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The continental distribution of *Theileria* and *Babesia* species in African wild mammals: A systematic review and meta–analysis of molecular prevalence

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ABSTRACT

Tick–borne piroplasmids of the genera *Theileria* and *Babesia* are emerging threats at the wildlife–livestock–human interface, particularly in Africa, where ecosystems are rapidly changing due to anthropogenic pressures. This systematic review and meta-analysis synthesizes current knowledge on their occurrence and molecular prevalence of these piroplasmids in African wild mammals. A total of 56 studies met the inclusion criteria, identifying 24 recognized species of *Babesia* and *Theileria* species, along with an additional 17 species that have provisional/uncertain denomination across nine African countries. Of these, 47 studies were suitable for meta-analysis, revealing a high overall molecular prevalence of *Theileria/Babesia* spp. in wild mammals (62.4 %; CI: 39.3–82.8 %), with *Babesia* spp. generally more prevalent in wild carnivores, while *Theileria* spp. predominated in wild ruminants. In African buffalo (*Syncerus caffer*), pooled prevalence of *T. parva*, the agent of East Coast fever and Corridor disease, was estimated at 62.9 % (CI: 37.5–85.0 %), with significant geographic differences. *Babesia bovis*, the most pathogenic agent of bovine babesiosis, was rare in buffalo (0.4 %; CI: 0–6.5 %), whereas the less pathogenic *B. occultans* reached 23.3 % (CI: 16.2–31.3 %) in the same species and 30 % (CI: 15.2–47.3 %) in blue wildebeest (*Connachaetes taurinus*). Zoonotic *B. microti* was detected in non-human primates, wild felids, and rodents, and a *B. odocoilei*–like organism was identified in lions (*Panthera leo*). Our findings underline the ecological complexity and hidden burden of piroplasms in African wildlife and the potential for spillover to domestic animals and humans. This review provides the first continental-level synthesis of *Theileria* and *Babesia* distribution in African wild mammals and emphasizes the need for expanded and enhanced molecular monitoring in underrepresented countries and animal taxa, as well as extensive taxonomic clarification.

1. Introduction

The balanced coexistence of multiple and diverse wildlife species is a hallmark of healthy ecosystems and successful species conservation. The exponential growth of the human population, now estimated at over 8 billion (United Nations, 2024), has drastically reshaped natural habitats worldwide, disrupting ecological balances and altering animal, vector and pathogen species distribution (Keck et al., 2025). Free-ranging wildlife is directly threatened by anthropogenic pressures, particularly in regions where undeveloped land is increasingly transformed for urban expansion, livestock, and crop farming, with consequent shrinking and fragmentation of natural habitats (Bradley and Altizer, 2007; Campbell et al., 2017; Cozim-Melges et al., 2024). Transformed areas are difficult to restore due to resource depletion, and soil and landscape degradation (AbdelRahman, 2023; Petrescu-Mag et al., 2024). As a result, the wildlife-livestock-human interface is expanding at a rapid pace, increasing the opportunities and risks for the spillover of infectious diseases (Gibb et al., 2024). Concurrently, the geographic spread of arthropod vectors driven by habitat encroachment and climate change is leading to the emergence and re-emergence of tick-borne pathogens (TBPs) in humans, domestic animals and wildlife (Nuttall, 2022).

Babesia and *Theileria* are two genera of protozoans (order Piroplasmida, phylum Apicomplexa) transmitted via tick bites, potentially causing severe disease in domestic animals. African wildlife appear to act as asymptomatic carriers of piroplasmids, likely reflecting a state of endemic stability and long–term host–parasite co-evolution (Seal et al.,

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2021; Squarre et al., 2020; Yabsley and Shock, 2013). The most significant piroplasmids include *Theileria parva,* a TBP present throughout a large part of eastern and southern Africa, primarily transmitted by *Rhipicephalus appendiculatus* ticks (Lawrence et al., 2004). *Theileria parva* causes an acute and often fatal lymphoproliferative disease in cattle. It invades and transforms the host lymphocytes, leading to fever, lymph node swelling, pulmonary edema and high mortality if untreated. In endemic regions, annual direct economic losses from *T. parva* infections are estimated at USD 168 million (Surve et al., 2023). Two clinically and epidemiologically distinct disease syndromes caused by *T. parva* are East Coast fever (ECF) and Corridor disease, each associated with different host and parasite dynamics. East Coast fever, caused by cattle–derived *T. parva* strains (formerly *T. parva parva*; Uilenberg, 1981), was introduced to countries south of the Zambezi River in 1901/02 following the importation of cattle from Tanzania. The disease was first reported in Zimbabwe in 1902. It was subsequently eradicated in southern Mozambique by 1917, Zimbabwe by 1954, South Africa by 1955, and Swaziland by 1960. However, it has continued to persist in the region north of the Zambezi River to this day (Morrison et al., 2020; Norval et al., 1992). Corridor disease was first described in Zimbabwe in 1934 and later emerged in South African cattle during the 1950s. This spread was attributed to spillover from infected buffalo via tick transmission (Neitz et al., 1992). The disease was subsequently associated with *T. parva* strains derived from buffalo, previously classified as *T. parva lawrencei* (Uilenberg, 1981). The key difference between the two diseases lies in their epidemiology and pathogenesis. East Coast fever is maintained within cattle populations, often leading to epidemics where the tick vector is present. Corridor disease, by contrast, does not transmit between cattle under natural conditions and arises only through tick-mediated exposure to infected buffalo, making it a spillover event rather than a sustainable transmission cycle in cattle. This epidemiological pattern is attributed to infection with buffalo-derived *T. parva* strains, which are genetically distinct from cattle-adapted strains and are responsible for Corridor disease. In cattle, these strains typically cause an acute, self-limiting infection in which animals either succumb before the parasite reaches the tick-infective piroplasm stage or, in survivors, parasitaemia rapidly declines to levels insufficient to sustain onward transmission. Recovered animals do not develop a true carrier state, as piroplasm parasitaemia is extremely low and the infection is generally cleared within weeks to months (Mbizeni et al., 2013). Consequently, the apparent lack of cattle-to-cattle transmission reflects biological mechanisms limiting piroplasm development and persistence in cattle, rather than reduced transmissibility *per se*, likely involving parasite-host incompatibilities that constrain completion of the parasite life cycle in both the vertebrate host and the tick vector.

Theileria equi and *Babesia caballi,* which are transmitted by ticks of the genera *Dermacentor, Rhipicephalus* and *Hyalomma*, cause equine piroplasmosis in domestic equids. This disease can present in an acute form, leading to severe clinical consequences in domestic equids, with symptoms including hemoglobinemia, hemoglobinuria and mortality rates ranging from 10 % to 50 % in naïve horses (Facile et al., 2025; Rothschild, 2013). These outcomes contribute to substantial direct and indirect global economic losses within the horse industry (Coultous et al., 2023; Kerber et al., 1999; Short et al., 2012).

Bovine babesiosis, commonly referred to as redwater, is a tick–borne disease of cattle caused by six *Babesia* species: *B. bigemina*, *B. bovis*, *B. divergens, B. major, B. occultans* and *B. ovata* (Decaro et al., 2013; Ros-García et al., 2011; World Organisation for Animal Health, 2021; Zintl et al., 2003). Among these, *B. bovis* (causing a disease called Asiatic redwater) is the most pathogenic, frequently resulting in acute illness characterized by fever, hemolytic anemia, hemoglobinuria, and, in severe cases, respiratory or neurological complications and up to 10 % mortality, even with treatment (CFSPH, 2018). The primary vectors responsible for the transmission of *B. bovis* are *Rhipicephalus annulatus* and *Rhipicephalus microplus*, while *Rhipicephalus decoloratus* can only transmit *B. bigemina* (Gray et al., 2019). Bovine babesiosis poses a significant threat to the global cattle industry due to its direct impact on animal health, productivity, and economic performance (Jacob et al., 2020). Although listed by the World Organisation of Animal Health (WOAH) and also included on the U.S. National Animal Health Reporting System (NAHRS), bovine babesiosis is not a notifiable disease in South Africa and several other African countries, mainly due to its endemic stability.

Seven *Babesia* species have been incriminated as causative organisms of clinical babesiosis of domestic canines (Birkenheuer et al., 2004; Leisewitz et al., 2023; Schoeman, 2009): four large piroplasms, namely *B. rossi* (the most virulent), *B. canis, B. vogeli* and *Babesia* sp. (coco), and three small *Babesia* spp., *i.e. B. gibsoni, B. conradae* and *B. vulpes* (formerly *T. annae*). While *B. canis, Babesia* sp. (coco), *B. gibsoni, B. conradae* and *B. vulpes* have traditionally been reported in Europe and/or North America and *B. vogeli* is found worldwide, whereas *B. rossi* is endemic to southern Africa.

To date, at least seven *Babesia* species have been implicated in human disease: *B. divergens*, *B. duncani*, *B. microti*, *B. motasi*, *B. venatorum, B. crassa* and *B. odocoilei* (Kumar et al., 2021). These species are known to cause a range of clinical manifestations, from mild flu-like symptoms to severe, life-threatening hemolytic anemia, particularly in immunocompromised individuals (Krause, 2019; Krause et al., 2008; Woolley et al., 2017). While human babesiosis is increasingly recognized as an emerging zoonosis in parts of Europe, Asia, and North America, there is a marked paucity of surveillance data from the African continent (Kumar et al., 2021). This gap in knowledge significantly limits our understanding of the potential zoonotic threat posed by *Babesia* spp. in African regions, particularly in areas with high levels of interactions between humans, wildlife and livestock.

Historically, piroplasm detection relied heavily on microscopy, which suffers from limited sensitivity and specificity (WOAH, 2018). Furthermore, although morphological characterization remains useful at the genus level, it is inadequate for differentiating closely related piroplasm species (Schnittger et al., 2012). Similarly, serological tests are prone to cross-reactivity and fail to distinguish between parasite strains (Moloi, 2010; Tirosh-Levy et al., 2020; Tirosh-Levy and Rothschild, 2020). Consequently, molecular tools are becoming the gold standard for piroplasm detection and identification. In particular, PCR–RLB (Reverse Line Blot) hybridization allows simultaneous detection of multiple piroplasm genera and species, while nested and real-time PCR assays offer high specificity and sensitivity, being able to successfully detect protozoans occurring with low parasitaemia (Berggoetz et al., 2014; Cossu, Ochai, et al., 2024; King’ori et al., 2018; Troskie et al., 2025; Wamuyu et al., 2015).

In this systematic review and meta-analysis, we collate and evaluate the epidemiological investigations of *Babesia* and *Theileria* spp. in African wildlife, with the goal to synthesize both the qualitative (host species, geographic distribution) and quantitative (molecular prevalence) findings across studies, in order to provide an evidence-based picture of piroplasm diversity, host range, and potential epidemiological roles within wild mammals in Africa.

2. Material and methods

2.1. Search strategy

To ensure methodological transparency, the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines were followed. The completed PRISMA statement and abstract checklists are provided in Supplementary Tables S1 and S2. To frame our research question and define eligibility criteria, we applied a modified version of the PICO (Population, Intervention, Comparison, Outcome) model: population was set to African wild mammals living on the African continent. investigation (instead of “Intervention”) was filtered to nucleic acid detection (e.g., PCR, RLB) tests, antigen-based assays, serological tests or direct microscopic identification. Comparison consisted of differences in detection outcomes across host family, species, geographic regions, and diagnostic techniques. Outcome was defined as the presence or absence of *Theileria* and/or *Babesia* species.

Based on this framework, our core research questions were: which *Theileria* and *Babesia* species have been reported in African wildlife? What is their molecular prevalence across different wild mammal hosts? What role might these wildlife species play in the broader epidemiology and transmission dynamics of these pathogens? To identify relevant studies, we formulated the following search algorithm: "Africa AND wildlife AND (theileria OR babesia)". This query was run across four electronic databases: PubMed, ScienceDirect, Scopus, and Web of Knowledge. All retrieved records were imported into Mendeley, and duplicates were removed.

2.2. Selection process

All studies retrieved through the defined search strategy were subjected to a preliminary screening of title and abstract, followed by a full-text review of potentially eligible articles. Studies were assessed according to predefined exclusion criteria. i) Study design not applicable. Only original research articles and official reports were included; reviews, editorials, and conference abstracts were excluded. ii) Population not applicable. Studies conducted on non-mammalian wildlife, such as birds or reptiles were excluded. iii) Study area not applicable. Studies involving African wild mammals housed in captivity outside the African continent (*e.g.*, in zoos) were not included. iv) Investigation tool not applicable. Studies focusing on therapeutic interventions rather than diagnostic detection were excluded. v) Outcome not applicable. Studies that investigated pathogens other than *Theileria* or *Babesia* were excluded. A detailed list of the reasons for exclusion at the full-text screening stage is provided in Supplementary Table S3. For the meta-analysis component, only studies that met the following additional inclusion criterion were retained: i) Use of quantitative molecular diagnostic methods suitable for prevalence estimation (excluding sequencing-only studies; refer to "Quantitative Analyses" section for details).

2.3. Data extraction and storage

Data extraction was performed for a total of 21 variables: publication details (reference key, authors, title, publication year, doi), animal specifics (common name, scientific name, sex, age, habitat type, clinical signs and/or lesions), sample specifics (sampling date, location, country, sample type, sampling strategy), details about the laboratory procedures (pathogens investigated, detection technique) and epidemiological data (number tested, number positive, variables correlated). Raw data were registered into a SQLite database from Aleph∞One, a customized web-based application built with PHP Laravel. Briefly, the registration forms of Aleph∞One are built with simple text and selection input fields designed to streamline and standardize the data entry process. Two naming authors (CA Cossu and C Blignaut) independently extracted the data in parallel and discrepancies were reviewed and resolved. All statistical analyses were performed using R studio software (version 2024.12.1 +563).

2.4. Critical assessment of included studies

Each included study was critical appraised to evaluate the risk of bias using a modified version of the Appraisal Tool for Cross-Sectional Studies (AXIS). This tool consists of 20 checklist items answered with "yes" or "no". Items related to non-responders were omitted as they are not applicable to animal-based studies. Studies were categorized based on the proportion of affirmative ("yes") responses: < 50 % indicates a high risk of bias; 50–70 % indicates a moderate risk of bias; 70 % or higher indicates a low risk of bias. Detailed results of the critical appraisal are presented in Supplementary Table S4. To ensure consistency and reduce reviewer bias, two authors (CA Cossu and C Blignaut) independently conducted the critical evaluations. Any discrepancies were resolved through discussion until consensus was reached.

2.5. Qualitative and quantitative analyses

A qualitative analysis was initially performed using descriptive statistics. Frequency distribution of the studies was performed, stratified by different variables, and visualized as bar and map charts with color legends. Tables were used to present more detailed and specific analytical information.

Quantitative analysis (meta-analysis) was conducted to estimate the pooled molecular prevalence of each pathogen species in African wild mammals. Molecular prevalence was defined as the proportion of animals testing positive for a given pathogen via nucleic acid detection at a specific time point.

Importantly, molecular sequencing studies were excluded from the meta-analysis because they do not provide numerical prevalence data (*i. e.* a proportion of positives to total tested) and often involve identification by interpretation of BLAST searches and phylogenetic analyses. Such studies were instead included in the qualitative analysis only, where their contribution to species characterization and discovery was emphasized.

The methods of our meta-analytical approach are provided elsewhere (Cossu, Cassini, et al., 2024; Cossu et al., 2023). The meta-analysis results were visualized in summary tables and maps. Codes and functions utilized can be retrieved from the GitHub website using the URL: https://github.com/CarlVet/Scientific_papers/blob/main/Meta_analysis_codes.

3. Results

3.1. Qualitative analysis

According to the search strategy and selection process applied in this study, a total of 56 papers were included in the qualitative analysis and 47 in the meta–analysis of molecular prevalence (Fig. 1). As a general trend, studies focused on selected protozoans in wildlife increased significantly starting from the year 2007 (52/56 studies; 82 %, Fig. 2**A**), highlighting a substantial increase in interest and research in this topic. Assays consisted mainly of nucleic acid detection tests (47/56 studies; 84 %, Fig. 2**B**) conducted on DNA extracted from whole blood samples (34/56 studies; 61 %, Fig. 2**C**), rarely from tissue samples.

All pathogen occurrences are documented in Supplementary Table S5 and categorized by animal species (together with their scientific nomenclature), country, detection method and corresponding references. Piroplasmids (*Theileria/Babesia* spp.) were reported in a total of 35 African wild mammal species (Fig. 3). All the studies where conducted in southern and eastern Africa, primarily in South Africa (25/56 studies; 45 %) and Kenya (10/56 studies; 18 %), with no reports from northern, western and central Africa.

Genus–specific assays detected *Babesia* spp. in nearly 30 species across 13 animal genera (Fig. 3), mostly in carnivores (9/30 species; 30 %), across six African countries (Fig. 4). A total of 13 recognized *Babesia* species were successfully characterized in African wild mammals. The most investigated species were *B. bovis*, *B. canis* and *B. microti* (16 studies each), followed by *B. felis* (15 studies), *B. bigemina, B. caballi* and *B. rossi* (14 studies). *Babesia bovis* was detected in African buffalo (*Syncerus caffer*) from Botswana (Eygelaar et al., 2015) and in four-–striped grass mice (*Rhabdomys pumilio*) from South Africa (Troskie et al., 2025). However, many other studies failed to detect *Babesia* spp. in other animal hosts investigated (Berggoetz et al., 2014; Brothers et al., 2011; Cossu, Ochai, et al., 2024; Nijhof et al., 2003; Oosthuizen et al., 2009; Oura et al., 2011b, 2011a; Pfitzer et al., 2011; Viljoen et al., 2020, 2021; Zimmermann et al., 2021). *Babesia canis* was not only detected in

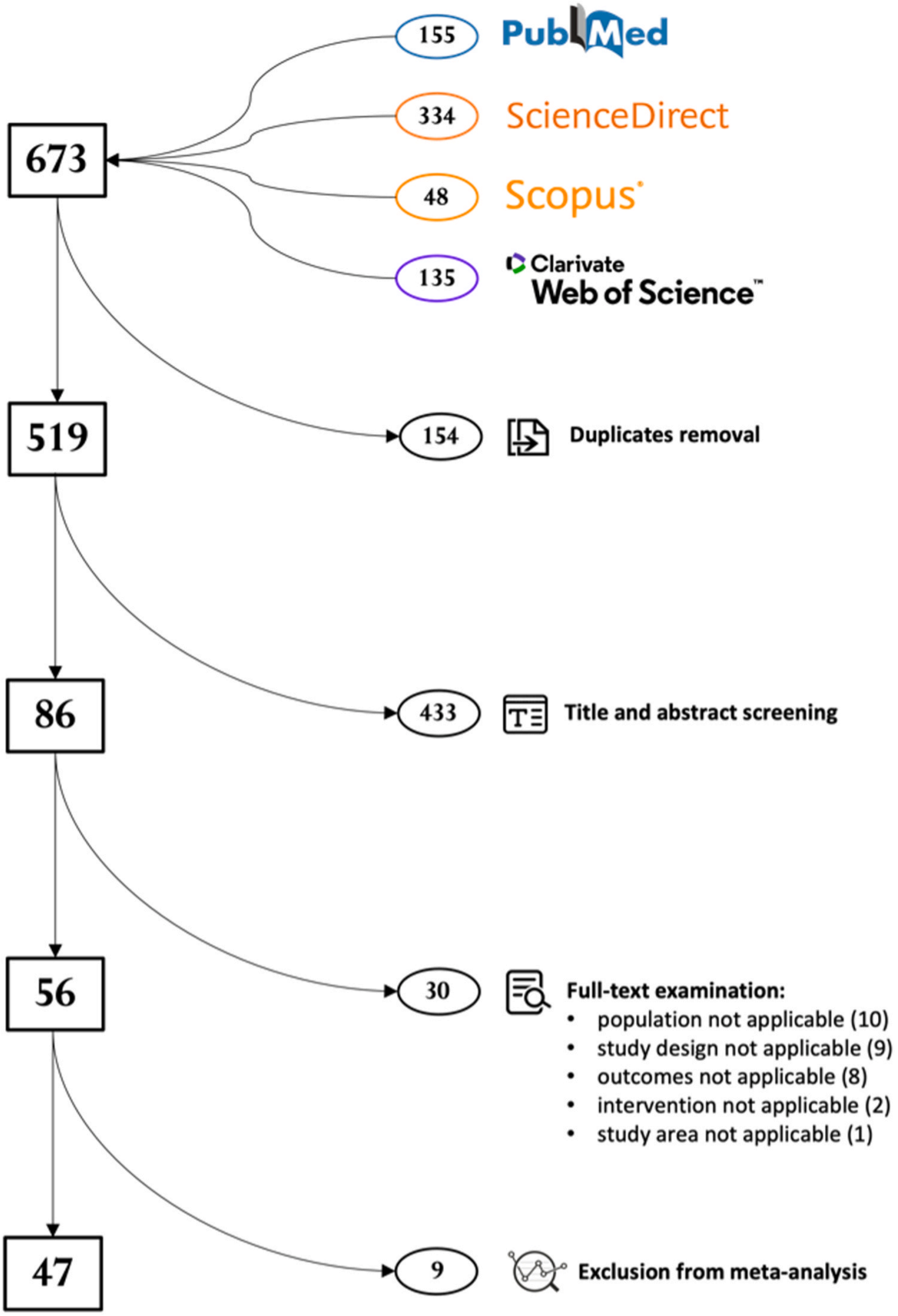

Fig. 1. Flow diagram depicting the steps performed in conducting the systematic search and selection. A total of 673 papers were initially retrieved from four search engines. Following the selection process, 56 papers were included in the qualitative analysis and 47 in quantitative analysis.

canid species, such as the African wild dog (*Lycaon pictus*) in South Africa using indirect immunofluorescence antibody test (Van Heerden et al., 1995), but also in lions (*Panthera leo*) from Botswana and South Africa (Broughton et al., 2021; McDermid et al., 2017). The zoonotic pathogen *B. microti* was found in wild felids from Botswana and South Africa (Broughton et al., 2021; McDermid et al., 2017; Viljoen et al., 2020), primates (grivet, baboon) from Kenya (Maamun et al., 2011) and rodents from South Africa (Troskie et al., 2025). Furthermore, three *Babesia* species with uncertain status were identified: *Babesia lengau*–like from spotted (*Crocuta crocuta*) and brown (*Parahyaena brunnea*) hyenas in Namibia and South Africa (Burroughs et al., 2017), *Babesia odocoilei*–like from lions in Zimbabwe (Kelly et al., 2014) and *Babesia leo*–like from yellow baboons (*Papio cynocephalus*) in Zambia (Nakayima et al., 2014). Lastly, four new *Babesia* spp. have been sequenced in lions from Botswana (McDermid et al., 2017), African wild dog from Zambia (Squarre et al., 2020), as well as in giraffe (*Giraffa camelopardalis*) and roan antelope (*Hippotragus equinus*) from South Africa (Oosthuizen et al., 2009), and await formal taxonomic designation.

In contrast, members of the *Theileria* genus were detected in 20 species belonging to 6 animal genera (Fig. 3), mostly wild bovids (9/20 species; 45 %) from South Africa, Namibia and Kenya (Fig. 5). A total of 11 recognized *Theileria* species were successfully characterized in

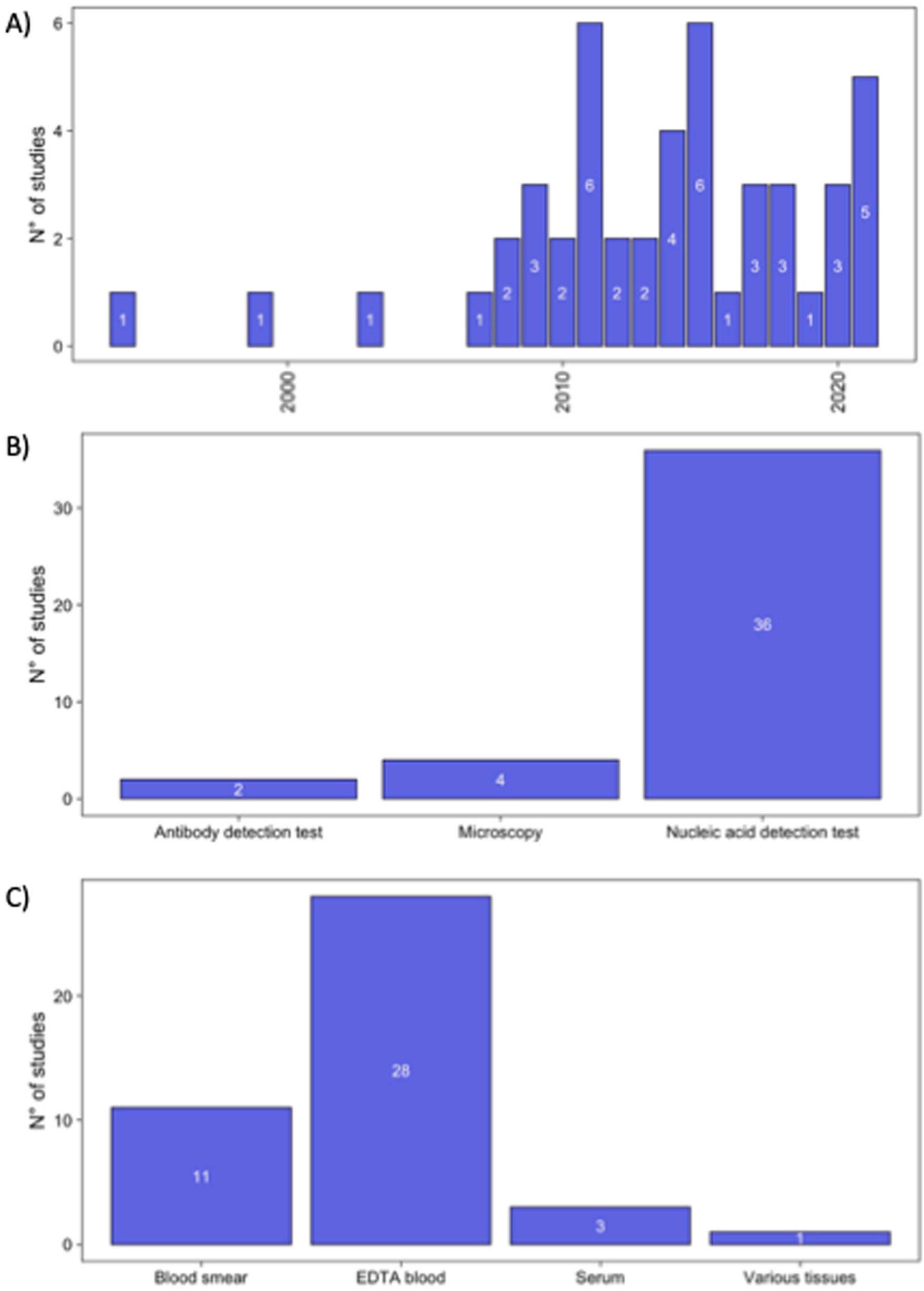

Fig. 2. Frequency distribution of studies included in qualitative analysis stratified by the main covariates: A) publication year; B) laboratory detection technique; C) sample type.

African wild mammals. *Theileria parva* was by far the most extensively investigated species, appearing in 23 studies, nine of which identified *T. parva* in buffalo from Botswana (Eygelaar et al., 2015), Namibia (Pascucci et al., 2011), South Africa (Pienaar et al., 2018), Zambia (Choopa et al., 2024; Munang'andu et al., 2009; Squarre et al., 2020), and Zimbabwe (Caron et al., 2013). Following *T. parva*, 18 studies detected *T. buffeli* in 11 animal species from Botswana, South Africa and Uganda, *T. equi* in plains (*Equus quagga*), mountain (*Equus zebra*) and Grévy'szebras (*Equus grevyi*) as well as white (*Ceratotherium simum*) and black rhinoceros (*Diceros bicornis*) from Kenya, Namibia and South Africa. Additionally, two *Theileria* species with uncertain classification were identified: *Theileria sable*–like in bushbuck (*Tragelaphus sylvaticus*),

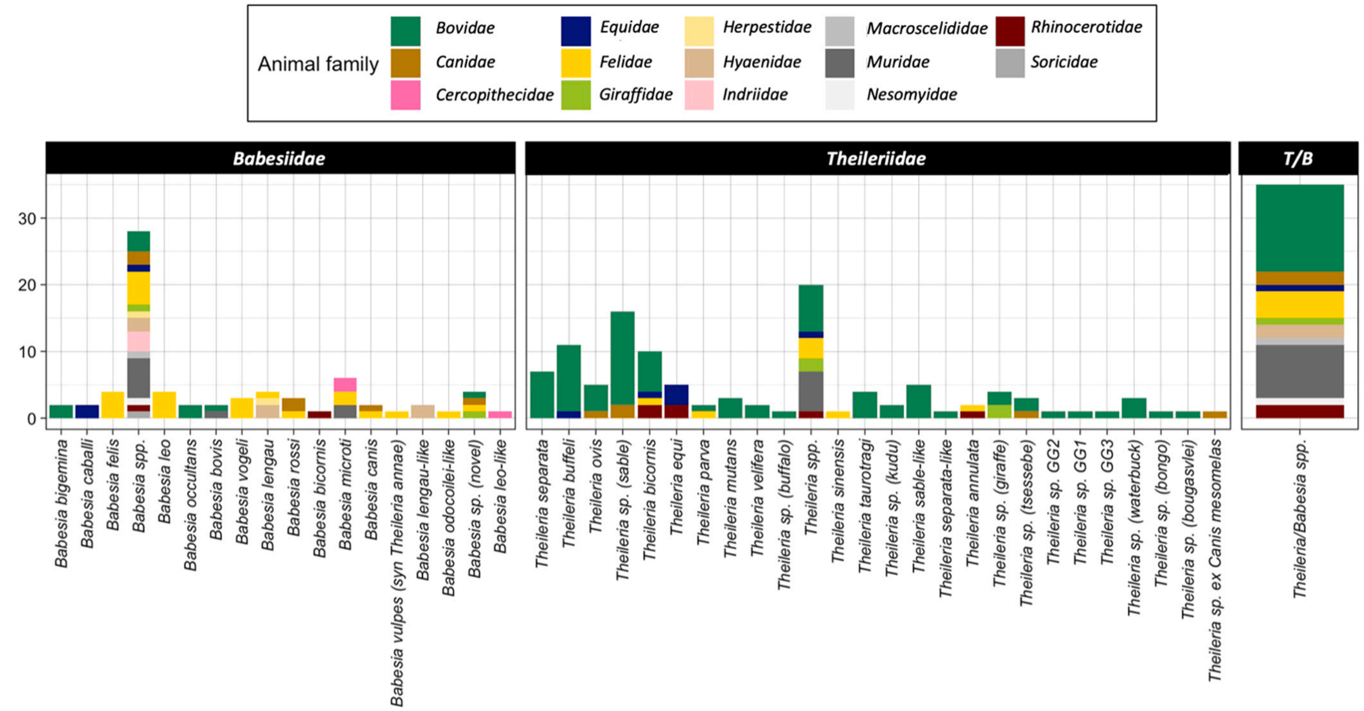

Fig. 3. Count of animal species infected with different pathogens stratified by animal family.

waterbuck (*Kobus ellipsiprymnus*), black (*Connachaetes gnou*) and blue wildebeest (*Connachaetes taurinus*) from South Africa, as well as in sable antelope (*Hippotragus niger*) from Zambia (Pienaar et al., 2018); and *Theileria separata*–like in blue wildebeest from Kenya (Wamuyu et al., 2015). Finally, the studies identified 12 *Theileria* spp. with provisional identification, with *Theileria* sp. (sable) being the most commonly reported, appearing in nine studies involving 16 animal species across South Africa, Namibia, Botswana and Zambia (Figs. 3 and 5).

3.2. Quantitative analysis

A meta–analysis was performed on 11 target pathogens detected using molecular tests in African wildlife, utilizing data from 47 articles. Meta–analysis was performed for a total of 39 pathogens, including the genus–specific targets (*Theileria/Babesia* spp., *Theileria* spp. and *Babesia* spp.). Pooled prevalences, confidence and prediction intervals, and heterogeneity indices are displayed in Table 1. The subgroup analysis highlighted that the factors mostly associated with pathogen prevalence were the animal species and the country where the sampling occurred (observed in 19/39 pathogen targets) (Supplementary Table S6).

As a general trend, *Babesia* spp. seem to occur at high prevalence in wild carnivores (felids, canids and hyaenids), while they are found at low prevalence in wild ruminant species (bovids and giraffids). The opposite holds for *Theileria* spp., which infect almost 75 % of wild bovids, about 1 % of wild felids, and remaining completely undetected in wild canids (Fig. 6). Regarding the geographic distribution (Fig. 7), *Babesia* spp. have been detected at high prevalences in lions in Botswana (McDermid et al., 2017), indriids in Madagascar (Qurollo et al., 2018), carnivores, equids and rodents in South Africa (Cossu, Ochai, et al., 2024; Penzhorn and Chaparro, 1994; Shabangu et al., 2021; Troskie et al., 2025; Viljoen et al., 2020, 2021). In contrast, *Theileria* spp. have primarily been found in wild ruminants from Kenya (Ghai et al., 2016; Githaka et al., 2012, 2013, 2014) and South Africa (Cossu, Ochai, et al., 2024; Pfitzer et al., 2011).

The molecular prevalence estimates for each pathogen in various wildlife species are summarized in Tables 2 and 3. For *Theileria* parasites, we highlight: high prevalence of *T. parva* in buffalo populations (62.9 %; CI: 37.5–85 %); widespread infection with *T. bicornis* in black (37.6 %; CI: 0–100 %) and white rhinoceros (35.4 %; CI: 28.8–42.2 %), impala (77.7 %; CI: 0–100 %), nyala (52.6 %; CI: 42.7–62.4 %), roan (100 %; CI: 82–100 %) and sable antelopes (100 %; CI: 59.2–100 %); *T. buffeli* in non–buffalo bovids such as bushbuck (100 %; CI: 71.3–100 %), eland (49.3 %; CI: 0–100 %; *Taurotragus oryx*), kudu (27.2 %; CI: 0–100 %), impala (43.1 %; CI: 0–100 %; *Aepyceros melampus*), nyala (87.6 %; CI: 80.4–93.4 %; *Tragelaphus angasii*), roan (68.3 %; CI: 0–100 %) and sable antelopes (100 %; CI: 59.2–100 %); high prevalences of the malignant *Theileria* sp. (sable) in numerous antelopes species, especially black (57.2 %; CI: 0–100 %) and blue wildebeests (69.5 %; CI: 2.9–100 %), blesbok (66.7 %; CI: 14.4–99.8 %; *Damaliscus pygargus phillipsi*), bushbuck (26.9 %; CI: 12–45.2 %), gemsbok (83.7 %; CI: 0–100 %; *Oryx gazella*), and, again, roan (100 %; CI: 100–100 %) and sable antelopes (62.5 %; CI: 0–100 %). For *Babesia* parasites, we estimated the prevalence of *B. bovis* in buffalo to be as low as 0.4 % (CI: 0–6.5 %); *B. rossi* was estimated to be present in 6 % of wild dogs (CI: 0–31.5 %), 8.6 % of jackal (CI: 0–100 %; *Lupulella mesomelas*) and 8.4 % of lions (4.9–12.8 %); while *B. microti* was found in 46.7 % of caracals (CI: 29.4–64.4 %; *Caracal caracal*), 35.7 % of lions (CI: 0–100 %), 23.1 % of yellow baboons (CI: 13.7–34 %) and 20 % of grivets (CI: 10.9–31 %; *Chlorocebus aethiops*).

4. Discussion

Our review highlights a growing interest in wildlife piroplasms across Africa over more than 20 years, driven largely by advances in molecular diagnostics. Among available sample types, blood remains the most suitable matrix for piroplasm detection, given the persistence of these protozoa in the bloodstream and lack of confirmed latency in organ tissues. Research has been focused in southern and eastern Africa, with a notable absence of studies from northern, western, and central regions. Nearly half of the studies originated in South Africa, reflecting the country's long-standing leadership in piroplasm research. This tradition dates back to the early 20th century, with foundational work by Sir Arnold Theiler and colleagues at Onderstepoort, who first described *T. parva* as the causative agent of ECF, separate from redwater

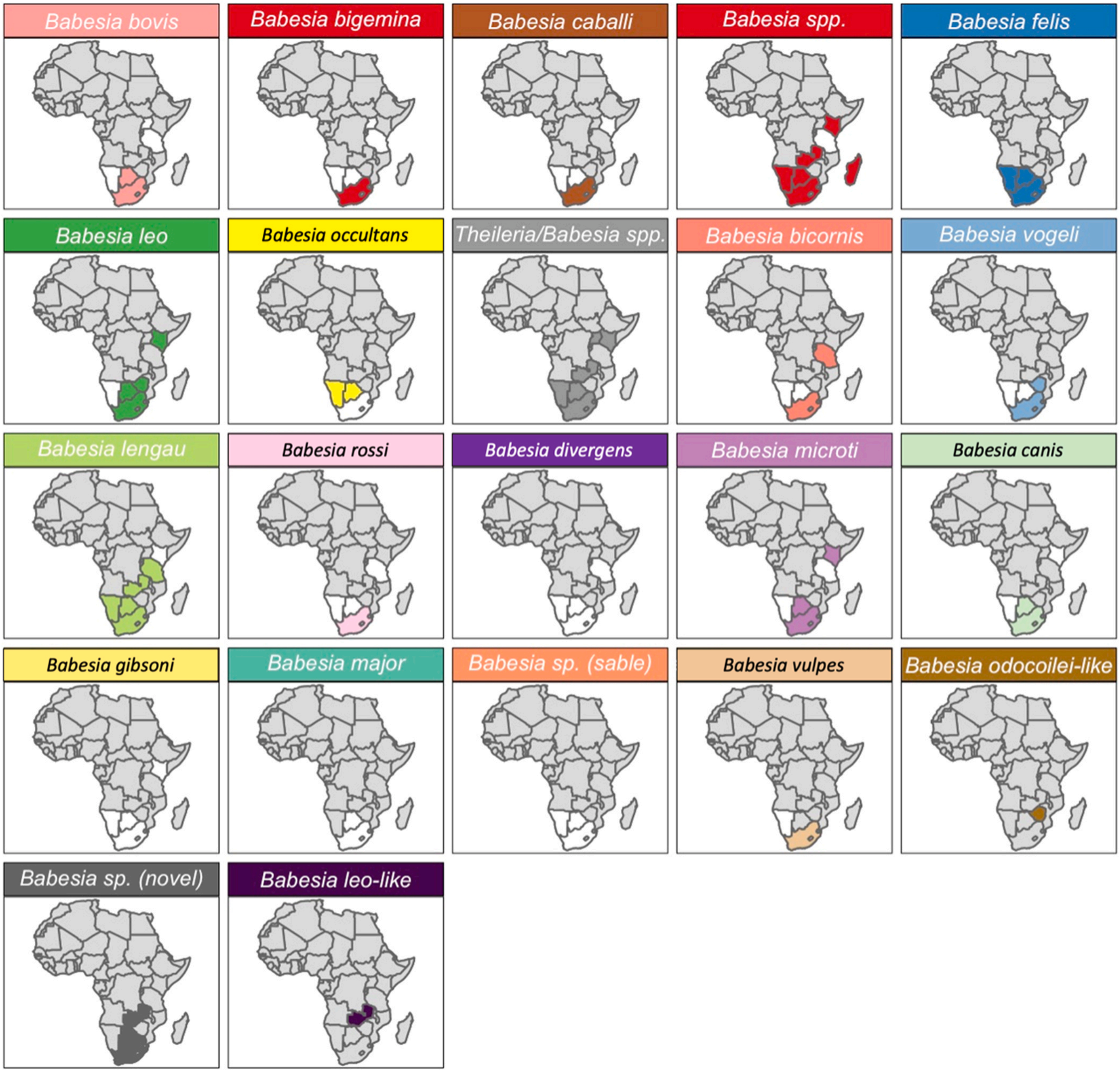

Fig. 4. Geographic distribution of Babesiidae species detected in African wildlife. For each map, colored countries indicate the occurrence of the pathogen species named above the panel. Countries where the pathogen was investigated but not detected are shown in white, while countries with no available data are shaded grey.

caused by *B. bovis* and *B. bigemina* (Theiler, 1912). The continued investment in veterinary research infrastructure in South Africa has sustained its prominence in this field. In contrast, limited research output from other African regions likely reflects disparities in research capacity, resources, priorities and political stability rather than a true absence of piroplasm diversity in their wildlife. Although the use of random-effects models and wide confidence and prediction intervals captures some of the uncertainty associated with data sparsity, additional data from under-represented regions may substantially influence future pooled estimates. Consequently, the current prevalence estimates should be interpreted as reflecting mainly southern and eastern African wildlife systems rather than the African continent as a whole. Importantly, zero pooled prevalences or occurrences for certain species-specific targets (e.g. *Theileria lestoquardi*, *Babesia vulpes*, *Babesia* sp. (sable)) should not be interpreted as evidence of true absence. Instead, they likely reflect a combination of limited surveillance in competent wildlife hosts, low infection prevalence below the detection threshold or insufficient sensitivity or specificity of available molecular assays. In this context, zero-prevalence estimates are best viewed as indicators of current knowledge gaps rather than definitive epidemiological conclusions.

4.1. Prevalence of piroplasms in African wildlife

Our meta–analysis revealed a high overall pooled prevalence of *Babesia/Theileria* spp. (62.4 %, CI: 39.3–82.8 %), with subgroup analyses indicating 35.9 % (CI: 13.3–62.6 %) for *Babesia* spp. and 27.7 % (CI: 4.7–60.4 %) for *Theileria* spp. (Table 1). Notably, most studies included in the review focused on clinically healthy animals, with only four studies reporting clinical signs or mortality associated with piroplasmid infection (Bosman et al., 2007; Githaka et al., 2012; Gray et al.,

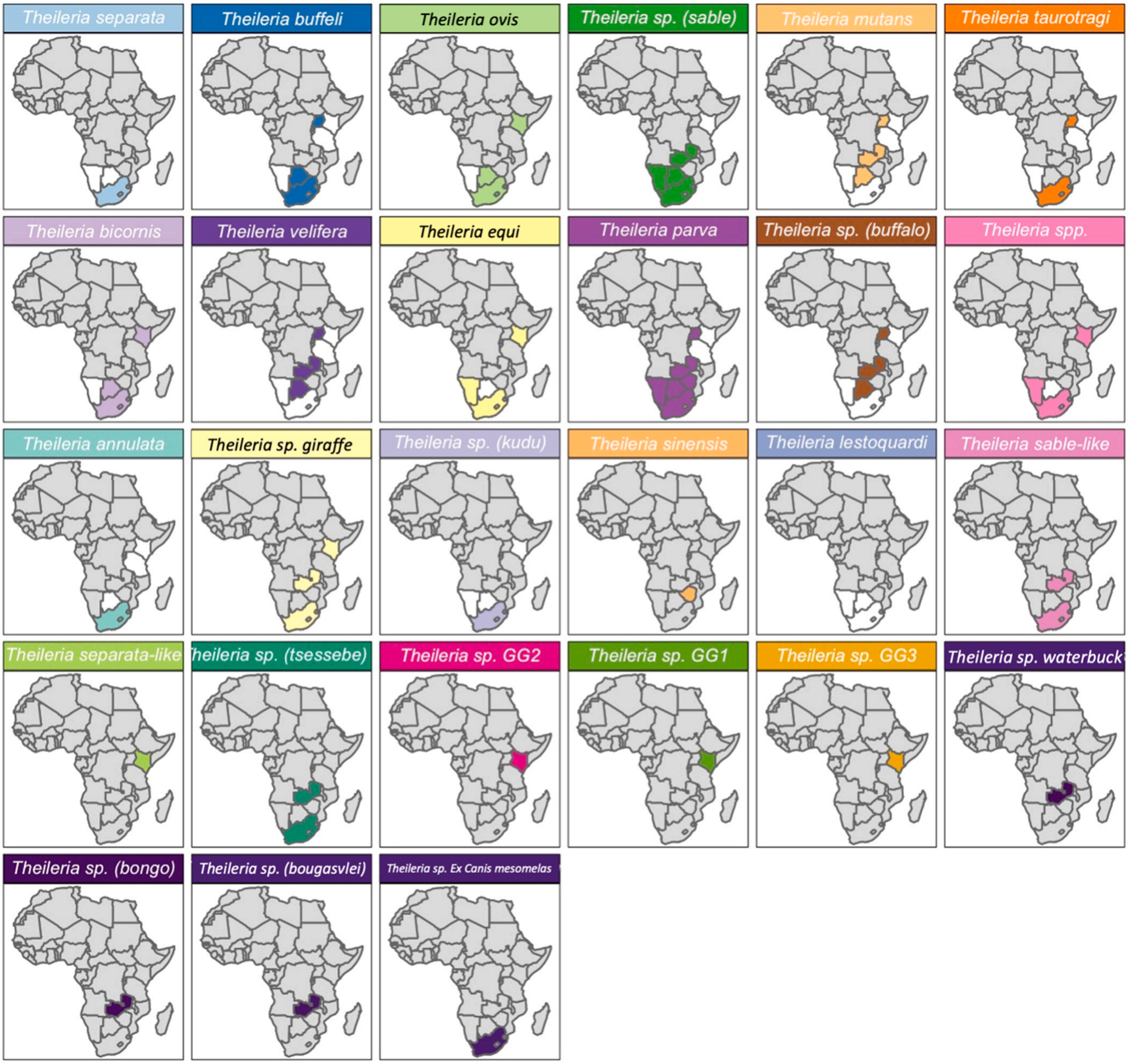

Fig. 5. Geographic distribution of *Theileriidae* species detected in African wildlife. For each map, colored countries indicate the occurrence of the pathogen species named above the panel. Countries where the pathogen was investigated but not detected are shown in white, while countries with no available data are shaded grey.

2019; King'ori et al., 2018). The rare occurrence of clinical disease suggests a state of immunological tolerance in wildlife hosts, likely developed through evolutionary pressures (Seal et al., 2021), or, alternatively, the maintenance of herd immunity leading to a state of enzootic stability. However, clinical babesiosis or theileriosis has been observed under conditions of physiological stress such as translocation, drought or nutritional stress, or captivity. For instance, Githaka et al. (2012) documented severe babesiosis in captive lions in Nairobi with concurrent mineral deficiencies, while fatal outcomes of disease were recorded in free-roaming black rhinoceroses (Nijhof et al., 2003) and roan antelopes (Nijhof et al., 2005) after capture and relocation.

These findings have important implications for wildlife management and translocation practices. Enhanced pathogen surveillance, both at the point of origin and destination, can inform risk assessments and guide decisions of wildlife movement, reducing the likelihood of disease outbreaks that could compromise the survival of already vulnerable or endangered species (Baker et al., 2022). Additionally, improving captive care conditions and reducing capture– and transport–associated stress are critical measures to prevent the reactivation of latent infections and reduce associated morbidity and mortality (Pohlin et al., 2020). Understanding the role of asymptomatic carriers in wildlife is crucial for predicting spillover risks, both within conspecific populations, where infection may spread from infected to naïve individuals, and across species boundaries, particularly to domestic animals when the pathogen exhibits a generalist host range (*e.g. T. bicornis, T. separata, B. bigemina, B. microti*). Future research should explore the immunological mechanisms underlying tolerance in natural hosts and assess how ecological changes might disrupt these complex host–pathogen relationships.

4.2. *Theileria parva* is widespread in African buffalo populations

Our meta–analysis estimated a pooled prevalence of *T. parva* in

Table 1
Meta–analysis results of *Theileria* and *Babesia* species in African wild mammals.

Pathogen species	N. studies	N. animals tested	N. animals positive	Pooled prevalence	95 %CI	PI	I^2
Theileria/Babesia spp.	24	2286	996	62.4	39.3–82.8	0–100	98.7
Babesia spp.	20	2316	647	35.9	13.3–62.6	0–100	98.8
Babesia bicornis	10	956	16	0.8	0–6.8	0–37.7	85.5
Babesia bigemina	13	1368	2	0	0–0.1	0–0.7	0
Babesia bovis	15	1849	6	0.1	0–0.3	0–0.9	18.3
Babesia caballi	13	1467	15	0.2	0–1.4	0–8.9	79.1
Babesia canis	13	1550	18	0.1	0–0.8	0–4.5	81.6
Babesia divergens	9	899	0	0	0–0	0–0.2	0
Babesia felis	14	1688	205	3.5	0–14.7	0–68.5	98.6
Babesia gibsoni	11	1165	0	0	0–0	0–0.1	0
Babesia lengau	6	505	59	4.5	0–31.5	0–91.6	97
Babesia leo	10	1003	185	11.2	1–30.2	0–82	98
Babesia major	6	697	0	0	0–0	0–0.3	0
Babesia microti	15	2009	195	3.4	0–11.8	0–55	97.7
Babesia occultans	5	522	37	2.3	0–17.5	0–62.1	95.1
Babesia rossi	13	1555	70	1.3	0–5.1	0–25.2	93.7
Babesia sp. (sable)	8	748	0	0	0–0	0–0.2	0
Babesia vogeli	12	1389	47	0.5	0–3.2	0–18.1	93
Babesia vulpes (syn *Theileria annae*)	8	1049	1	0	0–0.1	0–0.4	0
Theileria spp.	15	1730	401	27.7	4.7–60.4	0–100	99.1
Theileria annulata	12	1151	10	0.1	0–0.9	0–3.7	67.2
Theileria bicornis	14	1601	227	8.1	1.1–20.9	0–70.6	97.5
Theileria buffeli	17	1550	211	6.3	0.5–18.2	0–73.2	97.9
Theileria equi	16	1707	374	15.9	0.5–46.6	0–100	99.4
Theileria lestoquardi	8	912	0	0	0–0	0–0.2	0
Theileria mutans	15	1191	132	3.2	0–15.7	0–77.7	98.1
Theileria ovis	11	1153	10	0.3	0–1.6	0–6.9	69.5
Theileria parva	20	2237	527	7.9	0.5–22.6	0–89.5	98.9
Theileria sable–like	1	522	76	14.6	11.7–17.7	NA–NA	NA
Theileria separata	10	897	22	1.1	0–6.4	0–32.2	88.1
Theileria sinensis	1	99	1	1	0–3.9	NA–NA	NA
Theileria sp. (buffalo)	14	1414	61	0.8	0–4.9	0–30.7	94.7
Theileria sp. (giraffe)	2	39	11	30	0–100	NA–NA	97.9
Theileria sp. (kudu)	12	1310	114	1.9	0–13.4	0–69.3	98.2
Theileria sp. (sable)	14	1941	225	10.5	0.7–29.7	0–91.9	97.5
Theileria taurotragi	16	1954	46	0.6	0–3.1	0–20.8	89.6
Theileria velifera	16	1492	88	1.1	0–7.8	0–54.6	97.3

African buffalo populations at 62.9 % (95 % CI: 37.5–85.0 %). Prevalence varied significantly by both geographic region and diagnostic method. Notably higher prevalence was recorded in Zimbabwe (88.2 %; CI: 69.2–98.7 %), South Africa (79.0 %; CI: 74.6–83.1 %), Zambia (76.7 %; CI: 63.1–88.0 %) and Namibia (61.1 %; CI: 51.1–70.6 %) using real–time PCR or nested PCR techniques, compared to Botswana (30.0; CI: 24.4–35.9 %) and Uganda (42.2 %; CI: 34.8–49.7 %), where studies employed the RLB assay. These differences are likely attributable to the lower sensitivity of RLB in detecting *T. parva*, highlighting the need for more sensitive molecular diagnostics in wildlife surveillance.

The consistently high prevalence in buffalo across multiple southern African countries underscores their critical role as long–term reservoirs of *T. parva*, sustaining transmission cycles in natural ecosystems. These findings have important implications for transboundary disease management and integrated tick control programs. While immunization of cattle remains constrained to the infection-and-treatment method with available parasite stocks (*e.g.* Muguga, Katete, Chitongo), which has limitations such as inducing carrier status and the potential introduction of foreign strains, understanding buffalo–livestock interactions is essential for refining control strategies in areas where contact is increasing due to land-use changes and expanding wildlife–livestock interfaces (Mwamuye et al., 2020). Future studies should prioritize sensitive and standardized diagnostic protocols and longitudinal surveillance to better understand regional transmission patterns and how co-infections with piroplasms of other *Theileria* species affect *T. parva* infection dynamics and disease outcome (or severity).

While research on *T. parva* has predominantly focused on African buffalo and cattle, infections in other members of the Bovidae family, such as antelope species, remain poorly investigated. This knowledge gap limits our ability to fully assess the maintenance host community of the parasite. Expanding surveillance across diverse wild bovid species may therefore be important for more accurate risk assessment, particularly at wildlife–livestock interfaces where cross-species transmission may occur.

4.3. Zebras are the ancestral and maintenance hosts of equine piroplasms

Phylogenetic analyses have suggested that *T. equi* likely originated in African zebra species (Bhoora et al., 2020). In the present review, *T. equi* prevalence was estimated at 100 % in Grevy's and mountain zebras, 50 % in plains zebras (Table 2) and occasional detections in white and black rhinoceroses (Govender et al., 2011; Zimmermann et al., 2021), all showing no overt clinical signs, suggesting a broader host range within the order Perissodactyla. These findings support the hypothesis of long–term co–evolution between *T. equi* and its perissodactyl hosts. In contrast, *B. caballi* exhibited markedly lower prevalence in zebras and was not detected in rhinoceroses, highlighting its more restricted host specificity. Notably, *B. caballi* was only detected in zebra by means of real–time PCR (Bhoora, Buss, et al., 2010; Smith et al., 2019), while detection with RLB failed in plain zebras from South Africa and Namibia (Cossu, Ochai, et al., 2024). These results underscore once again the importance of using high–sensitivity molecular diagnostics for the effective surveillance of piroplasmids in wildlife, particularly for detecting infections characterized by low parasitaemia (Bhoora, Quan, et al., 2010).

These considerations raise concerns over the translocation of zebras as potential asymptomatic carriers, which may facilitate the spread of equine piroplasmosis into previously non-endemic regions, potentially causing outbreaks among domestic equids (Cossu et al., 2022; Smith et al., 2019). The movement of wildlife hosts with subclinical infections,

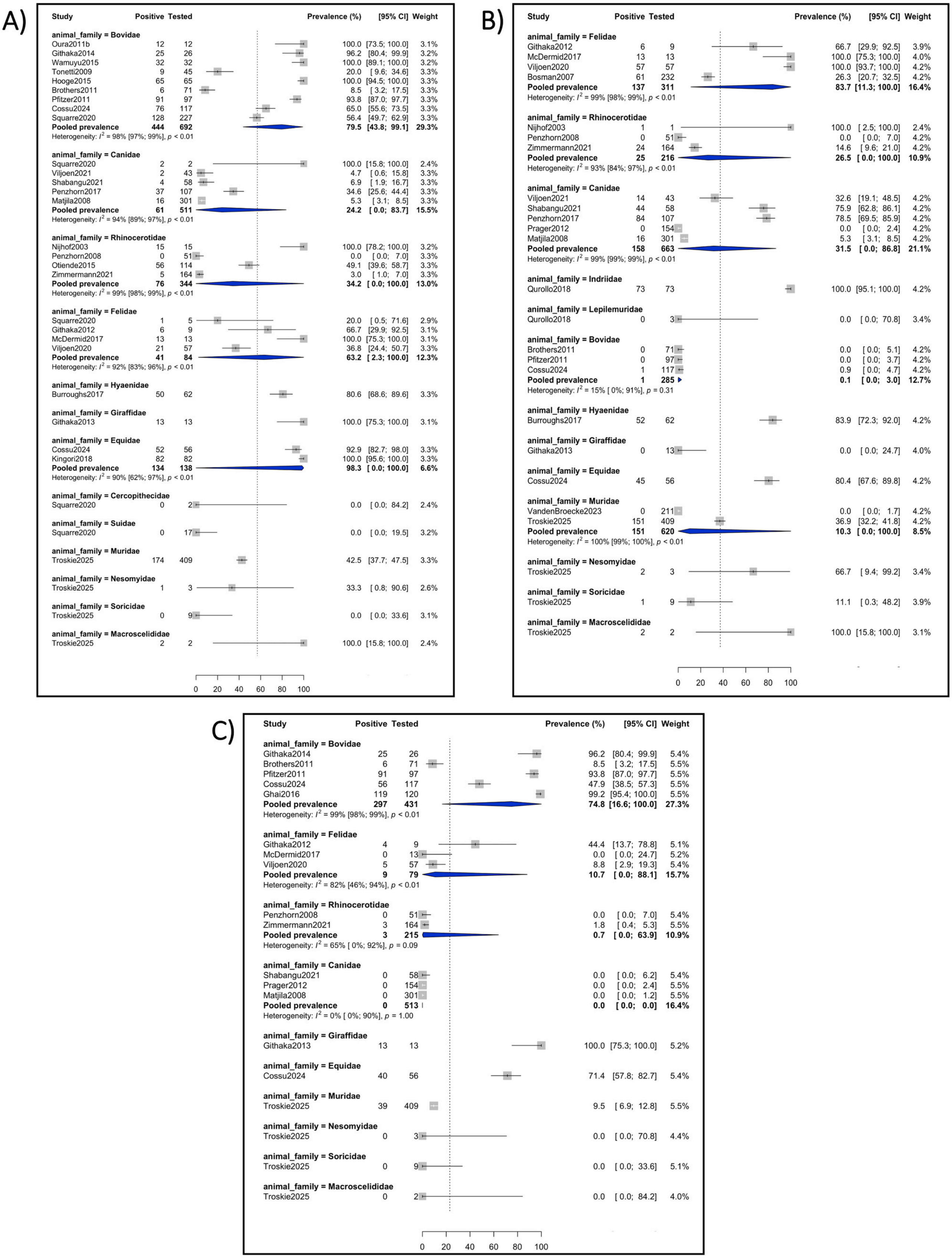

Fig. 6. Forest plots illustrating the results of meta–analysis on the molecular prevalence of A) *Theileria/Babesia*, B) *Babesia* spp. and C) *Theileria* spp. in African wildlife, stratified by animal family. The pooled prevalence can be seen as a blue diamond at the bottom of each plot, where the vertices represent the confidence intervals. The weight of each study is calculated based on the inverse–variance method.

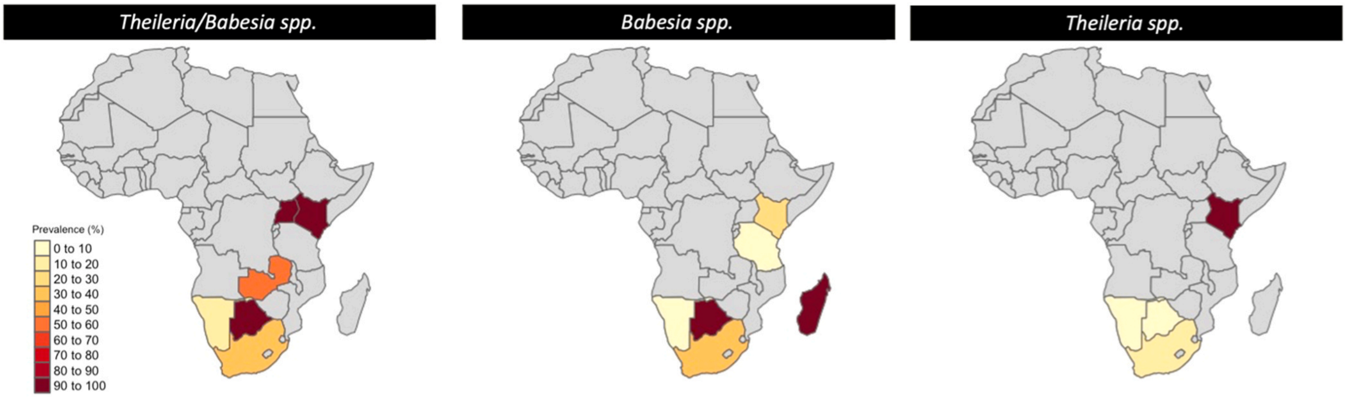

Fig. 7. Choropleth maps showing the molecular prevalence of *Theileria* and *Babesia* genera in African wildlife. Only the estimates showing a significant association with the variable "country" are displayed. Countries where the pathogen has not been investigated with molecular tests suitable for inclusion in the quantitative analysis or have not been investigated at all, are represented in grey.

which may exhibit low levels of parasitaemia, can pose serious biosecurity threats to animal health and conservation programs, especially in regions where wildlife–livestock interfaces are intensifying due to land–use changes.

4.4. Implications of canine Babesia spp. in wild felids

In the present review, we collate reports of *Babesia* spp. in African carnivores, though some identifications warrant careful interpretation. For instance, *B. canis* was reported in lions from South Africa (Broughton et al., 2021) and Botswana confirmed with sequencing (McDermid et al., 2017), yet the occurrence of *B. canis sensu stricto* in African wildlife is considered highly improbable, given that its primary vector (*Dermacentor reticulatus*) is restricted to Europe. Similarly, *B. vogeli* has been described in lions (Broughton et al., 2021), African wildcat and servals (Kelly et al., 2014), although the ecological relevance of this finding is uncertain because its vector, *Rhipicephalus sanguineus*, is rarely encountered in wildlife populations. In contrast, reports of *B. rossi* in lions (Broughton et al., 2021), African wild dogs (Matjila et al., 2008; Shabangu et al., 2021) and jackals (Penzhorn et al., 2017) are more plausible, as its principal vector (*Haemaphysalis elliptica*) is widespread in African carnivores. Attempts to detect *B. gibsoni* in wild carnivores, including wild canids and felids, have been consistently unsuccessful, suggesting that this parasite is poorly adapted to African ecosystems and the tick vectors present on the continent (Githaka et al., 2012; Matjila et al., 2008; Penzhorn et al., 2017; Shabangu et al., 2021; Viljoen et al., 2020, 2021).

The detection of canine *Babesia* spp. in apparently healthy wild felids raises important epidemiological questions. These animals may act as amplifying hosts or contribute to the maintenance of the host community (Haydon et al., 2002), potentially aiding in latent transmission cycles. Alternatively, they may represent incidental spillover hosts with limited epidemiological significance. The role of tick vectors that parasitize both wild carnivores and domestic dogs, such as *Haemaphysalis elliptica*, is especially relevant at the wildlife–domestic interface, where cross–species transmission could occur. Further studies are needed to confirm the identity and pathogenic potential of *Babesia* spp. in wild felids, using comprehensive molecular and phylogenetic tools.

4.5. Bovine babesiosis in African wildlife: underestimated or irrelevant?

In this review, the prevalence of *B. bovis* in African wildlife was estimated to be as low as 0.4 % (95 % CI: 0–6.5 %) in African buffalo, suggesting that this species is unlikely to be a significant reservoir. Instead, infections may be incidental, due to shared tick vectors with domestic cattle, or misidentified, due to false positive reactions. However, this may be underestimated due to the limited sensitivity of the molecular methods employed in most studies, primarily RLB. Similarly, *B. bigemina* was only sporadically detected in antelope species, including kudu (1/8) and impala (1/7) on South African game farms (Berggoetz et al., 2014). In contrast, *B. occultans*, a species typically associated with mild or subclinical infections (CFSPH, 2018), appears to be the most prevalent bovine *Babesia* species circulating in African wildlife: pooled prevalence was estimated at 23.3 % (CI: 16.2–31.3 %) in African buffalo and 30 % (CI: 15.2–47.3 %) in blue wildebeest (Table 3).

Given the low occurrence of the pathogenic *B. bovis* and *B. bigemina*, and the comparatively high prevalence of the less virulent *B. occultans*, it remains questionable whether African wildlife can serve as effective reservoirs for transmission of pathogenic bovine *Babesia* species to domestic cattle. Conversely, the possibility that livestock may act as sources of pathogenic *Babesia* for wildlife, particularly in species with limited prior exposure, deserves more attention. This scenario raises conservation concerns, especially where livestock and susceptible wildlife co–occur. Future research should focus on elucidating the directionality of transmission at the wildlife–livestock interface and assessing the impact of potential spillover events on vulnerable or naïve wildlife populations.

4.6. Carnivores, rodents and primates harbour zoonotic Babesia spp

We highlight the detection of *B. microti* in non–human primates from the Makueni and Kajiado districts of Kenya by means of nested PCR (Maamun et al., 2011), and in wild felids and rodents from multiple peri-urban and rural areas of South Africa and Botswana by means of RLB (Broughton et al., 2021; McDermid et al., 2017; Troskie et al., 2025; Viljoen et al., 2020), as well as a *B. odocoilei*–like parasite in captive lions from Gweru, Zimbabwe (Kelly et al., 2014). Across all included studies, the pooled prevalence of *B. microti* was 3.4 % (195 positive out of 2009 animal tested), with a substantial proportion of positive detections originating from African lions in Kruger National Park, South Africa (104/190) and four-striped grass mouse (*Rhabdomys pumilio*) (47/298).

These findings offer evidence of the presence and circulation of zoonotic *Babesia* species within African wildlife populations, particularly in landscapes characterised by intense agricultural activity, livestock production, tourism and frequent human–wildlife contact. Although the present analysis does not permit a quantitative assessment of spillover risk, the spatial clustering of detections in peri-urban and wildlife–livestock interface areas suggests contexts in which zoonotic transmission may be more likely. Future studies should prioritize molecular and serological surveillance of *Babesia* in both human populations and potential reservoir hosts. Special attention should be given

Table 2
Estimated pooled prevalences of *Theileriidae* in African wild mammal species. Empty cells indicate that the animals were not tested.

Animal species	*T/B* spp.	*T.* spp.	*T. bicornis*	*T. buffeli*	*T. equi*	*T. mutans*	*T. ovis*	*T. parva*	*T. separata*	*T.* sp. (buffalo)	*T.* sp. (giraffe)	*T.* sp. (kudu)	*T.* sp. (sable)	*T. taurotragi*	*T. velifera*
African buffalo (*Syncerus caffer*)	**62.3 %** [48.9–74.7 %]		0 % [0–0 %]	**13.6 %** [0–82.7 %]	0 % [0–0.8 %]	**41 %** [0–100 %]	**1.7 %** [0–86.1 %]	**62.9 %** [37.5–85 %]	0 % [0–0 %]	**31.7 %** [0–100 %]		0 % [0–0.8 %]	**2.9 %** [0–60.2 %]	0 % [0–0 %]	**26.7 %** [0–100 %]
African wild dog (*Lycaon pictus*)	**34.3 %** [0–100 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–1.6 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–1.6 %]	0 % [0–0 %]		0 % [0–0 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–0 %]
African wildcat (*Felis lybica*)								0 % [0–15.2 %]							
Black rhinoceros (*Diceros bicornis*)	**32.7 %** [0–100 %]	**0.7 %** [0–63.9 %]	**37.6 %** [0–100 %]	0 % [0–0 %]	**1.9 %** [0.4–4.7 %]	0 % [0–0 %]	0 % [0–0.6 %]	0 % [0–0 %]	0 % [0–0.6 %]	0 % [0–0.6 %]		0 % [0–0.6 %]	0 % [0–0.6 %]	0 % [0–0 %]	0 % [0–0 %]
Black wildebeest (*Connachaetes gnou*)	0 % [0–11.5 %]		**5.6 %** [0–20.4 %]	**5.6 %** [0–20.4 %]	0 % [0–6.3 %]	0 % [0–28.7 %]	0 % [0–28.7 %]		**44.4 %** [22.9–67.2 %]				**57.2 %** [0–100 %]	0 % [0–0 %]	0 % [0–28.7 %]
Black–backed jackal (*Lupulella mesomelas*)	**17.2 %** [0–100 %]		0 % [0–2.2 %]	0 % [0–2.2 %]	0 % [0–2.2 %]	0 % [0–2.2 %]	**4.7 %** [0.5–12.9 %]	0 % [0–2.2 %]	0 % [0–2.2 %]	0 % [0–2.2 %]		0 % [0–2.2 %]	**4.7 %** [0.5–12.9 %]	0 % [0–2.2 %]	0 % [0–2.2 %]
Blesbok (*Damaliscus pygargus*)	0 % [0–28.7 %]		0 % [0–28.7 %]	0 % [0–28.7 %]		0 % [0–28.7 %]	**33.3 %** [0.2–85.6 %]		0 % [0–28.7 %]				**66.7 %** [14.4–99.8 %]	0 % [0–0 %]	0 % [0–28.7 %]
Blue wildebeest (*Connachaetes taurinus*)	**85.4 %** [0–100 %]	**33.3 %** [17.9–50.9 %]	0 % [0–0 %]	**16.5 %** [0–100 %]	0 % [0–3.2 %]	0 % [0–0 %]	**3.3 %** [0–100 %]	0 % [0–3.2 %]	**25.9 %** [0–100 %]	0 % [0–3.2 %]		0 % [0–3.2 %]	**69.5 %** [2.9–100 %]	0 % [0–0 %]	0 % [0–0 %]
Brants's whistling rat (*Parotomys brantsii*)	**25 %** [0.1–72 %]	**25 %** [0.1–72 %]													
Brown hyaena (*Parahyaena brunnea*)	**53.3 %** [28.7–77.1 %]														
Bush vlei rat (*MyOtomys unisulcatus*)	**50 %** [25–75 %]	**21.4 %** [4.7–45.8 %]													
Cape bushbuck (*Tragelaphus sylvaticus*)				**100 %** [71.3–100 %]		**66.7 %** [14.4–99.8 %]		0 % [0–28.7 %]		0 % [0–28.7 %]			**26.9 %** [12–45.2 %]	**49.3 %** [0–100 %]	0 % [0–28.7 %]
Cape short–eared gerbil (*Desmodillus auricularis*)	0 % [0–22.1 %]	0 % [0–22.1 %]													
Caracal (*Caracal caracal*)	**36.8 %** [24.9–49.7 %]	**8.8 %** [2.9–17.4 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]		0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]
Chacma baboon (*Papio ursinus*)	0 % [0–69 %]														
Cheetah (*Acynonyx jubatus*)	**28.4 %** [0–100 %]	**60 %** [18.7–94 %]						0 % [0–22.1 %]							
Common eland (*Tragelaphus oryx*)	0 % [0–7.2 %]		0 % [0–7.2 %]	**49.3 %** [0–100 %]	0 % [0–22.1 %]	**29 %** [0–100 %]	0 % [0–10.3 %]	0 % [0–15.2 %]	0 % [0–7.2 %]	0 % [0–15.2 %]			0 % [0–0 %]	**51.8 %** [0–100 %]	0 % [0–0 %]

(*continued on next page*)

Table 2 (*continued*)

Animal species	*T/B* spp.	*T.* spp.	*T. bicornis*	*T. buffeli*	*T. equi*	*T. mutans*	*T. ovis*	*T. parva*	*T. separata*	*T.* sp. (buffalo)	*T.* sp. (giraffe)	*T.* sp. (kudu)	*T.* sp. (sable)	*T. taurotragi*	*T. velifera*
Common tsessebe (*Damaliscus lunatus*)	**8.5 %** [3.2–16 %]	**8.5 %** [3.2–16 %]	0 % [0–1.3 %]	0 % [0–1.3 %]	0 % [0–1.3 %]	0 % [0–1.3 %]	0 % [0–1.3 %]	0 % [0–1.3 %]	**4.2 %** [0.8–10.1 %]	0 % [0–1.3 %]		0 % [0–1.3 %]	**8.5 %** [3.2–16 %]	0 % [0–1.3 %]	0 % [0–1.3 %]
Elephant shrew (*Elephantulus* spp.)	**100 %** [59.2–100 %]	0 % [0–40.8 %]													
Four–striped grass mouse (*Rhabdomys pumilio*)	**48.7 %** [43–54.3 %]	**8.4 %** [5.5–11.8 %]													
Gemsbok (*Oryx gazella*)	**88.9 %** [61.8–100 %]		0 % [0–69 %]	0 % [0–69 %]		0 % [0–69 %]	0 % [0–69 %]		0 % [0–69 %]				**83.7 %** [0–100 %]	0 % [0–0 %]	0 % [0–69 %]
Giraffe (*Giraffa camelopardalis*)			0 % [0–18 %]	0 % [0–18 %]		0 % [0–18 %]	0 % [0–18 %]		0 % [0–18 %]				0 % [0–0 %]	0 % [0–0 %]	0 % [0–18 %]
Grant's gazelle (*Nanger granti*)	**100 %** [98.5–100 %]	**99.2 %** [96.8–100 %]													
Greater kudu (*Tragelaphus strepsiceros*)	**25.1 %** [0–100 %]	**39.7 %** [28.5–51.5 %]	**12.4 %** [0–100 %]	**27.2 %** [0–100 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–1.4 %]	0 % [0–0 %]	0 % [0–1.4 %]		**39.7 %** [28.5–51.5 %]	**5.7 %** [0–86.7 %]	**23.3 %** [0–99.9 %]	0 % [0–0 %]
Grevy's Zebra (*Equus grevyi*)					**100 %** [94.1–100 %]										
House mouse (*Mus musculus*)	**25 %** [9–45.7 %]	**20 %** [5.9–39.8 %]													
Impala (*Aepyceros melampus*)	**94.4 %** [12.1–100 %]	**100 %** [95–100 %]	**77.7 %** [0–100 %]	**43.1 %** [0–100 %]	0 % [0–5 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–0 %]		0 % [0–5 %]	**12.1 %** [0–83.8 %]	0 % [0–0 %]	0 % [0–0 %]
Lechwe (*Kobus leche*)	0 % [0–10.3 %]														
Leopard (*Panthera pardus*)	**100 %** [59.2–100 %]	0 % [0–40.8 %]													
Lion (*Panthera leo*)	**71 %** [0–100 %]	**9.8 %** [0–100 %]	**3.1 %** [0–39.5 %]					**1.1 %** [0–4.4 %]							
Maasai and reticulated giraffes (*Giraffa* spp.)	**100 %** [92.8–100 %]	**100 %** [92.8–100 %]		0 % [0–7.2 %]		0 % [0–7.2 %]	0 % [0–7.2 %]	0 % [0–7.2 %]		0 % [0–7.2 %]	**84.6 %** [61–98.3 %]	0 % [0–7.2 %]		0 % [0–7.2 %]	0 % [0–7.2 %]
Mesic four–striped grass rat (*Rhabdomys dilectus*)	**28.1 %** [14.2–44.7 %]	**15.6 %** [5.3–30 %]													
Mountain zebra (*Equus zebra*)					**100 %** [100–100 %]										
Namaqua rock rat (*Micaelamys namaquensis*)	**12 %** [2.5–27.3 %]	**4 %** [0–15 %]													
Natal multimammate mouse (*Mastomys natalensis*)	**20 %** [2.3–48.8 %]	0 % [0–9.3 %]													

(*continued on next page*)

Table 2 (*continued*)

Animal species	*T/B* spp.	*T.* spp.	*T. bicornis*	*T. buffeli*	*T. equi*	*T. mutans*	*T. ovis*	*T. parva*	*T. separata*	*T.* sp. (buffalo)	*T.* sp. (giraffe)	*T.* sp. (kudu)	*T.* sp. (sable)	*T. taurotragi*	*T. velifera*
Nyala (*Tragelaphus angasii*)	**93.8 %** [88.2–97.7 %]	**93.8 %** [88.2–97.7 %]	**52.6 %** [42.7–62.4 %]	**87.6 %** [80.4–93.4 %]	0 % [0–1 %]	0 % [0–1 %]	0 % [0–1 %]	0 % [0–1 %]	0 % [0–1 %]	0 % [0–1 %]		**89.7 %** [82.9–94.9 %]	**18.6 %** [0–100 %]	**1.2 %** [0–100 %]	0 % [0–1 %]
Plains zebra (*Equus quagga*)	**98.3 %** [0–100 %]	**71.4 %** [59–82.4 %]	**1.4 %** [0–38.8 %]	**1.4 %** [0–38.8 %]	**50 %** [0–100 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–0 %]	0 % [0–1.7 %]		0 % [0–1.7 %]	0 % [0–0 %]	0 % [0–1.7 %]	0 % [0–1.7 %]
Red hartebeest (*Alcelaphus buselaphus*)	**18.1 %** [0–100 %]		0 % [0–6.3 %]	0 % [0–6.3 %]	0 % [0–6.3 %]				**6.7 %** [0–24.2 %]				**2.4 %** [0–100 %]	0 % [0–69 %]	
Roan antelope (*Hippotragus equinus*)	**100 %** [31–100 %]		**100 %** [82–100 %]	**68.3 %** [0–100 %]	0 % [0–18 %]				**12.9 %** [0–100 %]				**100 %** [100–100 %]		
Sable antelope (*Hippotragus niger*)	**100 %** [88.5–100 %]		**100 %** [59.2–100 %]	**100 %** [59.2–100 %]		0 % [0–40.8 %]	**100 %** [59.2–100 %]		**100 %** [59.2–100 %]				**62.5 %** [0–100 %]	0 % [0–0 %]	0 % [0–40.8 %]
Serval (*Leptailurus serval*)								0 % [0–40.8 %]							
Sitatunga (*Tragelaphus spekii*)	**75 %** [28–99.9 %]														
South African pouched mouse (*Saccostomus campestris*)	**33.3 %** [0.2–85.6 %]	0 % [0–28.7 %]													
Southern African vlei rat (*Otomys irroratus*)	**100 %** [59.2–100 %]	0 % [0–40.8 %]													
Spotted hyaena (*Crocuta crocuta*)	**89.4 %** [79.1–96.5 %]														
Springbok (*Antidorcas marsupialis*)	0 % [0–13.1 %]		0 % [0–15.2 %]	0 % [0–15.2 %]		0 % [0–15.2 %]	0 % [0–15.2 %]		**16.7 %** [0–53.5 %]				**2.7 %** [0–100 %]	0 % [0–0 %]	0 % [0–15.2 %]
Vervet monkey (*Chlorocebus pygerythrus*)	0 % [0–69 %]														
Warthog (*Phacocoerus africanus*)	0 % [0–5.5 %]		0 % [0–28.7 %]	0 % [0–28.7 %]	0 % [0–28.7 %]				0 % [0–28.7 %]				0 % [0–28.7 %]		
Waterbuck (*Kobus ellipsiprymnus*)	**96.2 %** [85.6–100 %]	**96.2 %** [85.6–100 %]		0 % [0–3.6 %]	0 % [0–3.6 %]	0 % [0–3.6 %]		0 % [0–3.6 %]		0 % [0–3.6 %]	0 % [0–3.6 %]	0 % [0–3.6 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–3.6 %]
White rhinoceros (*Ceratotherium simum*)	**65.6 %** [48.6–80.8 %]		**35.4 %** [28.8–42.2 %]	0 % [0–0.5 %]	**9.2 %** [5.6–13.7 %]	0 % [0–0.5 %]		0 % [0–0.5 %]		0 % [0–0.5 %]		0 % [0–0.5 %]	0 % [0–0.5 %]	0 % [0–0.5 %]	0 % [0–0.5 %]
White–toothed shrews (*Crocidura* spp.)	0 % [0–10.3 %]	0 % [0–10.3 %]													

Table 3

Estimated pooled prevalences of *Babesiidae* in African wild mammal species. *Babesia divergens, B. gibsoni*, *B. major, B. vulpes* and *Babesia* sp. (sable) were not included because they were not detected in any of the animals tested. Empty cells indicate that the animals were not tested.

Animal species	*B. bicornis*	*B. bigemina*	*B. bovis*	*B. caballi*	*B. canis*	*B. felis*	*B. lengau*	*B. leo*	*B. microti*	*B. occultans*	*B. rossi*	*B. spp.*	*B. vogeli*
African buffalo (*Syncerus caffer*)	0 % [0–0.8 %]	0 % [0–0 %]	**0.4 %** [0–6.5 %]	0 % [0–0.8 %]	0 % [0–0.8 %]	0 % [0–0.8 %]			0 % [0–0.8 %]	**23.3 %** [16.2–31.3 %]	0 % [0–0.8 %]		0 % [0–0.8 %]
African wild dog (*Lycaon pictus*)	0 % [0–1.6 %]	0 % [0–0.3 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–0 %]		0 % [0–1.6 %]	0 % [0–0 %]		**6 %** [0–31.5 %]	**17.2 %** [0–100 %]	0 % [0–0 %]
African wildcat (*Felis lybica*)								0 % [0–15.2 %]					**100 %** [84.8–100 %]
Black rhinoceros (*Diceros bicornis*)	**24.5 %** [0–100 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–0.6 %]	0 % [0–0.6 %]	0 % [0–0.6 %]		0 % [0–0.6 %]	0 % [0–0 %]	0 % [0–0.6 %]	0 % [0–0 %]	**26.5 %** [0–100 %]	0 % [0–0.6 %]
Black wildebeest (*Connachaetes gnou*)		0 % [0–28.7 %]	0 % [0–28.7 %]										
Black–backed jackal (*Lupulella mesomelas*)	0 % [0–2.2 %]	0 % [0–2.2 %]	0 % [0–2.2 %]	0 % [0–2.2 %]	0 % [0–0 %]	0 % [0–2.2 %]	0 % [0–2.2 %]	0 % [0–2.2 %]	0 % [0–2.2 %]	0 % [0–2.2 %]	**8.6 %** [0–100 %]	**56.6 %** [0–100 %]	0 % [0–0 %]
Black–footed cat (*Felis nigripes*)						0 % [0–11.5 %]		0 % [0–11.5 %]				**62.5 %** [28.7–90.5 %]	
Blesbok (*Damaliscus pygargus*)		0 % [0–28.7 %]	0 % [0–28.7 %]										
Blue wildebeest (*Connachaetes taurinus*)	0 % [0–3.2 %]	0 % [0–0 %]	0 % [0–0 %]	0 % [0–3.2 %]	0 % [0–3.2 %]	0 % [0–3.2 %]	0 % [0–3.2 %]	0 % [0–3.2 %]	0 % [0–3.2 %]	**30 %** [15.2–47.3 %]	0 % [0–3.2 %]	**3.3 %** [0–12.6 %]	0 % [0–3.2 %]
Brants's whistling rat (*Parotomys brantsii*)			0 % [0–22.1 %]						0 % [0–22.1 %]			0 % [0–22.1 %]	
Brown hyaena (Parah*yaena brunnea*)							**70.6 %** [47.5–89.2 %]					**66.7 %** [41.7–87.4 %]	
Bush vlei rat (*MyOtomys unisulcatus*)			0 % [0–6.7 %]						0 % [0–6.7 %]			**35.7 %** [13.7–61.6 %]	
Cape bushbuck (*Tragelaphus sylvaticus*)		0 % [0–28.7 %]	0 % [0–28.7 %]										
Cape short–eared gerbil (*Desmodillus auricularis*)			0 % [0–22.1 %]						0 % [0–22.1 %]			0 % [0–22.1 %]	
Caracal (*Caracal caracal*)	0 % [0–3.2 %]	0 % [0–3.2 %]	0 % [0–3.2 %]	0 % [0–3.2 %]	0 % [0–3.2 %]	**17.7 %** [0–100 %]	0 % [0–3.2 %]	**15.8 %** [0–100 %]	**46.7 %** [29.4–64.4 %]	0 % [0–3.2 %]	0 % [0–3.2 %]	**54 %** [0–100 %]	0 % [0–3.2 %]
Cheetah (*Acynonyx jubatus*)					0 % [0–18 %]	**6.9 %** [0–100 %]	0 % [0–18 %]	**28 %** [0–100 %]				**37.5 %** [0–100 %]	0 % [0–22.1 %]
Common eland (*Tragelaphus oryx*)		0 % [0–0 %]	0 % [0–0 %]										
Common tsessebe (*Damaliscus lunatus*)	0 % [0–1.3 %]	0 % [0–1.3 %]	0 % [0–1.3 %]	0 % [0–1.3 %]	0 % [0–1.3 %]	0 % [0–1.3 %]			0 % [0–1.3 %]		0 % [0–1.3 %]	0 % [0–1.3 %]	0 % [0–1.3 %]

(*continued on next page*)

Table 3 (*continued*)

Animal species	***B. bicornis***	***B. bigemina***	***B. bovis***	***B. caballi***	***B. canis***	***B. felis***	***B. lengau***	***B. leo***	***B. microti***	***B. occultans***	***B. rossi***	***B. spp.***	***B. vogeli***
Diademed sifaka (*Propithecus diadema*)												**100 %** [98.1–100 %]	
Eastern woolly lemur (*Avahi laniger*)												**100 %** [86.9–100 %]	
Elephant shrew (*Elephantulus* spp.)			0 % [0–40.8 %]						0 % [0–40.8 %]			**100 %** [59.2–100 %]	
Four–striped grass mouse (*Rhabdomys pumilio*)			**1.3 %** [0.4–3 %]						**15.8 %** [11.9–20.1 %]			**44 %** [38.4–49.6 %]	
Gemsbok (*Oryx gazella*)		0 % [0–69 %]	0 % [0–69 %]										
Giraffe (*Giraffa camelopardalis*)		0 % [0–18 %]	0 % [0–18 %]										
Greater kudu (*Tragelaphus strepsiceros*)	0 % [0–1.4 %]	**1.9 %** [0–100 %]	0 % [0–0 %]	0 % [0–1.4 %]	0 % [0–1.4 %]	0 % [0–1.4 %]	0 % [0–1.4 %]	0 % [0–1.4 %]	0 % [0–1.4 %]	0 % [0–1.4 %]	0 % [0–1.4 %]	0 % [0–1.4 %]	0 % [0–1.4 %]
Greater weasel lemur (*Lepilemur mustelinus*)												0 % [0–28.7 %]	
Grevy's Zebra (*Equus grevyi*)				0 % [0–5.9 %]									
Grivet (*Chlorocebus aethiops*)									**20 %** [10.9–31 %]				
House mouse (*Mus musculus*)			0 % [0–4.7 %]						0 % [0–4.7 %]			0 % [0–4.7 %]	
Impala (*Aepyceros melampus*)	0 % [0–5 %]	**1 %** [0–33.4 %]	0 % [0–0 %]	0 % [0–5 %]	0 % [0–5 %]	0 % [0–5 %]	0 % [0–5 %]	0 % [0–5 %]	0 % [0–5 %]	0 % [0–5 %]	0 % [0–5 %]	0 % [0–5 %]	0 % [0–5 %]
Indri (*Indri indri*)												**100 %** [93.7–100 %]	
Leopard (*Panthera pardus*)					0 % [0–40.8 %]	0 % [0–0 %]	0 % [0–40.8 %]	**100 %** [100–100 %]				**54.3 %** [0–100 %]	
Lion (*Panthera leo*)					**7.8 %** [0–98.8 %]	**25.5 %** [0–92.9 %]	**9.2 %** [0–100 %]	**31.8 %** [6–66.2 %]	**35.7 %** [0–100 %]		**8.4 %** [4.9–12.8 %]	**64.4 %** [0–100 %]	**13.9 %** [0.2–43.2 %]
Maasai and reticulated giraffes (*Giraffa* spp.)												0 % [0–7.2 %]	
Mesic four–striped grass rat (*Rhabdomys dilectus*)			0 % [0–3 %]						**3.1 %** [0–11.8 %]			**18.7 %** [7.4–33.9 %]	
Mountain zebra (*Equus zebra*)				**2.8 %** [0–90.2 %]									

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Table 3 (*continued*)

Animal species	*B. bicornis*	*B. bigemina*	*B. bovis*	*B. caballi*	*B. canis*	*B. felis*	*B. lengau*	*B. leo*	*B. microti*	*B. occultans*	*B. rossi*	*B. spp.*	*B. vogeli*
Namaqua rock rat (*Micaelamys namaquensis*)			0 % [0–3.8 %]						0 % [0–3.8 %]			**24 %** [9.7–42.3 %]	
Natal multimammate mouse (*Mastomys natalensis*)			0 % [0–9.3 %]						0 % [0–9.3 %]			**4.1 %** [0–100 %]	
Nyala (*Tragelaphus angasii*)	0 % [0–1 %]	0 % [0–1 %]	0 % [0–1 %]	0 % [0–1 %]	0 % [0–1 %]	0 % [0–1 %]			0 % [0–1 %]		0 % [0–1 %]	0 % [0–1 %]	0 % [0–1 %]
Plains zebra (*Equus quagga*)	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	**5.3 %** [0–100 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	0 % [0–1.7 %]	**80.4 %** [69–89.6 %]	
Sable antelope (*Hippotragus niger*)		0 % [0–40.8 %]	0 % [0–40.8 %]										
Serval (*Leptailurus serval*)						**33.3 %** [0.2–85.6 %]		0 % [0–0 %]				0 % [0–28.7 %]	**100 %** [59.2–100 %]
South African pouched mouse (*Saccostomus campestris*)			0 % [0–28.7 %]						0 % [0–28.7 %]			**66.7 %** [14.4–99.8 %]	
Southern African vlei rat (*Otomys irroratus*)			0 % [0–40.8 %]						0 % [0–40.8 %]			**50 %** [0.9–99.1 %]	
Spotted hyaena (*Crocuta crocuta*)							**55.8 %** [40.9–70.2 %]					**89.4 %** [79.1–96.5 %]	
Springbok (*Antidorcas marsupialis*)		0 % [0–15.2 %]	0 % [0–15.2 %]										
White rhinoceros (*Ceratotherium simum*)	0 % [0–0.5 %]	0 % [0–0.5 %]	0 % [0–0.5 %]	0 % [0–0.5 %]	0 % [0–0.5 %]	0 % [0–0.5 %]			0 % [0–0.5 %]		0 % [0–0.5 %]		
White–toothed shrews (*Crocidura* spp.)			0 % [0–10.3 %]						0 % [0–10.3 %]			**11.1 %** [0–38.2 %]	
Yellow baboon (*Papio cynocephalus*)									**23.1 %** [13.7–34 %]				

to individuals in rural and peri-urban areas with high tick exposure, such as farmers, wildlife professionals and bushmeat handlers. An integrated One Health approach will be essential to properly assess the zoonotic risk and implement evidence-based control strategies.

4.7. Limitations and future perspectives

Molecular testing has become the gold standard for diagnosis and differentiation of *Babesia* and *Theileria* in African wildlife, with a majority of the studies (47/56 studies; 84 %) utilizing this approach. Despite this widespread adoption, several important limitations persist. A recurrent challenge across many studies is the inability to definitively classify novel or divergent strains. Consequently, researchers often need to rely on provisional or uncertain nomenclature, such as *Theileria sp.* (waterbuck) or *Theileria* sp. (sable)-like, which highlights the need for more comprehensive genetic characterization and standardized taxonomy. One of the primary obstacles to accurate molecular identification lies in the technical difficulty of sequencing long DNA regions in the presence of co-infections, which is particularly problematic in wildlife, or the inability to isolate and establish axenic cultures of piroplasms *in vitro*, which are essential for whole-genome sequencing and formal species denomination. Advanced techniques such as full-length 18S rRNA gene sequencing (*e.g.*, via cloning or long-read next-generation sequencing) or even whole-genome sequencing offer significantly higher discriminatory power. In this review, only one study made use of next-generation sequencing in wildlife samples (Squarre et al., 2020). These approaches not only enhance species-level resolution but can also reveal insights into microbial evolution and host specificity (Cossu et al., 2025; Makgabo et al., 2023). As the cost of sequencing continues to decline and technical expertise becomes more widespread across African research institutions, it is expected that these methods will become increasingly accessible.

Among the studies employing molecular techniques, RLB remains the most commonly used approach (27/47; 57 %). While RLB offers a practical means to screen for and differentiate between multiple pathogens simultaneously, it also presents notable limitations. RLB probes are typically designed to target short hypervariable regions within conserved genes (primarily 16S and 18S rRNA genes) (Berggoetz et al., 2014; Bosman et al., 2007; Cossu, Ochai, et al., 2024; Eygelaar et al., 2015; Matjila et al., 2008; Nijhof et al., 2003; Penzhorn et al., 2017; Penzhorn and Chaparro, 1994; Troskie et al., 2025; Viljoen et al., 2020, 2021), resulting in cross–reaction between similar microbial oganisms, particularly in complex samples containing mixed infections or previously uncharacterized parasites. These challenges underscore the urgent need to supplement RLB with sequence-based methods in order to achieve accurate surveillance and robust phylogenetic analysis. RLB membranes specific for relevant pathogen species (*e.g. T. parva, B. bovis, B. rossi* etc.) may also be developed incorporating additional confirmatory genetic markers with higher species specificity, therefore improving diagnostic accuracy and reducing cross-reactivity.

Future research should prioritize the centralization of epidemiological data in a reliable and flexible digital platform, such as Aleph∞One (https://aleph-one.carlocossu.it/), to integrate heterogeneous infectious disease datasets. Such platforms can serve both as a primary information hub and a comprehensive data repository, enhancing collaboration, traceability and accessibility of surveillance data. Building on this foundation, we recommend three complementary, actionable strategies to maximize impact on understanding piroplasmid ecology and managing spillover risk at the wildlife-livestock-human interface: (i) structured observational surveillance, including retrospective, cross-sectional, and longitudinal designs, focused on high-risk wildlife species at interface zones to enable early detection of emerging infections; (ii) adopt advanced and cost-effective molecular diagnostics combining broad-range screening with confirmatory species-specific assays and high-resolution genomic approaches to improve taxonomic classification; and (iii) integrate ecological and host behavioral data alongside molecular results to model host-vector-parasite dynamics and identify critical control points. Collectively, these approaches provide a practical One Health–oriented framework to advance surveillance, risk assessment and management of *Babesia* and *Theileria* species circulating in African wildlife.

CRediT authorship contribution statement

Henriette van Heerden: Writing – review & editing, Validation, Supervision, Resources, Project administration, Investigation, Data curation, Conceptualization. **Carlo Andrea Cossu:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Coenraad Blignaut:** Writing – review & editing, Writing – original draft, Investigation, Data curation. **Raksha Vasantrai Bhoora:** Writing – review & editing, Validation, Supervision, Data curation. **Luis Neves:** Writing – review & editing, Validation, Data curation. **Andeliza Smit:** Writing – review & editing, Validation, Data curation. **Sibeko Kgomotso:** Writing – review & editing, Validation, Data curation. **Darshana Morar-Leather:** Writing – review & editing, Validation, Data curation. **Nicola Collins:** Writing – review & editing, Validation, Data curation. **Oosthuizen Marinda C:** Writing – review & editing, Validation, Data curation.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.prevetmed.2026.106813.

References

AbdelRahman, M.A.E., 2023. An overview of land degradation, desertification and sustainable land management using GIS and remote sensing applications. Rend. Lince.. Sci. Fis. e Nat. 34 (3), 767–808. https://doi.org/10.1007/s12210-023-01155-3.

Baker, R.E., Mahmud, A.S., Miller, I.F., Rajeev, M., Rasambainarivo, F., Rice, B.L., Takahashi, S., Tatem, A.J., Wagner, C.E., Wang, L.F., Wesolowski, A., Metcalf, C.J.E., 2022. Infectious disease in an era of global change. Nat. Rev. Microbiol. 20 (4), 193–205. https://doi.org/10.1038/s41579-021-00639-z.

Berggoetz, M., Schmid, M., Ston, D., Wyss, V., Chevillon, C., Pretorius, A.-M., Gern, L., 2014. Tick-borne pathogens in the blood of wild and domestic ungulates in South Africa: Interplay of game and livestock. Ticks Tick. borne Dis. 5 (2), 166–175. https://doi.org/10.1016/j.ttbdis.2013.10.007.

Bhoora, R., Buss, P., Guthrie, A.J., Penzhorn, B.L., Collins, N.E., 2010. Genetic diversity of piroplasms in plains zebra (*Equus quagga burchellii*) and Cape mountain zebra (*Equus zebra zebra*) in South Africa. Vet. Parasitol. 174 (1–2), 145–149. https://doi.org/10.1016/j.vetpar.2010.08.014.

Bhoora, R.V., Collins, N.E., Schnittger, L., Troskie, C., Marumo, R., Labuschagne, K., Smith, R.M., Dalton, D.L., Mbizeni, S., 2020. Molecular genotyping and epidemiology of equine piroplasmids in South Africa. Ticks Tick. Borne Dis. 11 (2), 101358. https://doi.org/10.1016/j.ttbdis.2019.101358.

Bhoora, R., Quan, M., Franssen, L., Butler, C.M., Van der Kolk, J.H., Guthrie, A.J., Zweygarth, E., Jongejan, F., Collins, N.E., 2010. Development and evaluation of real-time PCR assays for the quantitative detection of *Babesia caballi* and *Theileria equi* infections in horses from South Africa. Vet. Parasitol. 168 (3–4), 201–211.

Birkenheuer, A.J., Neel, J., Ruslander, D., Levy, M.G., Breitschwerdt, E.B., 2004. Detection and molecular characterization of a novel large *Babesia* species in a dog. Vet. Parasitol. 124 (3–4), 151–160. https://doi.org/10.1016/j.vetpar.2004.07.008.

Bosman, A.M., Venter, E.H., Penzhorn, B.L., 2007. Occurrence of *Babesia felis* and *Babesia leo* in various wild felid species and domestic cats in Southern Africa, based on reverse line blot analysis. Vet. Parasitol. 144 (1–2), 33–38. https://doi.org/10.1016/j.vetpar.2006.09.025.

Bradley, C.A., Altizer, S., 2007. Urbanization and the ecology of wildlife diseases. Trends Ecol. Evol. 22 (2), 95–102. https://doi.org/10.1016/j.tree.2006.11.001.

Brothers, P.S., Collins, N.E., Oosthuizen, M.C., Bhoora, R., Troskie, M., Penzhorn, B.L., 2011. Occurrence of blood-borne tick-transmitted parasites in common tsessebe (*Damaliscus lunatus*) antelope in Northern Cape Province, South Africa. Vet. Parasitol. 183 (1–2), 160–165. https://doi.org/10.1016/j.vetpar.2011.06.015.

Broughton, H., Govender, D., Serrano, E., Shikwambana, P., Jolles, A., 2021. Equal contributions of feline immunodeficiency virus and coinfections to morbidity in African lions. Int. J. Parasitol. Parasites Wildl. 16, 83–94. https://doi.org/10.1016/j.ijppaw.2021.07.003.

Burroughs, R.E.J., Penzhorn, B.L., Wiesel, I., Barker, N., Vorster, I., Oosthuizen, M.C., 2017. Piroplasms in brown hyaenas (*Parahyaena brunnea*) and spotted hyaenas (*Crocuta crocuta*) in Namibia and South Africa are closely related to *Babesia lengau*. Parasitol. Res 116 (2), 685–692. https://doi.org/10.1007/s00436-016-5334-5.

Campbell, B.M., Beare, D.J., Bennett, E.M., Hall-Spencer, J.M., Ingram, J.S.I., Jaramillo, F., Ortiz, R., Ramankutty, N., Sayer, J.A., Shindell, D., 2017. Agriculture production as a major driver of the earth system exceeding planetary boundaries. Ecol. Soc. 22 (4). https://doi.org/10.5751/ES-09595-220408.

Caron, A., Miguel, E., Gomo, C., Makaya, P., Pfukenyi, D.M., Foggin, C., Hove, T., de Garine-Wichatitsky, M., 2013. Relationship between burden of infection in ungulate populations and wildlife/livestock interfaces. Epidemiol. Infect. 141 (7), 1522–1535. https://doi.org/10.1017/s0950268813000204.

CFSPH, 2018. Bov. Babesiosis. ⟨www.cfsph.iastate.edu⟩.

Choopa, C.N., Muleya, W., Fandamu, P., Mukolwe, L.D., Sibeko-Matjila, K.P., 2024. p67 gene alleles sequence analysis reveals *Theileria parva* parasites associated with East Coast fever and Corridor disease in buffalo from Zambia. Vet. Parasitol. 330, 110240. https://doi.org/10.1016/j.vetpar.2024.110240.

Cossu, C.A., Bhoora, R.V., Cassini, R., van Heerden, H., 2022. The significance of viral, bacterial and protozoan infections in zebra: a systematic review and meta-analysis of prevalence. Hystrix Ital. J. Mammal. https://doi.org/10.4404/hystrix-00501-2021.

Cossu, C.A., Cassini, R., Bhoora, R.V., Menandro, M.L., Oosthuizen, M.C., Collins, N.E., Wentzel, J., Quan, M., Fagir, D.M., van Heerden, H., 2024. Occurrence and molecular prevalence of *Anaplasmataceae, Rickettsiaceae* and *Coxiellaceae* in African wildlife: A systematic review and meta-analysis. In: In Preventive Veterinary Medicine, 230. Elsevier B.V. https://doi.org/10.1016/j.prevetmed.2024.106257.

Cossu, C.A., Collins, N.E., Oosthuizen, M.C., Menandro, M.L., Bhoora, R.V., Vorster, I., Cassini, R., Stoltsz, H., Quan, M., van Heerden, H., 2023. Distribution and Prevalence of *Anaplasmataceae, Rickettsiaceae* and *Coxiellaceae* in African Ticks: A Systematic Review and Meta-Analysis. In: In Microorganisms, 11. MDPI. https://doi.org/10.3390/microorganisms11030714.

Cossu, C.A., Garofolo, G., Janowicz, A., De Massis, F., Wentzel, J., Ledwaba, M.B., Sabeta, C., De Klerk, L.M., Godfroid, J., Vergnaud, G., van Heerden, H., 2025. Phylogenomics of *Brucella abortus* isolated from African Buffalo in Kruger National Park: New perspectives on wildlife-cattle disease dynamics. Vet. Microbiol. 304. https://doi.org/10.1016/j.vetmic.2025.110493.

Cossu, C.A., Ochai, S.O., Troskie, M., Hartmann, A., Godfroid, J., de Klerk, L.-M., Turner, W., Kamath, P., van Schalkwyk, O.L., Cassini, R., Bhoora, R., van Heerden, H., 2024. Detection of Tick-Borne Pathogen Coinfections and Coexposures to Foot-and-Mouth Disease, Brucellosis, and Q Fever in Selected Wildlife From Kruger National Park, South Africa, and Etosha National Park, Namibia. Transbound. Emerg. Dis. 2024 (1). https://doi.org/10.1155/tbed/2417717.

Coultous, R.M., Sutton, D.G.M., Boden, L.A., 2023. A risk assessment of equine piroplasmosis entry, exposure and consequences in the UK. Equine Vet. J. 55 (2), 282–294. https://doi.org/10.1111/evj.13579.

Cozim-Melges, F., Ripoll-Bosch, R., Veen, G.F., Oggiano, P., Bianchi, F.J.J.A., van der Putten, W.H., van Zanten, H.H.E., 2024. Farming practices to enhance biodiversity across biomes: a systematic review. Npj Biodivers. 3 (1). https://doi.org/10.1038/s44185-023-00034-2.

Decaro, N., Larocca, V., Parisi, A., Losurdo, M., Lia, R.P., Greco, M.F., Miccolis, A., Ventrella, G., Otranto, D., Buonavoglia, C., 2013. Clinical bovine piroplasmosis caused by *Babesia occultans* in Italy. J. Clin. Microbiol. 51 (7), 2432–2434. https://doi.org/10.1128/JCM.00713-13.

Eygelaar, D., Jori, F., Mokopasetso, M., Sibeko, K.P., Collins, N.E., Vorster, I., Troskie, M., Oosthuizen, M.C., 2015. Tick-borne haemoparasites in African buffalo (*Syncerus caffer*) from two wildlife areas in Northern Botswana. Parasit. Vectors 8, 26. https://doi.org/10.1186/s13071-014-0627-y.

Facile, V., Magliocca, M., Dini, F.M., Imposimato, I., Mariella, J., Freccero, F., Urbani, L., Rinnovati, R., Sel, E., Gallina, L., Castagnetti, C., Galuppi, R., Battilani, M., Balboni, A., 2025. Molecular Diagnosis and Identification of Equine Piroplasms: Challenges and Insights from a Study in Northern Italy. Animals 15 (3). https://doi.org/10.3390/ani15030437.

Ghai, R.R., Mutinda, M., Ezenwa, V.O., 2016. Limited sharing of tick-borne hemoparasites between sympatric wild and domestic ungulates. Vet. Parasitol. 226, 167–173. https://doi.org/10.1016/j.vetpar.2016.07.005.

Gibb, R., Ryan, S.J., Pigott, D., Fernandez, M. del P., Muylaert, R.L., Albery, G.F., Becker, D.J., Blackburn, J.K., Caceres-Escobar, H., Celone, M., Eskew, E.A., Frank, H.K., Han, B.A., Hulland, E.N., Jones, K.E., Katz, R., Kucharski, A., Limmathurotsakul, D., Lippi, C.A., … Carlson, C.J. (2024). The anthropogenic fingerprint on emerging infectious diseases. https://doi.org/10.1101/2024.05.22.24307684.

Githaka, N., Konnai, S., Bishop, R., Odongo, D., Lekolool, I., Kariuki, E., Gakuya, F., Kamau, L., Isezaki, M., Murata, S., Ohashi, K., 2014. Identification and sequence characterization of novel *Theileria* genotypes from the waterbuck (*Kobus defassa*) in a *Theileria parva*-endemic area in Kenya. Vet. Parasitol. 202 (3–4), 180–193. https://doi.org/10.1016/j.vetpar.2014.02.056.

Githaka, N., Konnai, S., Kariuki, E., Kanduma, E., Murata, S., Ohashi, K., 2012. Molecular detection and characterization of potentially new *Babesia* and *Theileria* species/variants in wild felids from Kenya. Acta Trop. 124 (1), 71–78. https://doi.org/10.1016/j.actatropica.2012.06.013.

Githaka, N., Konnai, S., Skilton, R., Kariuki, E., Kanduma, E., Murata, S., Ohashi, K., 2013. Genotypic variations in field isolates of *Theileria* species infecting giraffes (*Giraffa camelopardalis tippelskirchi* and *Giraffa camelopardalis reticulata*) in Kenya. Parasitol. Int. 62 (5), 448–453. https://doi.org/10.1016/j.parint.2013.06.002.

Govender, D., Oosthuisen, M.C., Penzhorn, B.L., 2011. Piroplasm parasites of white rhinoceroses (*Ceratotherium simum*) in the Kruger National Park, and their relation to anaemia. J. South Afr. Vet. Assoc. 82 (2), 36–40. https://doi.org/10.4102/jsava.v82i2.60.

Gray, J.S., Estrada-Peña, A., Zintl, A., 2019. Vectors of Babesiosis. Annu. Rev. Entomol. 64 (1), 149–165. https://doi.org/10.1146/annurev-ento-011118-111932.

Haydon, D.T., Cleaveland, S., Taylor, L.H., Laurenson, M.K., 2002. Identifying reservoirs of infection: A conceptual and practical challenge. Emerg. Infect. Dis. 8 (12), 1468–1473. https://doi.org/10.3201/eid0812.010317.

Jacob, S.S., Sengupta, P.P., Paramanandham, K., Suresh, K.P., Chamuah, J.K., Rudramurthy, G.R., Roy, P., 2020. Bovine babesiosis: An insight into the global perspective on the disease distribution by systematic review and meta-analysis. Vet. Parasitol. 283. https://doi.org/10.1016/j.vetpar.2020.109136.

Keck, F., Peller, T., Alther, R., Barouillet, C., Blackman, R., Capo, E., Chonova, T., Couton, M., Fehlinger, L., Kirschner, D., Knüsel, M., Muneret, L., Oester, R., Tapolczai, K., Zhang, H., Altermatt, F., 2025. The global human impact on biodiversity. Nature. https://doi.org/10.1038/s41586-025-08752-2.

Kelly, P., Marabini, L., Dutlow, K., Zhang, J., Loftis, A., Wang, C., 2014. Molecular detection of tick-borne pathogens in captive wild felids, Zimbabwe. Parasit. Vectors 7, 514. https://doi.org/10.1186/s13071-014-0514-6.

Kerber, A.E., Ferreira, C.E., Pereira, F.G., 1999. Control of equine piroplasmosis in Brazil. Onderstepoort J. Vet. Res. 66.

King'ori, E.M., Obanda, V., Ndambiri, E.M., Runo, S.M., Chiyo, P.I., 2018. Adding injury to infection: The relationship between injury status and genetic diversity of *Theileria* infecting plains zebra, *Equus quagga*. Infect. Genet. Evol. 58, 269–278. https://doi.org/10.1016/j.meegid.2018.01.010.

Krause, P.J., 2019. Human babesiosis. In: In International Journal for Parasitology, 49. Elsevier Ltd, pp. 165–174. https://doi.org/10.1016/j.ijpara.2018.11.007.

Krause, P.J., Gewurz, B.E., Hill, D., Marty, F.M., Vannier, E., Foppa, I.M., Furman, R.R., Neuhaus, E., Skowron, G., Gupta, S., McCalla, C., Pesanti, E.L., Young, M., Heiman, D., Hsue, G., Gelfand, J.A., Wormser, G.P., Dickason, J., Bia, F.J., Spielman, A., 2008. Persistent and relapsing babesiosis in immunocompromised patients. Clin. Infect. Dis. 46 (3), 370–376. https://doi.org/10.1086/525852.

Kumar, A., O'bryan, J., Krause, P.J., 2021. The global emergence of human babesiosis. In: In Pathogens, 10. MDPI. https://doi.org/10.3390/pathogens10111447.

Lawrence, J.A., Perry, B.D., Williamson, S.M., 2004. East Coast Fever. In: Coetzer, In.J.A. W., Tustin, R.C. (Eds.), Infectious Diseases of Livestock, 2nd ed., 1. Oxford University Press, pp. 448–467.

Leisewitz, A.L., Mrljak, V., Dear, J.D., Birkenheuer, A., 2023. The Diverse Pathogenicity of Various *Babesia* Parasite Species That Infect Dogs. In: In Pathogens, 12. Multidisciplinary Digital Publishing Institute (MDPI). https://doi.org/10.3390/pathogens12121437.

Maamun, J.M., Suleman, M.A., Akinyi, M., Ozwara, H., Kariuki, T., Carlsson, H.E., 2011. Prevalence of *Babesia microti* in free-ranging baboons and African green monkeys. J. Parasitol. 97 (1), 63–67. https://doi.org/10.1645/ge-2391.1.

Makgabo, S.M., Brayton, K.A., Oosthuizen, M.C., Collins, N.E., 2023. Unravelling the diversity of *Anaplasma* species circulating in selected African wildlife hosts by targeted 16S microbiome analysis. Curr. Res. Microb. Sci. 5. https://doi.org/10.1016/j.crmicr.2023.100198.

Matjila, P.T., Leisewitz, A.L., Jongejan, F., Bertschinger, H.J., Penzhorn, B.L., 2008. Molecular detection of *Babesia rossi* and *Hepatozoon* sp. in African wild dogs (*Lycaon pictus*) in South Africa. Vet. Parasitol. 157 (1–2), 123–127. https://doi.org/10.1016/j.vetpar.2008.07.016.

Mbizeni, S., Potgieter, F.T., Troskie, C., Mans, B.J., Penzhorn, B.L., Latif, A.A., 2013. Field and laboratory studies on Corridor disease (*Theileria parva* infection) in cattle population at the livestock/game interface of uPhongolo-Mkuze area, South Africa. Ticks Tick. Borne Dis. 4 (3), 227–234. https://doi.org/10.1016/j.ttbdis.2012.11.005.

McDermid, K.R., Snyman, A., Verreynne, F.J., Carroll, J.P., Penzhorn, B.L., Yabsley, M.J., 2017. Surveillance for viral and parasitic pathogens in a vulnerable African lion (*Panthera leo*) population in the northern Tuli game reserve, Botswana. J. Wildl. Dis. 53 (1), 54–61. https://doi.org/10.7589/2015-09-248.

Moloi, T.P., 2010. Serol. Mol. Epidemiol. strain Divers. Equine piroplasms South Afr. [Univ. Free State]. ⟨http://hdl.handle.net/11660/1862⟩.

Morrison, W.I., Hemmink, J.D., Toye, P.G., 2020. *Theileria parva*: a parasite of African buffalo, which has adapted to infect and undergo transmission in cattle. In: In International Journal for Parasitology, 50. Elsevier Ltd, pp. 403–412. https://doi.org/10.1016/j.ijpara.2019.12.006.

Munang'andu, H.M., Siamudaala, V., Matandiko, W., Mulumba, M., Nambota, A., Munyeme, M., Mutoloki, S., Nonga, H., 2009. Detection of *Theileria parva* antibodies in the African buffalo (*Syncerus caffer*) in the livestock–wildlife interface areas of Zambia. Vet. Parasitol. 166 (1–2), 163–166. https://doi.org/10.1016/j.vetpar.2009.08.010.

Mwamuye, M.M., Odongo, D., Kazungu, Y., Kindoro, F., Gwakisa, P., Bishop, R.P., Nijhof, A.M., Obara, I., 2020. Variant analysis of the sporozoite surface antigen gene reveals that asymptomatic cattle from wildlife-livestock interface areas in northern

Tanzania harbour buffalo-derived *T. parva*. Parasitol. Res. 119 (11), 3817–3828. https://doi.org/10.1007/s00436-020-06902-1.

Nakayima, J., Hayashida, K., Nakao, R., Ishii, A., Ogawa, H., Nakamura, I., Moonga, L., Hang'ombe, B.M., Mweene, A.S., Thomas, Y., Orba, Y., Sawa, H., Sugimoto, C., 2014. Detection and characterization of zoonotic pathogens of free-ranging non-human primates from Zambia. Parasit. Vectors 7, 490. https://doi.org/10.1186/s13071-014-0490-x.

Neitz, W.O., Canham, A.S., Kluge, E.B., 1992. Corridor disease: a fatal form of bovine theileriosis encountered in Zululand. J. South Afr. Vet. Assoc. 26 (2), 79–87.

Nijhof, A.M., Penzhorn, B.L., Lynen, G., Mollel, J.O., Morkel, P., Bekker, C.P.J., Jongejan, F., 2003. *Babesia bicornis* sp. nov. and *Theileria bicornis* sp. nov.: Tick-Borne Parasites Associated with Mortality in the Black Rhinoceros (*Diceros bicornis*. J. Clin. Microbiol. 41 (5), 2249–2254. https://doi.org/10.1128/JCM.41.5.2249-2254.2003.

Nijhof, A.M., Pillay, V., Steyl, J., Prozesky, L., Stoltsz, W.H., Lawrence, J.A., Penzhorn, B. L., Jongejan, F., 2005. Molecular characterization of *Theileria* species associated with mortality in four species of African antelopes. J. Clin. Microbiol. 43 (12), 5907–5911. https://doi.org/10.1128/JCM.43.12.5907-5911.2005.

Norval, R.A., Perry, B.D., Young, A.S., 1992. The Epidemiology of Theileriosis in Africa. Academic Press.

Nuttall, P.A., 2022. Climate change impacts on ticks and tick-borne infections. In: In Biologia, 77. Springer Science and Business Media Deutschland GmbH, pp. 1503–1512. https://doi.org/10.1007/s11756-021-00927-2.

Oosthuizen, M.C., Allsopp, B.A., Troskie, M., Collins, N.E., Penzhorn, B.L., 2009. Identification of novel Babesia and Theileria species in South African giraffe (*Giraffa camelopardalis*, Linnaeus, 1758) and roan antelope (*Hippotragus equinus*, Desmarest 1804). Vet. Parasitol. 163 (1–2), 39–46. https://doi.org/10.1016/j.vetpar.2009.03.045.

Oura, C.A.L., Tait, A., Asiimwe, B., Lubega, G.W., Weir, W., 2011b. *Theileria parva* genetic diversity and haemoparasite prevalence in cattle and wildlife in and around Lake Mburo National Park in Uganda. Parasitol. Res 108 (6), 1365–1374. https://doi.org/10.1007/s00436-010-2030-8.

Oura, C.A.L., Tait, A., Asiimwe, B., Lubega, G.W., Weir, W., 2011a. Haemoparasite prevalence and *Theileria parva* strain diversity in Cape buffalo (*Syncerus caffer*) in Uganda. Vet. Parasitol. 175 (3–4), 212–219. https://doi.org/10.1016/j.vetpar.2010.10.032.

Pascucci, I., Capobianco Dondona, A., Cammà, C., Marcacci, M., Di Domenico, M., Lelli, R., Scacchia, M., Jago, M., Khaiseb, S., Hager, A.L., Tjipura-Zaire, G., Caporale, V., 2011. Survey of ixodid ticks and two tick-borne pathogens in African buffaloes, *Syncerus caffer*, from the Caprivi Strip, Namibia. J. Zoo. Wildl. Med 42 (4), 634–640. https://doi.org/10.1638/2011-0014.1.

Penzhorn, B.L., Chaparro, F., 1994. Prevalence of *Babesia cynicti* Infection in Three Populations of Yellow Mongooses (*Cynictis penicillata*) in the Transvaal, South Africa. J. Wildl. Dis. 30 (4), 557–559. https://doi.org/10.7589/0090-3558-30.4.557.

Penzhorn, B.L., Vorster, I., Harrison-White, R.F., Oosthuizen, M.C., 2017. Black-backed jackals (*Canis mesomelas*) are natural hosts of *Babesia rossi*, the virulent causative agent of canine babesiosis in sub-Saharan Africa. Parasit. Vectors 10 (1), 124. https://doi.org/10.1186/s13071-017-2057-0.

Petrescu-Mag, R.M., Hartel, T., Reti, K.O., Mocanu, C., Petrescu-Mag, I.V., Macicasan, V., Petrescu, D.C., 2024. Land degradation: Addressing the vulnerability of local people through the lens of transformative change. Heliyon 10 (18). https://doi.org/10.1016/j.heliyon.2024.e37891.

Pfitzer, S., Oosthuizen, M.C., Bosman, A.-M., Vorster, I., Penzhorn, B.L., 2011. Tick-borne blood parasites in nyala (*Tragelaphus angasii*, Gray 1849) from KwaZulu-Natal, South Africa. Vet. Parasitol. 176 (2–3), 126–131. https://doi.org/10.1016/j.vetpar.2010.11.006.

Pienaar, R., Latif, A.A., Mans, B.J., 2018. Investigations into the host specificity of *Theileria taurotragi*. Vet. Parasitol. 254, 30–35. https://doi.org/10.1016/j.vetpar.2018.03.003.

Pohlin, F., Hofmeyr, M., Hooijberg, E.H., Blackhurst, D., Reuben, M., Cooper, D., Meyer, L.C.R., 2020. Challenges to animal welfare associated with capture and long road transport in boma-adapted black (*Diceros bicornis*) and semi-captive white (*Ceratotherium simum*) rhinoceroses. J. Wildl. Dis. 56 (2), 294–305. https://doi.org/10.7589/2019-02-045.

Qurollo, B.A., Larsen, P.A., Rakotondrainibe, H.H., Mahefarisoa, K., Rajaonarivelo, T., Razafindramanana, J., Breitschwerdt, E.B., Junge, R.E., Williams, C.V., 2018. Molecular surveillance of novel tick-borne organisms in Madagascar's lemurs. Ticks Tick. Borne Dis. 9 (3), 672–677. https://doi.org/10.1016/j.ttbdis.2018.02.012.

Ros-García, A., M'Ghirbi, Y., Bouattour, A., Hurtado, A., 2011. First detection of *Babesia occultans* in *Hyalomma* ticks from Tunisia. Parasitology 138 (5), 578–582. https://doi.org/10.1017/S0031182011000060.

Rothschild, C.M., 2013. Equine Piroplasmosis. J. Equine Vet. Sci. 33 (7), 497–508. https://doi.org/10.1016/j.jevs.2013.03.189.

Schnittger, L., Rodriguez, A.E., Florin-Christensen, M., Morrison, D.A., 2012. Babesia: A world emerging. Infect. Genet. Evol. 12 (8), 1788–1809. https://doi.org/10.1016/J.MEEGID.2012.07.004.

Schoeman, J.P., 2009. Canine babesiosis: tick-borne diseases. Onderstepoort J. Vet. Res 76 (1). https://doi.org/10.4102/ojvr.v76i1.66.

Seal, S., Dharmarajan, G., Khan, I., 2021. Evol. Pathog. Toler. Emerg. Infect. A Missing Exp. Paradig. 0, 68874. https://doi.org/10.7554/eLife.

Shabangu, N., Penzhorn, B.L., Oosthuizen, M.C., Vorster, I., van Schalkwyk, O.L., Harrison-White, R.F., Matjila, P.T., 2021. A shared pathogen: *Babesia rossi* in domestic dogs, black-backed jackals (*Canis mesomelas*) and African wild dogs (*Lycaon pictus*) in South Africa. Vet. Parasitol. 291, 109381. https://doi.org/10.1016/j.vetpar.2021.109381.

Short, M.A., Clark, C.K., Harvey, J.W., Wenzlow, N., Hawkins, I.K., Allred, D.R., Knowles, D.P., Corn, J.L., Grause, J.F., Hennager, S.G., Kitchen, D.L., Traub-Dargatz, J.L., 2012. Outbreak of equine piroplasmosis in Florida. J. Am. Vet. Med. Assoc. 240 (5), 588–595. https://doi.org/10.2460/javma.240.5.588.

Smith, R.M., Bhoora, R.V., Kotzé, A., Grobler, J.P., Lee Dalton, D., 2019. Translocation a potential corridor for equine piroplasms in Cape mountain zebra (*Equus zebra zebra*). Int. J. Parasitol. Parasites Wildl. 9, 130–133. https://doi.org/10.1016/j.ijppaw.2019.04.010.

Squarre, D., Nakamura, Y., Hayashida, K., Kawai, N., Chambaro, H., Namangala, B., Sugimoto, C., Yamagishi, J., 2020. Investigation of the piroplasm diversity circulating in wildlife and cattle of the greater Kafue ecosystem, Zambia. Parasites Vectors 13 (1), 599. https://doi.org/10.1186/s13071-020-04475-7.

Surve, A.A., Hwang, J.Y., Manian, S., Onono, J.O., Yoder, J., 2023. Economics of East Coast fever: a literature review. In: In Frontiers in Veterinary Science, 10. Frontiers Media SA. https://doi.org/10.3389/fvets.2023.1239110.

Theiler, A., 1912. The Immunisation of Cattle against East Coast Fever. Cape Times Limited, Government Printers, *Cape Town*. ⟨https://repository.up.ac.za/bitstream/handle/2263/15426/Thl_266-314.pdf?sequence=1⟩.

Tirosh-Levy, S., Gottlieb, Y., Fry, L.M., Knowles, D.P., Steinman, A., 2020. Twenty years of equine piroplasmosis research: Global distribution, molecular diagnosis, and phylogeny. Pathogens 9 (11), 1–32. https://doi.org/10.3390/pathogens9110926.

Tirosh-Levy, S., Rothschild, C.M., 2020. Equine piroplasmosis. J. Equine Vet. Sci. 33 (7), 497–508. https://doi.org/10.1016/j.jevs.2013.03.189.

Troskie, M., Matthee, S., Penzhorn, B.L., Jansen, R., Oosthuizen, M., 2025. Occurrence of tick-borne haemoparasites in South African rodent species and evidence of *Babesia microti*-like sequence variants in two *Rhabdomys* species. Int. J. Parasitol. Parasites Wildl. 26, 101051. https://doi.org/10.1016/j.ijppaw.2025.101051.

Uilenberg, G. (1981). Theilerial Species of Domestic Livestock. In M. P. and Y. A. S. Irvin A. D. and Cunningham (Ed.), Advances in the Control of Theileriosis: Proceedings of an International Conference held at the International Laboratory for Research on Animal Diseases in Nairobi, 9–13th February, 1981 (pp. 4–37). Springer Netherlands. https://doi.org/10.1007/978-94-009-8346-5_2.

United Nations, 2024. World Popul. Prospects 2024 Summ. Results. ⟨https://population.un.org/wpp/assets/Files/WPP2024_Summary-of-Results.pdf⟩.

Van Heerden, J., Mills, M.G., Van Vuuren, M.J., Kelly, P.J., Dreyer, M.J., 1995. An investigation into the health status and diseases of wild dogs (*Lycaon pictus*) in the Kruger National Park. J. S Afr. Vet. Assoc. 66 (1), 18–27.

Viljoen, S., O'Riain, M.J., Penzhorn, B.L., Drouilly, M., Serieys, L.E.K., Cristescu, B., Teichman, K.J., Bishop, J.M., 2020. Molecular detection of tick-borne pathogens in caracals (*Caracal caracal*) living in human-modified landscapes of South Africa. Parasit. Vectors 13 (1), 220. https://doi.org/10.1186/s13071-020-04075-5.

Viljoen, S., O'Riain, M.J., Penzhorn, B.L., Drouilly, M., Vorster, I., Bishop, J.M., 2021. Black-backed jackals (*Canis mesomelas*) from semi-arid rangelands in South Africa harbour *Hepatozoon canis* and a *Theileria* species but apparently not *Babesia rossi*. Vet. Parasitol. Reg. Stud. Rep. 24, 100559. https://doi.org/10.1016/j.vprsr.2021.100559.

Wamuyu, L., Obanda, V., Kariuki, D., Gakuya, F., Makanda, M., Otiende, M., Ommeh, S., 2015. Molecular Detection and Characterization of *Theileria* Infecting Wildebeest (*Connochaetes taurinus*) in the Maasai Mara National Reserve, Kenya. Pathogens 4 (3), 626–638. https://doi.org/10.3390/pathogens4030626.

WOAH. (2018). Chapter 3.4.15. Theileriosis in cattle (infection with Theileria annulata, T. orientalis and T. parva). ⟨https://www.woah.org/fileadmin/Home/eng/Health_standards/tahm/3.04.15_THEILIERIOSIS.pdf⟩.

Woolley, A.E., Montgomery, M.W., Savage, W.J., Achebe, M.O., Dunford, K., Villeda, S., Maguire, J.H., Marty, F.M., 2017. Post-babesiosis warm autoimmune hemolytic Anemia. N. Engl. J. Med. 376 (10), 939–946. https://doi.org/10.1056/nejmoa1612165.

World Organisation for Animal Health, 2021. Terr. Man. Chapter 3. 4. 2. Bov. babesiosis. ⟨https://www.woah.org/fileadmin/Home/fr/Health_standards/tahm/3.04.02_BABESIOSIS.pdf⟩.

Yabsley, M.J., Shock, B.C., 2013. Natural history of Zoonotic *Babesia*: role of wildlife reservoirs. Int. J. Parasitol. Parasites Wildl. 2 (1), 18–31. https://doi.org/10.1016/j.ijppaw.2012.11.003.

Zimmermann, D.E., Penzhorn, B.L., Vorster, I., Troskie, M., Oosthuizen, M.C., 2021. *Babesia bicornis, Theileria bicornis* and *Theileria equi* in metapopulations of two black rhinoceros (*Diceros bicornis*) subspecies in South Africa and their potential impact on conservation. Ticks Tick. Borne Dis. 12 (2), 101635. https://doi.org/10.1016/j.ttbdis.2020.101635.

Zintl, A., Mulcahy, G., Skerrett, H.E., Taylor, S.M., Gray, J.S., 2003. *Babesia divergens*, a bovine blood parasite of veterinary and zoonotic importance. Clin. Microbiol. Rev. 16 (4), 622–636. https://doi.org/10.1128/CMR.16.4.622-636.2003.