions, as well as the pathogen exposure and indirect indicators of immune system activation in the selected indicator species wild boar (*Sus scrofa*) in a network of 18 study sites in the Iberian Peninsula. Our findings revealed that wild mammal richness and diversity were greater and antibody prevalences and multiple pathogen co-exposure in wild boar were lower in the presence of domestic ruminants. When grazing livestock is not present, an apparent amplification effect occurs.

Overall, the results suggest that traditional ruminant livestock grazing is associated with greater biodiversity and more balanced communities, as well as with improved indicators of ecosystem health, influencing pathogen transmission dynamics through potential replacement as less-susceptible hosts. These findings highlight the potential of traditionally managed livestock systems to support global health by enhancing biodiversity while mitigating disease risks. Such systems may reduce opportunities for pathogen spillover at the wildlife-livestock-human interface and contribute to more resilient socio-ecological landscapes.

1. - Introduction

Pathogens as components of ecological systems circulate within complex communities where interactions between vertebrates and their environment drive their persistence and spread (Dobson and Hudson, 1986; Tompkins et al., 2011). The structures formed by pathogens, host communities and their environment can be understood as episystems, that is, the set of biological, environmental, and epidemiological elements of infections on defined geographic and temporal scales (Tabachnick, 2010; Hassell et al., 2021). The dynamics of generalist pathogens in biodiverse episystems remains a major frontier for disease ecology and has significant management implications. Changes in land use and increasing human pressure on the natural environment impact on biodiversity and on the distribution, abundance and connectivity of

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vertebrates, as well as on the emergence, spread and persistence of pathogens, with consequences for both biodiversity conservation and health (Isbell et al., 2017; Schmeller et al., 2020; Shepon et al., 2023).

Globally, the increase in the number of domestic ruminant heads over time has been associated to increases in infectious disease outbreaks in wildlife and a higher number of threatened wild species (Morand, 2020), thereby linking livestock, pathogens and biodiversity. However, partially modified natural grazing areas are a source of resources for millions of people worldwide and contribute to ecological and social health and well-being (Godde et al., 2020). European traditionally managed unfertilized grasslands, shrublands and open forests with low profitability, constitute regenerative grazing areas characterised by high richness in animal and plant species (Envall et al., 2021). In Mediterranean drylands, livestock grazing might benefit biodiversity through the creation and maintenance of lentic waterbodies (Thiere et al., 2009), their role as ecosystem engineers avoiding woody encroachment (Derner et al., 2009), and direct resource competition with wild ungulates, avoiding overabundance (Chaikina and Ruckstuhl, 2006). Thus, ruminant grazing in Europe can have positive impacts both on biodiversity (Angerer et al., 2021), aligning with the European Biodiversity Strategy for 2030 (European Commission, 2020), and on human well-being (Godde et al., 2020).

These traditional livestock systems in Europe have co-evolved with the ecosystem. Therefore, they constitute complex socio-ecological systems that interconnect the factors determining ecosystem health with the socio-cultural determinants of well-being and human activity (Berkes, 2017; Manzano et al., 2021). Within these systems, management policies and decision-making determine how these connections are formed, and they must be adequately grounded in scientific evidence, local knowledge and best practices for the rational use of resources to provide highly resilient systems (Berkes, 2017).

However, although livestock grazing contributes to shape not only biodiversity but also host-pathogen dynamics in grasslands, the effects of ruminant livestock grazing on pathogen circulation remain poorly studied. Thus, investigations of host-community responses to disease may benefit from considering anthropogenic land uses including livestock grazing (Barrile et al., 2021). In grassland episystems a few key actors, such as ruminant livestock and wild ungulates, can significantly affect pathogen circulation with highly susceptible reservoir species driving disease dynamics in the episystem (Power and Mitchell, 2004; Tanner et al., 2019). This illustrates the crucial role of host-community structure in determining the dynamics of generalist pathogens (Dobson, 2004). Consequently, the control of shared infections often requires targeting several hosts or even managing the entire host community and its habitat, i.e., the episystem (Crispell et al., 2019).

Environmental and host-community assemblage determinants of vertebrate and ecosystem health have been seldomly investigated in the framework of extensive livestock grazing, in part due to the controversial expected effects over the health of the diverse array of vertebrate hosts in these complex episystems (Barroso et al., 2023; Barroso and Gortázar, 2024). Appropriate sentinel species for ecosystem health have rarely been widely identified either. However, in Iberian episystems, Eurasian wild boar (*Sus scrofa*), an abundant, widespread and easy to sample generalist species prone to develop antibodies against a broad range of circulating pathogens, has been recently suggested as a key indicator species of ecosystem health (Barroso et al., 2024). Similarly, there is no agreement on the pathogens or markers representing better indicators of episystem health (Barroso et al., 2023). Analysing host-community structure and diversity and screening for a broad range of pathogens and markers, measuring the proportion of co-exposures, should allow to overcome these barriers.

Further studies are needed to inform management policies that enhance ecosystem resilience while supporting the long-term viability of rural socio-ecological systems under a One Health framework. We assessed the interaction of ruminant livestock grazing, biodiversity, and dynamics of generalist pathogens, thereby addressing a major knowledge gap in ecology and epidemiology (Dobson, 2004). We hypothesize that ruminant livestock grazing could improve mammal diversity by limiting wild ungulate overabundance and, thereby, potentially reduce pathogen circulation.

2. - Methods

2.1. - Study areas

This study was conducted at 18 monitoring sites across the Iberian Peninsula, 15 in Spain and three in Portugal, that participated in a pilot network for integrated wildlife monitoring (Barroso et al., 2023). The sites were selected to represent the five bioregions recognized in the Wildlife Health Surveillance Plan of Spain: (1) Atlantic Spain; (2) Cereal plains; (3) Continental Mediterranean ecosystems; (4) Inland mountains (5) Southern and Eastern coast (Muñoz et al., 2010). Domestic ruminants (i.e., sheep, goats and/or cattle); were present in ten of the 18 locations (55.6%; Fig. 1a).

2.2. - Sample collection

Ten ml of blood were collected in additive-free tubes by puncturing the cavernous sinus (Arenas-Montes et al., 2013) from 1109 wild boar hunted-harvested between 2020 and 2024 in the 18 study sites (see Table S1 for sample size per site). The samples were centrifuged at 1500 g for 10 min to separate the serum, which was then stored at −20 °C until antibody detection and indirect health status marker testing.

2.3. - Health status assessment

The pathogens *Brucella* spp., *Salmonella* spp., *Coxiella burnetii*, *Erysipelothrix rhusiopathiae*, *Mycobacterium tuberculosis* complex (MTC), *Mycoplasma hyopneumoniae*, Aujeszky's disease virus (ADV), influenza virus (IV), porcine circovirus 2 (PCV2), canine distemper virus (CDV), hepatitis E virus (HEV), Crimean-Congo haemorrhagic fever virus (CCHFV), epizootic haemorrhagic disease virus (EHDV), and *Toxoplasma gondii* were selected for integrated monitoring to include zoonotic, livestock-relevant and wildlife-specific agents that reflect a broad spectrum of ecological interfaces (Zlotowski et al., 2009; Meng, 2010; Roest et al., 2011; Barasona et al., 2019; Ruiz-Fons et al., 2024). Wild boar was used as the sentinel species due to its wide distribution, ecological adaptability and frequent interactions with both domestic animals and humans, making it a key indicator of ecosystem health (Barroso et al., 2023, 2024). Table S1 lists the tests employed for antibody detection by enzyme-linked immunosorbent as the say (ELISA) of the pathogens analysed.

Three approaches were used as proxies of ecosystem health: pathogen co-exposure both at community and individual scale, and individual assessment of indirect non-specific health status markers. At the community scale (i.e., study site), we calculated a co-exposure degree index (*CEd*), considering the number of pathogens to which each wild boar individual was seropositive. To generate this *CEd*, the individual wild boars were classified as *degree 0* when no antibodies against any of the analysed pathogens where detected or antibodies were detected against a single pathogen; *degree 1* when antibodies against two to three pathogens were detected; *degree 2* when antibodies against four to six pathogens were detected; and *degree 3* when antibodies against seven or more pathogens were detected. The co-exposure degree of a study site was calculated using the following formula:

$$CEd\ (\%) = \frac{G1 + 2G2 + 3G3}{3} \times 100$$

where "*G1*", "*G2*" and "*G3*" correspond to the proportion at study site of wild boar classified as degree 1, 2 or 3 individuals, respectively. This co-exposure degree index was therefore a weighted indicator for each study

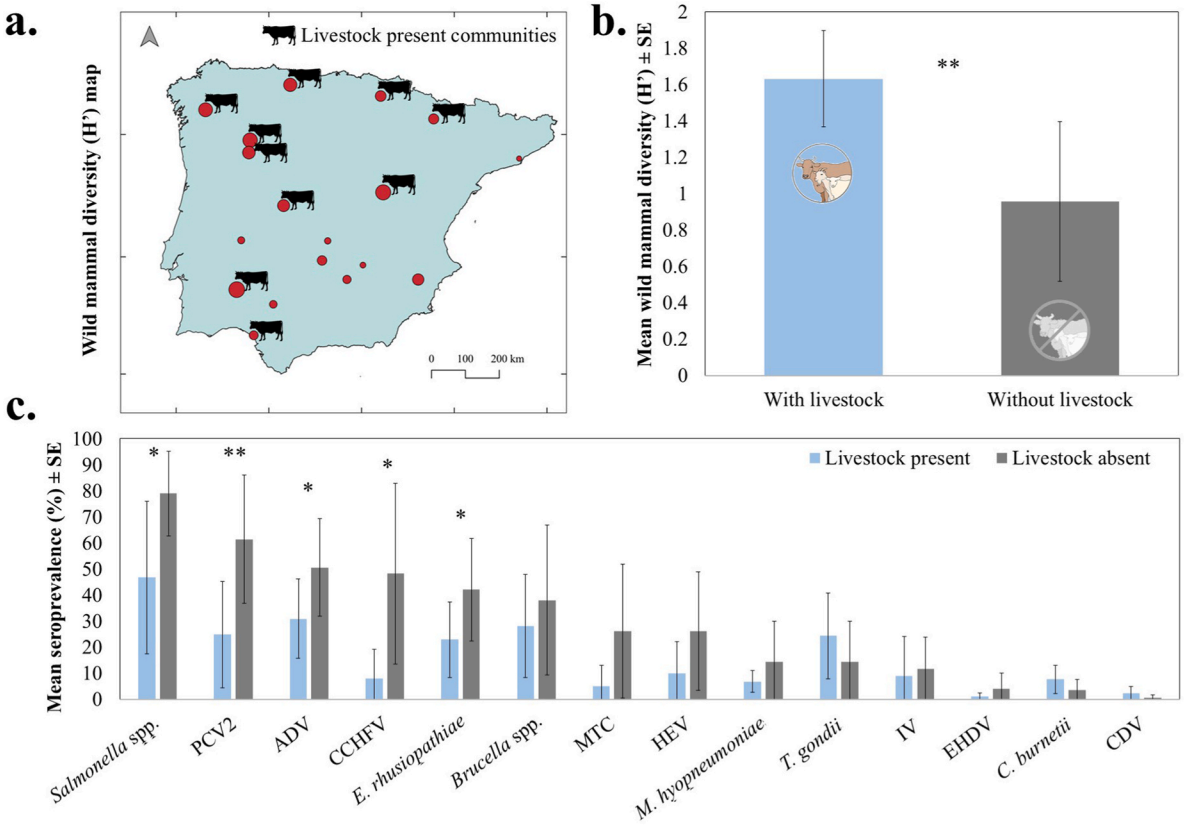

Fig. 1. Spatial distribution of study sites **(a)**: the circle size represents the wild mammal diversity (H′) and the cattle figures represents livestock presence. Comparison of mammal diversity **(b)** and pathogen seroprevalence in wild boar **(c)** between communities with and without livestock. PCV2 - porcine circovirus type 2; ADV - Aujeszky disease virus; CCHFV - Crimea-Congo haemorrhagic fever virus; MTC - *Mycobacterium tuberculosis* complex; HEV - hepatitis E virus; IV - influenza virus; EHDV - epizootic haemorrhagic disease virus; CDV - canine distemper virus. Data in the bar chart is represented as mean ± SE. Significance: *$p < 0.05$ and **$p < 0.01$.

site conceived as a community-level indicator of cumulative multi-pathogen exposure in a sentinel wildlife species rather than a measure of pathogen transmission or immunological burden. This approach allows accounting for the overall pathogen exposure pressure experienced by wild boar populations across study sites.

The individual pathogen co-exposure rate was calculated as the percentage of tested pathogens for which antibodies were detected in each wild boar. It provides a standardized measure of pathogen richness, the proportion of pathogens to which an individual has been exposed. It was calculated as follows:

$$Individual\ co-exposure\ rate = \frac{number\ of\ pathogens\ with\ detected\ antibodies\ in\ an\ individual}{total\ number\ of\ pathogens\ analyzed\ in\ that\ individual} \times 100$$

As an indirect marker of the health status of ecosystems, the serum concentrations of a marker of inflammatory response (adenosine deaminase -ADA-) was determined in the wild boar sera. The measurements were run in an automated analyser (Olympus AU 600, Beckman Coulter) following previously established protocols (Contreras-Aguilar et al., 2020). The assay was specifically validated for the indicator species included in this study, with inter- and intra-assay variation coefficients below 15% and demonstrated linearity across serial dilutions in saline solution.

2.4. - Mammal community monitoring

At each study site, a random grid of unbaited camera traps (average 18 camera traps per site, range 11–30; model Browning Strike Force HD ProX 1080, Browning Arms Company, Morgan, Utah, USA) was deployed annually for approximately two months between October and May, during the period 2020 to 2024. The camera traps were positioned facing north, approximately 40 cm above the ground, and angled to be parallel to the ground. The camera traps were set to operate 24 h a day, capturing eight consecutive photos per activation (rapid fire) with a minimum triggering interval of 1 s between activations. The images from cameras that were operational for less than five days due to technical issues were excluded from the analyses. The survey effort was then standardized to 450 camera-days per site. Species detections spaced more than 2 min apart were considered as independent encounters. Standardized encounters per survey efforts (number of cameras and days) constitute a reliable relative abundance parameter (Wearn and Glover-Kapfer, 2017).

The 18 ecological communities were classified according to livestock presence. Sites with a mean relative abundance less than 0.03 for domestic ruminants were considered livestock-free. In this study, all the areas with livestock consisted of free-ranging grazing systems with low to medium stocking densities. The status of each study site regarding presence or absence of livestock is also reported in Fig. 1a and Table S1.

To obtain relative estimates of mammal diversity, the data from the camera trap grids were used to list mammal species (overall richness and wild mammal richness) and to calculate the Shannon diversity index (H′) for mammals. These measures were based on the presence/absence data and encounters per camera trap for each species, respectively, by using the *ggvegan* package of v. 4.4.1 of R. Shannon diversity index (H') was performed using data from years 2022 to 2023.

2.5. - Ecological networks

We defined spatio-temporal coincidences as the detection of pairs of species by the same camera trap within a 24-h time window, based on the environmental survival of the targeted pathogens (Kukielka et al., 2013; Niedballa et al., 2019). Using these data, 18 static networks, one per site, were constructed using the R package *igraph*. In the ecological network analyses, nodes represented species while links corresponded to the frequency of pairs of species recorded by the same camera within 24 h at each site. The weight of each link was calculated as the number of co-occurrences of the two species per site, divided by the sum of the total number of encounters of each species individually at each study site. This correction was applied to account for differences in species abundance, allowing for the identification of true co-occurrences rather than connections driven simply by the higher abundance of some species. Node and network level centrality measures were calculated for all study sites using the R package *igraph* v. 4.4.1 (Martínez-López et al., 2009). Ecological networks were performed using data from years 2022 to 2023.

2.6. - Pathogen networks

In the pathogen network analyses, nodes represented pathogens, while links corresponded to the number of wild boar co-exposed to each pair of pathogens per study site. The weight of each link was calculated by dividing the number of co-exposed wild boar by the sum of the number of wild boar positive for each individual pathogen at each study site. This correction was applied to minimize the influence of seroprevalence differences and to better reflect true co-exposure patterns rather than connections driven solely by the high prevalence of individual pathogens within the communities. Pathogen strength and network level centrality measures were calculated for all study sites using the R package *igraph* v. 4.4.1 (Martínez-López et al., 2009).

2.7. - statistical analysis

Bivariate analyses were conducted to explore the relationships between biodiversity metrics, pathogen seroprevalences, ADA concentrations, and network measures for both pathogen and ecological networks, considering the presence or absence of livestock as independent variable. The differences among the study site groups defined by livestock presence were assessed using Wilcoxon rank-sum tests in R (Tables S1, S2 and S3).

Two generalized linear mixed models (GLMMs) were developed to assess the combined effect of livestock presence and biodiversity on the health status of communities. The first model included the direct health indicator (individual co-exposure rate) as response variable, while in the second model the indirect health indicator ADA was selected as response variable, due to its recognized role as a biomarker of immune activation and physiological stress in suids (Tecles et al., 2018; Cerón et al., 2022). The explanatory variables for both models were wild mammal richness, livestock presence (yes/no), their interaction, and latitude. Study site was included as random effect in both models. Latitude was incorporated as a covariate to account for potential geographic variation, since communities with and without livestock were unevenly distributed along the north–south gradient of the study area (Fig. 1a). Collinearity among predictor variables was assessed through the variance inflation factor (VIF) using the *car* R package. The statistical significance was set at $p < 0.05$. Model selection was carried out based on the corrected Akaike Information Criterion (AICc) using the *MuMIn* R package (see Tables S8 and S9 for model selection). All models were performed with the *lme4* package in R software v. 4.4.1.

3. - results

3.1. - Biodiversity

Diversity rates and species richness by study site are shown in Table S2. Wild mammal diversity (Shannon index) was significantly higher in sites with livestock ($W = 4$; $p = 0.001$; Fig. 1a and b; Table S2).

3.2. - Disease markers

The mean serum concentration of ADA is shown in Table S5. The values did not significantly differ between sites with and without livestock in the bivariate analysis. However, ADA was retained as a significant factor by the GLMM (see 3.5. "Livestock as a modulator of the relationship between biodiversity and disease"; Fig. 4b; Table 2).

Table S1 displays the seroprevalence rates for each pathogen, co-exposure rates and sample size by study site. A significantly higher seroprevalence of PCV2 ($W = 69$; $p < 0.01$), ADV ($W = 65$; $p = 0.03$), CCHFV ($W = 65$; $p = 0.03$), *E. rusiopathiae* ($W = 63$; $p = 0.04$) and *Salmonella* spp. ($W = 64$; $p = 0.03$) was observed in communities without ruminant livestock compared to communities with livestock (Fig. 1c; Table S1). Furthermore, the percentage of wild boar co-exposed to multiple pathogens ($W = 71$, $p < 0.01$) and the co-exposure degree ($W = 71$, $p < 0.01$) were also higher in the communities without livestock (Table S1).

3.3. - Ecological networks

The ecological networks from each study site are shown in Fig. 2. The network metrics and node centrality measures are compiled in Table S3 (doi: https://doi.org/10.5281/zenodo.15881912). Overall, red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), lagomorphs, wild boar and red fox (*Vulpes vulpes*) were the most connected species, i.e., the species with the highest centrality measures. Significant differences in centrality measures were observed between sites with and without livestock. Red deer strength was significantly higher ($W = 41$, $p = 0.03$) in communities without livestock, while roe deer strength ($W = 0$, $p < 0.01$) and degree ($W = 3$, $p = 0.03$) significantly differed between both community types (Table S4). In all the cases, these generalist species tended to be less connected in sites with livestock.

As for network measures, there were no statistically significant differences depending on the presence of livestock.

3.4. - Pathogen co-occurrence networks

Fig. 3 shows the pathogen co-occurrence networks and Table S6 (doi: https://doi.org/10.5281/zenodo.15881912) summarizes the network and node centrality measures. The pathogen networks from sites without livestock had significantly higher density, clustering coefficient and mean pathogen strength compared to those from sites with livestock ($W = 68$ $p = 0.01$; $W = 72$ $p < 0.01$; and $W = 5954.5$ $p < 0.01$). Statistically significant differences were observed between communities with and without livestock in the co-occurrence of the following pathogens with others (i.e., higher pathogen strength in livestock absent communities): PCV2 ($W = 56.5$; $p = 0.05$), *Brucella* spp. ($W = 62$; $p = 0.05$), ADV ($W = 61.5$; $p = 0.05$), HEV ($W = 27$; $p = 0.03$), EHDV ($W = 16$; $p = 0.03$), CCHFV ($W = 28$; $p = 0.02$) and MTC ($W = 19.5$; $p = 0.03$; Table S7).

3.5. - Livestock as a modulator of the relationship between biodiversity and pathogens

In episystems without livestock, increasing wild mammal species richness was associated with higher mean individual co-exposure rate, suggesting an epidemiological pattern consistent with an apparent amplification effect. However, in systems with livestock there was no

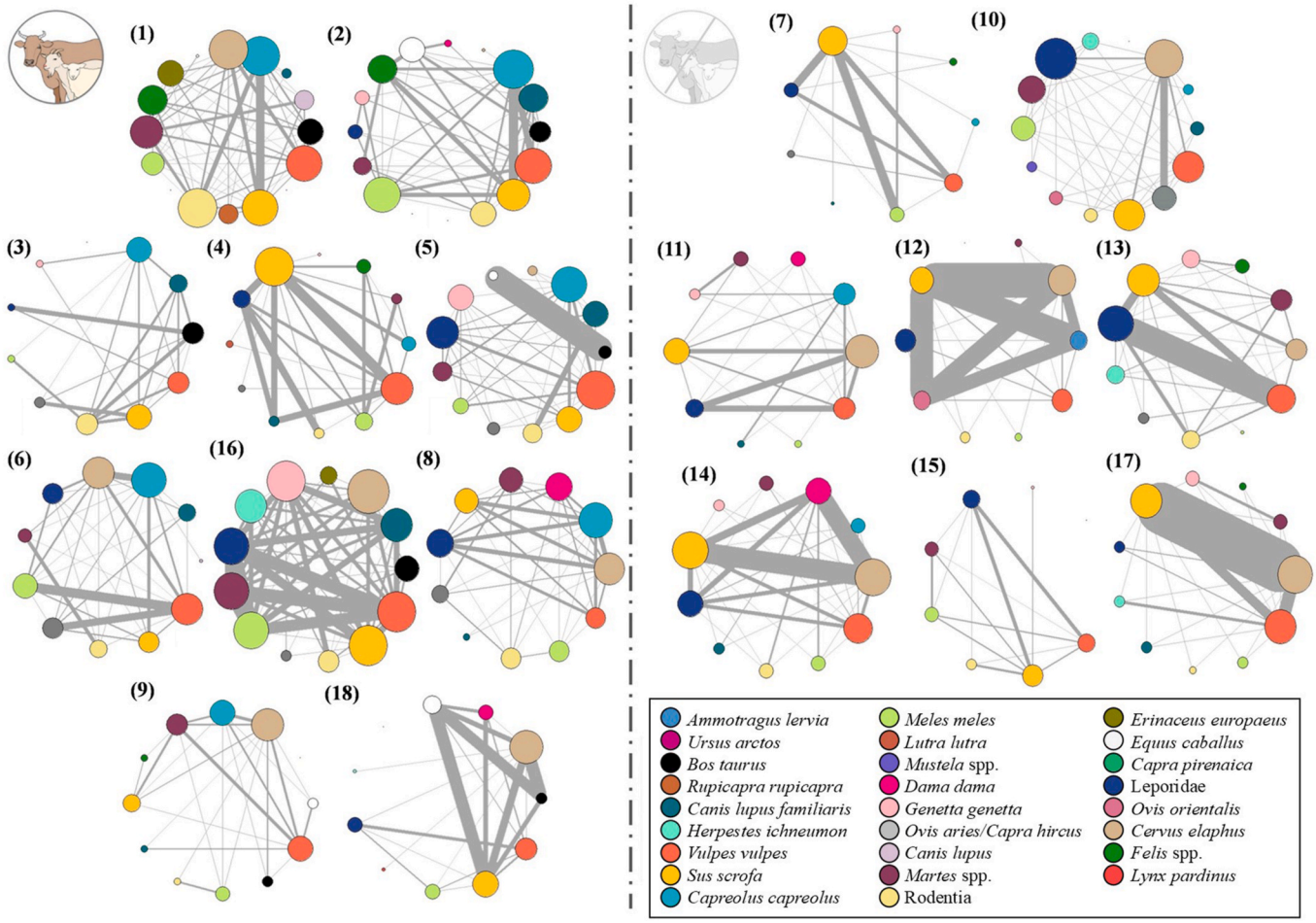

Fig. 2. Ecological networks of study sites with (left panel) and without livestock (right panel). Nodes represent species and edges represent spatial coincidences recorded by camera traps. The size of the nodes represents the degree, and the width of the edges represents the number of spatial coincidences between nodes.

such effect, suggesting that livestock could influence wildlife-pathogen dynamics (Fig. 4a; Table S8). Additionally, we identified a significant south-north latitudinal gradient, with pathogen richness declining at higher latitudes (Table 1). Wild boar serum ADA concentrations were not influenced by the interplay between wildlife diversity and livestock, but solely by livestock presence (Table 2; Fig. 4b; Table S9). The wild boars living in sympatry with livestock had lower ADA concentrations.

4. - Discussion

This study offers new insights into how the presence of ruminant livestock, community composition and diversity, and interaction patterns influence the circulation of shared pathogens and the consequent increase in the immune system response and inflammation. Our findings show the multifaceted impact of livestock grazing on wildlife and pathogen communities, affecting ecological interactions, pathogen exposure rates and physiological responses. This highlights the necessity and advantage of developing community-based wildlife health indicators, which can help to identify areas and species of high risk and inform management strategies.

Livestock grazing and wildlife abundance drive host-pathogen dynamics (Barrile et al., 2021). The increase in the individual co-exposure rate of wild boars with higher mammal species richness in the sites without livestock (Fig. 4a) could fit with an increased disease risk under increased species diversity conditions, known as an amplification effect of biodiversity (Dobson, 2004; Keesing et al., 2006). However, our results derive from an observational design, hindering the confirmation of a likely amplification effect. In the Iberian Peninsula, wild ungulate overabundance is a consequence of rural abandonment and could favour pathogen maintenance and spread (Gortázar et al., 2006; Barroso and Gortázar, 2024).

However, the presence of domestic ruminants seemed to influence such correlation between pathogen circulation and biodiversity (Fig. 4a), increasing biodiversity (Fig. 1b) and reducing pathogen prevalence (Fig. 1a) and pathogen co-occurrence (Fig. 3, Table 1). Livestock presence reduced the connectivity of central generalist host species (Fig. 2), suggesting a potential disruption in their interactions with other species. This in turn would have effects on pathogen circulation (Fig. 3). Such lower connectivity and epidemiological relevance could be explained by competition for resources and space (Young et al., 2005; Chaikina and Ruckstuhl, 2006; Gordon, 2018) and would promote biodiversity (Barroso et al., 2023). While higher stocking rates in livestock farming lead to the loss of favourable conditions for some mammal species (Ripple et al., 2015), low-density, grazing-based livestock systems tend to have less noticeable or even positive impacts on certain taxa (Evans et al., 2015), agreeing with the higher diversity of mammal species in the study sites with livestock in our study (Fig. 1a and b).

Wild ungulates can act as reservoirs of shared and zoonotic pathogens (Woolhouse and Gowtage-Sequeria, 2005). Through competition, domestic ruminants could reduce the abundance of susceptible hosts below the minimum required density and connectedness among hosts necessary to uphold transmission (Kermack and McKendrick, 1927; Black, 1966). However, our results may also reflect changes in community competence beyond a simple reduction in host density. For example, Johnson et al. (2013) demonstrated for trematode infection in amphibians that increasing host diversity can lead to a predictable

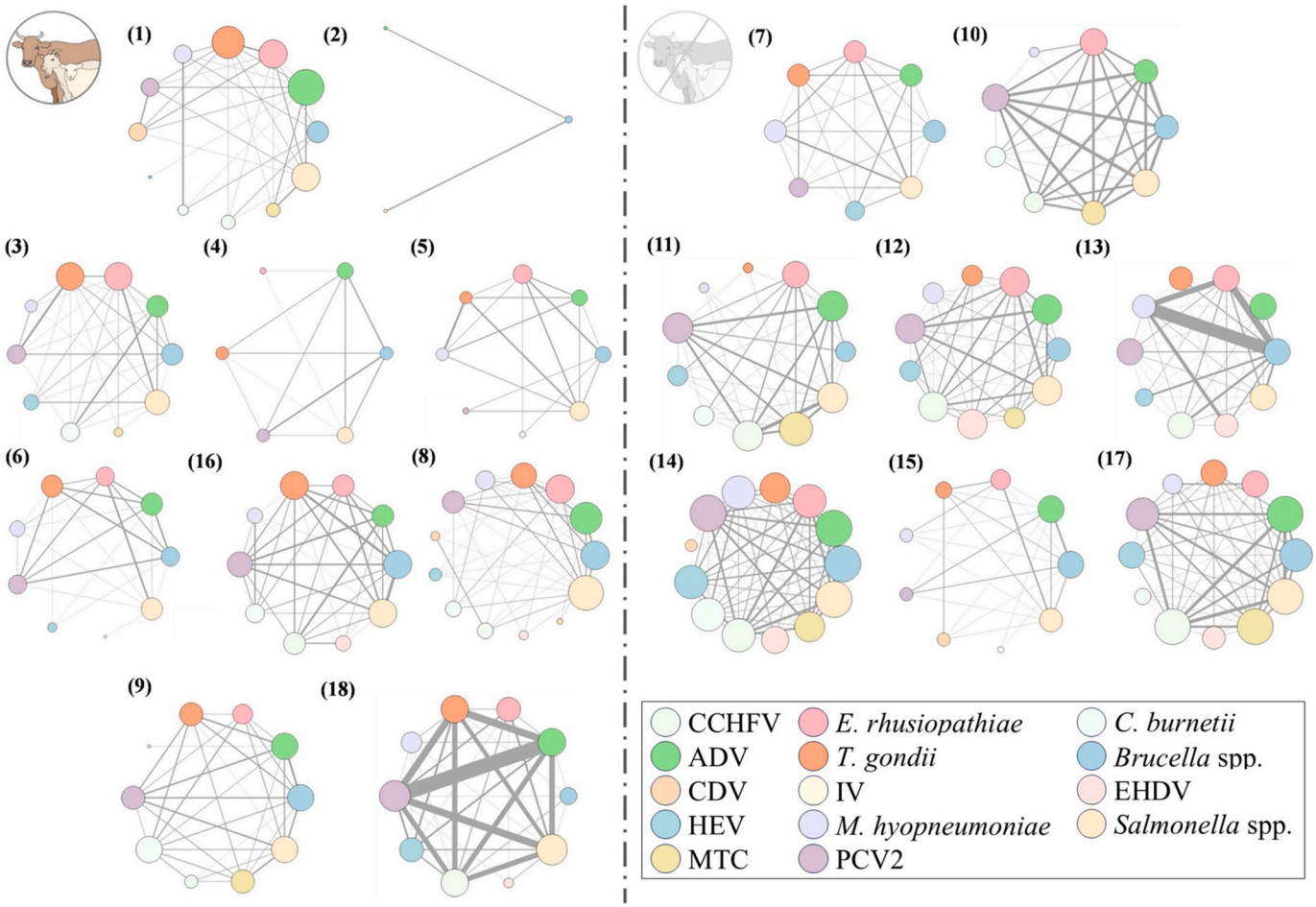

Fig. 3. Pathogen co-exposure networks of study sites with (left panel) and without livestock (right panel), derived from individual serological data. Nodes represent pathogens and edges represent individual co-exposure rates. Node size represents their degree (multiplied by 4-four for representation) and the width of the edges represents the number of individuals showing each co-exposure (multiplied by 25 for representation). ADV - Aujeszky disease virus; CCHFV - Crimea-Congo haemorrhagic fever virus; CDV - canine distemper virus; EHDV - epizootic haemorrhagic disease virus; HEV - hepatitis E virus; IV - influenza virus; MTC - *Mycobacterium tuberculosis* complex; PCV2 - porcine circovirus type 2.

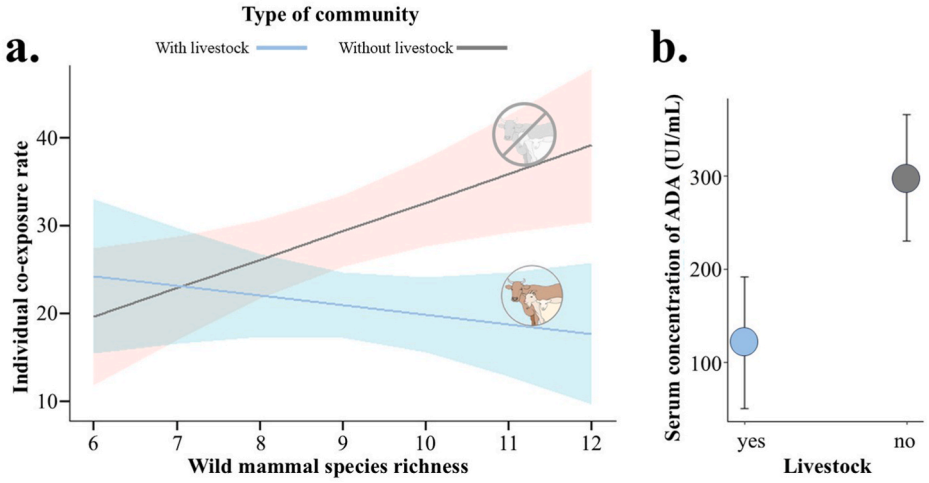

Fig. 4. Livestock as a modulator of the relationship between biodiversity and pathogens. **(a)** GLMM representation comparing wild boar individual co-exposure rate (pathogen richness) dynamics between communities with and without livestock when wild mammal richness increase (Table 1; Table S6). **(b)** GLMM representation of immune system activation differences between communities with and without livestock (Table 2; Table S7). Shaded bands and error bars represent confidence intervals (CI95%).

Table 1
Results of the generalized linear mixed model on the effect of ruminant livestock grazing, wild mammal richness and latitude on wild boar individual co-exposure rates.

Fixed effects	Estimate coefficient	Standard error	Degrees of freedom	*p*-value
Intercept	0.30	0.14	14.26	0.05
Wild mammal richness	0.29	0.11	14.69	0.02
Ruminant livestock presence	−0.47	0.18	12.57	0.02
Latitude	−0.25	0.09	12.42	0.02
Interaction between wild mammal richness and ruminant livestock presence	−0.38	0.16	13.61	0.03

Table 2
Results of the generalized linear mixed model on the effect of ruminant livestock grazing on immune system activation (ADA).

Fixed effects	Estimate coefficient	Standard error	Degrees of freedom	*p*-value
Intercept	0.23	0.10	10.87	0.03
Ruminant livestock presence	−0.49	0.14	12.15	<0.01

dilution of community competence when less competent hosts are progressively incorporated into more biodiverse communities. In our study sites, the presence of livestock could similarly alter the functional composition of the host community, favouring mammalian richness and biodiversity and reducing the overall transmission capacity independently of density effects. Moreover, treatment and/or management and eradication programs against some pathogens investigated in this study are applied in domestic ruminants, having a likely contribution to reduce the susceptible population (Horan et al., 2008), and potentially slightly influencing the observed patterns. Altogether, the findings would agree with a trend towards a dilution effect in presence of livestock, reducing pathogen circulation by reducing contacts among competent hosts (Keesing et al., 2006; Barroso and Gortázar, 2024).

Not all pathogens originate in wildlife. Management policies can account for the net and overall influences of anthropogenic modifications to the environment, such as the establishment of traditionally managed livestock systems. However, decision-making regarding the management of these systems must consider that domestic animals themselves are sometimes the main reservoirs of certain pathogens, such as *C. burnetii*, and therefore potentially responsible for their circulation in the episystem (Roest et al., 2011). Consequently, reductions in wildlife pathogen prevalence may not directly translate into lower zoonotic risk, highlighting the need for integrated and pathogen-specific risk assessments.

The negative relationship between latitude and individual pathogen co-exposure of the wild boar is most likely explained by a combination of environmental variables, such as temperature, favouring pathogen richness with decreasing latitude (Guernier et al., 2004; Becvarik et al., 2023) and management practices such as fencing and supplementary feeding which increase host abundance, density and aggregation in southern Iberia, as described for pathogens such as MTC, PCV2, ADV and CCHFV, among others (Vicente et al., 2004, 2005, 2007; Cuadrado-Matías et al., 2022).

Indirect serum markers of inflammation have been proposed to monitor the health status of wildlife populations without the need for specific tests for each and all of the potential diseases (Ráez-Bravo et al., 2015; Barroso et al., 2023). Specifically, ADA is considered a reliable biomarker of immune system activation and inflammation in suids (Tecles et al., 2018; Contreras-Aguilar et al., 2020; Cerón et al., 2022). In turn, pathogens can either suppress or stimulate the immune response of the host, thus mutually influencing each other (Lello et al., 2004; Telfer et al., 2010). The higher serum ADA concentration in the wild boar from the study sites without livestock presence (Fig. 4b–Table 2) could result from the higher pathogen exposure in those communities (Figs. 1c, 3 and 4a; Table 1), inducing an overall higher immune system activation and/or diseases with an inflammatory component.

This study has several limitations. The results and conclusions of this study could be widened by adding complementary methods, such as track tubes and live traps, to include small mammals, amphibians, reptiles and birds in the assessment of biodiversity. Camera traps are known to show lower performance for small mammals and species with neophobic behaviour, which may result in an incomplete characterisation of the mammal community (Glen et al., 2013). Given that small mammals can act as reservoirs for some of the pathogens studied, such as *C. burnetii* or CCHFV (Pascucci et al., 2015; Celina et al., 2025), their underrepresentation may therefore influence the interpretation of community-level effects on pathogen dynamics. While the wild boar has been proposed as the sentinel species in the studied ecosystems (Barroso et al., 2023), it is not the only suitable indicator species and not the best one to monitor pathogens like EHDV (Ruiz-Fons et al., 2024). So, widening the pathogens investigated and the sentinel species would strengthen the conclusions. Although serology reflects past exposure rather than active infection, sampling over different years and the expected partial renewal of wild boar populations due to hunting activities could make these serological data relatively reliable indicators of present circulation of the analysed pathogens. This study uses spatio-temporary coincidences as a species interaction proxy. The assessment of direct interactions among species would require other methodological approaches, such as GPS-collaring (Barasona et al., 2014). The 18 study sites were selected opportunistically to develop a health surveillance network rather than for this research (Barroso et al., 2023), with some livestock-free areas coinciding with game estates in central and southern regions where wild ungulate overabundance is common, potentially introducing geographic bias that was controlled for by including latitude as an explanatory variable in all models. Site-specific livestock management data, such as stocking density, or seasonal movement patterns, was not available at the spatial resolution required for this study, limiting the results to the influence of livestock presence at the study sites. Furthermore, this study did not account for species-specific effects of livestock; it is known that the impact of small domestic ruminants on the ecosystem may be slightly different from that of cattle, primarily due to differences in grazing behaviour (Rook et al., 2004).

Livestock grazing conforms socio–ecological systems based on traditional knowledge, where herders act not only as episystemic actors but as holders of adaptive ecological knowledge shaped through long-term co-evolution in Mediterranean ecosystems. This knowledge promotes management practices that enhance ecosystem resilience, biodiversity, and resource efficiency (Berkes, 2017; Manzano et al., 2021; Varela et al., 2022; Per et al., 2025). These practices situate grazing within broader agroecological and circular economy frameworks, highlighting its relevance for the establishment of sustainable food systems.

Overall, our results suggest that the absence of grazing livestock is associated with a lower diversity of wild mammals and a greater complexity in pathogen communities, which translates into higher co-occurrence and prevalence of pathogens in the sentinel species. This situation, which might also occur in other regions of the northern hemisphere, could reflect an imbalance in ecological interactions with implications for ecosystem health.

CRediT authorship contribution statement

Alberto Perelló: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Patricia Barroso:**

Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jorge Ramón López-Olvera:** Writing – review & editing, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis. **David Relimpio:** Writing – review & editing, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis. **Ángela Marín-Rojo:** Writing – review & editing, Validation, Methodology, Investigation. **María Escobar:** Writing – review & editing, Validation, Methodology, Investigation. **Francisco Ruiz-Fons:** Writing – review & editing, Validation, Methodology, Investigation, Funding acquisition. **José Joaquín Cerón:** Writing – review & editing, Validation, Methodology, Investigation, Funding acquisition. **Ana Balseiro:** Writing – review & editing, Validation, Methodology, Investigation, Funding acquisition. **Christian Gortázar:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors have no potential conflicts of interest to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2026.129842.

Data availability

Data are available at ZENODO repository (doi: https://doi.org/10.5281/zenodo.15881912). Further supplementary information and data are available from the corresponding authors upon reasonable request.

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