Wild bovid habitat and infectious disease risk in Thailand

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Abstract

Wild bovids are a diverse group of typically large, hoofed ruminant mammals that play crucial functions in ecosystems as seed transporters and prey for predators to maintain biodiversity. However, their conservation status varies from least concern to critically endangered with extinction, depending on the regions and remaining population. The expansion of agricultural areas and livestock farming has led to habitat loss and natural resource sharing, likely increasing the risk of disease transmission and pathogen circulation between humans, wildlife, and domestic animals at the shared habitats or the interface areas.

This thesis aims to identify the habitat suitability of five wild bovids remaining in Thailand, understand the consequences of introducing infectious disease into the population, and identify where there is a risk of disease transmission. Therefore, three main studies were conducted: 1) identifying suitable areas for five wild bovid species, including gaur, banteng, wild water buffalo, mainland serow and Chinese goral in Thailand; 2) simulating the impact of infectious diseases of cattle on wild bovid populations, and; 3) mapping potential risk areas between wild bovids and cattle.

Initially, I used ecological niche modelling to identify the habitat suitability of five wild bovids remaining in Thailand. Due to poor model predictions for two species (mainland serow and Chinese goral), I excluded these two models from further analyses. The results indicated that over 50% of the potentially suitable areas for the three modelled species (gaur, banteng, wild water buffalo) were located outside protected areas close to human populations and agricultural areas. Then, I simulated the number of animals in a model gaur population with and without infections over 100 years with 100 repetitions using stochastic mathematical models. I selected six bovine infectious diseases with different traits, such as incubation and infectious periods or fatality probabilities, including anthrax, bovine tuberculosis, haemorrhagic septicaemia, lumpy skin disease, foot and mouth disease and brucellosis. I introduced an individual infected animal into a closed population for each infectious disease. The disease-free gaur population grew over time, with infections with different traits having different impacts. The populations infected with chronic diseases (e.g. bovine tuberculosis and bovine brucellosis) showed the greatest decline, while diseases with high mortality but acute disease or high transmission rates with low mortality had less impact on the populations. Finally, I mapped the potential risk areas for disease transmission, assuming that high cattle density and habitat suitability increased transmission risk between wild bovids and livestock. The results also indicated that the potential high-risk areas were at the interface areas at the forest edges where interactions between wildlife and cattle occur.

All my studies and findings will require further investigation and validation to gain a deeper and better understanding of the complexity of infectious diseases within wildlife populations and the dynamics of their distributions, but they contribute to supporting wildlife conservation and implementing disease mitigation measures to prevent disease transmission among the populations by highlighting where wild bovids might have suitable habitat, what types of infections may be problems and where mitigation may be better targeted.

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Chapter 1

Introduction

1.1 Global biodiversity crisis with disease and conservation overview

Biodiversity and global change

Biodiversity plays a crucial role in maintaining ecosystem health, global safety and sustainability (Cardinale et al., 2012; Dinerstein et al., 2020; Pennekamp et al., 2018). Biodiversity is quantified by measuring variation at the genetic, species and ecosystem levels. Loss of biodiversity may affect the dynamics and function of ecosystems of living creatures and natural resources which link to human well-being (Naeem et al., 2016). Human activities impact ecosystems, biodiversity(Ripple et al., 2015), and species extinction rates (Andermann et al., 2020). Human activities that lead to land changes impact the environment in direct and indirect ways. From 1982 to 2016, it was estimated that 40% of global land change was due to indirect changes such as via climate change, and 60% of global land change from direct human activities (e.g. deforestation, urbanization, expanding agricultural area), which both influence local biodiversity loss (Song et al., 2018), species richness and abundance (Chapin Iii et al., 2000; Díaz et al., 2019; Dirzo et al., 2014). Even though tree canopies have increased, forest areas have been converted to other land use types such as agricultural areas and cropland (Song et al., 2018). Currently, the species extinction rate is predicted to have accelerated to around 1,000 times the background rate due to human disturbance (Pimm et al., 2014). At least 20% of native species abundance in terrestrial biomes has declined since 1990, around 1 million species are challenged with extinction, and 25% of evaluated species are threatened (Díaz et al., 2019). The global vertebrate species populations indicator, Living Planet Index (LPI), reports declines of 69% from 1970 to 2018 (range: 63% to75%) at different rates in different regions (WWF, 2020).

Biodiversity in Southeast Asia

Asia has high-biodiversity hotspots throughout the continent, particularly in the Southeast Asia (SEA) region (Sodhi et al., 2004). The largest proportion of the world's forested area (~45% of the total forests) are in the tropical zone, including SEA (FAO, 2020). SEA contains ~25% of plant and animal species of the world across four biogeographic subregions, from tropical rain forests to savannas, and is one of the world's mammal richness and diversity hotspots (Woodruff, 2010). According to analyses of the global hotspots of mammal distributions (Ceballos & Ehrlich, 2006), SEA has a high number of threatened species and habitat loss rate due to high human population density (Sodhi et al., 2010). Strong evidence from previous studies demonstrated that human development impacts deforestation and wildlife extinctions in Asia (Dirzo et al., 2014; Sodhi et al., 2010). More unknown are the gaps in identifying wildlife habitat suitability, the risk of infectious disease transmission and its consequence between wildlife and domestic animal populations. Filling in this gap may support conservation and disease prevention methods in this region.

Emerging infectious diseases and biodiversity

Emerging infectious diseases (EID) are one threat to human, domestic and wild animal, as well as ecological health, with an increasing trend of events over time (Schmeller et al., 2020). Most reported events (72%) are zoonoses from natural wildlife reservoirs (Jones et al., 2008), such as HIV, Ebola, West Nile virus, severe acute respiratory syndrome (SARS), Middle Eastern Respiratory Syndrome coronavirus (MERS-CoV) and Avian Influenza (Field, 2009; Mandl et al., 2015; May et al., 2004). Most notably, likely SARS-CoV-2, the cause of coronavirus disease (COVID-19) (Zhou et al., 2020). There are multiple drivers of infectious disease emergence. For example, there is evidence of EID outbreaks linked to wildlife trade, hunting or habitat encroachment (Karesh et al., 2005). In Asia, the SARS outbreak in 2002 that infected more than 8,000 people was suspected to have originated from small carnivores (Asian palm civets *Paradoxurus hermaphroditus* and raccoon dogs *Nyctereutes procyonoides*) sold in wildlife markets and restaurants in China (Peiris et al., 2003). In Africa, Ebola virus disease outbreaks in humans may have resulted from direct exposure to wildlife by contact or meat consumption (Leroy et al., 2009; Leroy et al., 2004). Ebola virus outbreaks can cause up to 88% mortality in humans (Marí Saéz et al., 2015) and led to a rapid decline of western lowland gorillas and common chimpanzee populations (Leroy et al., 2004). While direct human-animal contact is likely necessary for infection transmission, land use change is a likely driver that is leading to an increased in the frequency of Ebola virus disease outbreaks, with several analyses having linked forest fragmentation to EVD outbreak risk (Olivero et al., 2017; Rulli et al., 2017; Wilkinson et al., 2018). Land use change, and subsequent changes in animal ecology (Eby et al., 2023), is likely leading to differing opportunities for infectious disease emergence both locally and globally.

Therefore, the risk factors drives the emerging of infectious disease warrants further investigation (Muylaert et al., 2023) and addressing these drivers is one proposed approach to reduce the likelihood of infectious disease emergence (Authored by the members of the One Health High-Level Expert Panel et al., 2023).

Dilution effect

Losing biodiversity might itself drive infectious disease transmission and outbreaks in plants, wild animals and humans (Keesing et al., 2010; Schmeller et al., 2020). Declines in host biodiversity, changes in host density and behaviour can increase EID transmission in humans and wildlife (Civitello et al., 2015; Keesing et al., 2006). For example, it has been reported that Lyme disease incidence in humans and vector infection prevalence was reduced in areas with highly diverse host communities (LoGiudice et al., 2003). Similarly, the prevalence and host density of hantavirus was increased when researchers removed the non-reservoir host from the area (Suzán et al., 2009). This concept has been called the dilution effect. It has been proposed, therefore, that conserving biodiversity and reducing its loss would help prevent the transmission of infectious disease from wildlife to livestock and to humans, which refer to the dilution effect (Keesing et al., 2010) and the positive correlation between biodiversity and emerging infectious disease events mentioned by Rohr et al. (2020).

Wildlife diseases and threats to wildlife

Wildlife infectious diseases are one of the threats to species populations, causing decline and potentially extinction, particularly among smaller, declining populations and when there is a lack of gene flow between populations (Glassock et al., 2021). The huge impact from chytridiomycosis, an amphibian fungal disease, on amphibian populations has caused mass mortality of over 200 amphibian species (Cunningham et al., 2017), with some estimates reaching 500 species impacted and with many tens of extinctions (Scheele et al., 2019). Canine distemper, a viral disease of Carnivora, has also caused population declines, including among already endangered populations such as Amur tigers (*Panthera tigris altaica*) (Gilbert et al., 2020), black-foot ferrets (*Mustela nigripes*) (Williams et al., 1988) and Ethiopian wolves (*Canis simensis*) (Gordon et al., 2015). African Swine Fever (ASF), a viral disease of swine, emerged from Africa reaching as far as Southeast Asia in 2019 and has killed more than one hundred million domestic pigs in affected countries, such as China, Vietnam and Philippines (Luskin et al., 2020). African swine fever can cause high mortality rate (reaching ~100%) in wild boar (*Sus scrofa*) and also reported spreading to wild Suidae (Galindo & Alonso, 2017; Luskin et al., 2020). Another SEA animal disease outbreak is African Horse Sickness (AHS), which occurred in 2020 due to horse trade and the movement of horses from Africa to Thailand. This outbreak killed approximately 500 domestic horses with 90% mortality rate (Castillo-Olivares, 2021).

1.2 Bovidae and infectious diseases

Bovidae is a mammalian family in the order Artiodactyla comprised of 139 cloven-hoofed (or even-toed), ruminant species (IUCN, 2024). Crucially, the family includes cattle, sheep, and goats, which are Eurasian bovid species now found throughout the world due to their domestication. Only some plants and Carnivora (e.g. dogs and cats) have been as widely and deliberately distributed by people since domestication, with other species such as peri-domestic rodents accidentally moved. Several other bovids, such as water buffalo (*Bubalus bubalis*) and yak (*Bos grunniens*), have been domesticated, but remain within the range of their wild ancestors (Shi et al., 2016; Zhang et al., 2020). There are currently estimated to be 1.43 billion cattle, and 1.87 billion sheep and goats (Robinson et al., 2014) on earth through domestication and movement. Therefore, the impact of this on land use globally is significant.

Infectious pathogens can be subdivided into two broad groups 1) macroparasites and 2) microparasites. Macroparasites are typically large and complex eukaryotic organisms including helminths and ectoparasites, while microparasites are single-cell organisms including viruses, bacteria, protozoa (single-celled eukaryotes), and prions (non-living infectious proteins) (Keeling & Rohani, 2008; Schmid-Hempel & Cremer, 2020). Some infections, such as protozoa, can have traits of both micro- and macroparasites. Most microparasites reproduce and amplify within the host. However, some microorganisms can endure outside the host in a suitable environment for specific periods or tolerate environmental conditions. For example, sporulating bacteria (e.g. *Bacillus* spp., *Clostridium* spp.) have been observed to survive for decades in soil (Barandongo et al., 2023; Swick et al., 2016). The primary mode of transmission for microorganisms like viruses and bacteria is direct transmission from infectious to susceptible animals. However, certain pathogens can also survive within feces, urine, water, or food for a suitable period after excreting from animals which can be spread to new hosts or locations via vectors (e.g. insects, mammals) or natural processes (e.g. wind, water). While this increases the risk of transmission to susceptible hosts, it can concurrently reduce the probability of infection, as the pathogens may decrease infectivity, quantity, and virulence after residing outside the host (Plowright et al., 2008). For macroorganisms, the route of transmission is typically by indirectly ingesting eggs or infective larvae while grazing on a contaminated environment, potentially in the sharing habitats as helminths life cycle circulates in multiple host species and can live in the environment. For instance, more than 400 nematode species were reported in wild and domestic ungulates (Walker & Morgan, 2014).

Wild Bovidae are infected by similar infections to domestic cattle, such as foot and mouth disease (FMD), anthrax, bovine tuberculosis (bTB; *Mycobacterium bovis*), Bovine viral diarrhea (BVD), bovine brucellosis (*Brucella abortus*), haemorrhagic septicaemia (*Pasteurella multocida*), Infectious bovine rhinotracheitis (IBR) and vector-borne diseases (e.g. lumpy skin disease, Bluetongue, rickettsia) (Smith et al., 2017; Weaver et al., 2013). Most of the bovine infectious pathogens can circulate and infect both domestic and wild bovids globally (Caron et al., 2013; Wiethoelter et al., 2015). These diseases affect livestock, economic losses, food supply, native animals and human health concerns (Tomley & Shirley, 2009). One example is the dramatic decline of some North American bighorn sheep (*Ovis canadensis*) populations from ovine respiratory disease (*Mycoplasma ovipneumoniae*) because of free-grazing domestic sheep (Carpenter et al., 2014). In China, bovine brucellosis, pleuropneumonia and haemorrhagic fever from domesticated yak have impacted wild yak (*Bos mutus*) populations (Shi et al., 2016).

Bacterial infections are a persistent ongoing issue in wildlife and livestock populations, particularly involving two primary pathogens: bovine brucellosis and bTB (Wiethoelter et al., 2015) which are widely distributed (Khurana et al., 2021; Reis et al., 2021; Simpson et al., 2021; Zimpel et al., 2020) in multi-host species (e.g. cattle, sheep, goats, and wildlife) (Khurana et al., 2021; Wilber et al., 2019). Bovine brucellosis, a zoonotic intracellular bacterium, can be transmitted through direct contact with infected animal via secretions, semen, blood, aborted fetuses, placenta and vaginal discharge, and indirectly through contaminated sources such as ingesting milk, drinking water, and animal products (Khurana et al., 2021). Bovine brucellosis transmission among bison (*Bison bison*), elk (*Cervus canadensis*) and domestic cattle populations in Yellowstone, USA, has occurred (Cotterill et al., 2020). The disease lead to retained placenta, abortion, stillbirth (Higgins et al., 2012; Olsen, 2010) and reduced pregnancy rates in seropositive elk (A. Yang et al., 2019). For domestic cattle, brucellosis causes reproductive disorders in both female (e.g. abortion and placentitis) and male (e.g. orchitis and epididymitis) cattle, decreasing productivity and increasing the cost of production through diagnosis, quarantine and culling (Andrews et al., 2008).

Bovine tuberculosis, caused by a gram-positive, acid-fast bacilli, sometimes has complicated transmission and interactions between wildlife, livestock, and the environment. Direct inhalation of small aerosol droplets shed from infected animal lesions is a common route of transmission (Domingo et al., 2014; Neill et al., 2001), but indirect contact is also common and the pathogen can persist in the environment (e.g. in water, soil, hay, and mineral licks) (Barasona et al., 2017; Fine et al., 2011; Kaneene et al., 2017). Based on patterns of contact (Drewe et al., 2013), indirect contacts between wild badgers and cattle were more frequently observed, while direct contacts were rare in open pasture. Thus, both indirect and direct contact could be relatively important depending on contact behaviour and species population (Böhm et al., 2009). The bacteria can be excreted into the environment, which could be sources of infection transmitted to susceptible animals through inhalation and ingestion (Cowie et al., 2016; Renwick et al., 2007). Infected animals can develop chronic inflammation, firm nodule lesions, with white to yellowish abscesses that are frequently detected in the lung, thoracic lymph nodes, and thoracic cavity (Domingo et al., 2014; Neill et al., 2001). Although a small number of bacteria can start the lesions, other factors like the frequency, pattern, and type of contact are related to the likelihood of transmission, as shown by analyses of contact networks between badgers and cattle, cattle and wild bovids, and cervids (Wilber et al., 2019).

Both bovine tuberculosis and brucellosis are chronic infections that may cause life-long infection, having slow development of clinical signs that require prolonged population monitoring (Gorsich et al., 2015). Some studies indicate that while there may be low disease prevalence in populations, there is the potential for this to have a significant impact on animals of specific ages and sex. In the adult African wild buffalo population, bovine brucellosis can increase mortality rates and reduce the overall population growth rate (Gorsich et al., 2015) whereas bovine tuberculosis infection may lead to a reduction in both survival rate and fecundity rate (Jolles et al., 2005).

Tuberculosis and brucellosis are both caused by bacterial infections. However, viral infections were the majority (60%) of the total infectious diseases reported between wildlife and livestock, compared to other pathogens (Wiethoelter et al., 2015). FMD is one of the most highly contagious viral diseases known, and can be transmitted among most, if not all, even-toed ungulates. The disease is caused by viruses from the *Aphthovirus* genus in the *Picornaviridae* family, which comprises 7 serotypes: SAT1, SAT2, SAT3, C, O, A, Asia1 (WOAH, 2021b). Serotypes O, A, Asia1 commonly cause outbreaks in Asia, while serotypes SAT 1-3 are predominantly spread in Africa, and serotype C has not been reported since the 2004 outbreak in Brazil and Kenya (Paton et al., 2021). The pathogen can spread by aerosol droplets or direct contact with vesicles or secretions from infected animals. However, indirect contact through environmental exposure is also possible, as the virus can survive outside animal's body, particularly in manure, for up to six months in winter, depending on the environmental condition (e.g. temperature, precipitation, humidity, pH), type of contaminated material, and quantity (Alexandersen et al., 2003; Andrews et al., 2008). The incubation period ranges from 7 to 14 days. After exposure, animals may have high fever, and develop generalised vesicles on the skin or mucosa inside the oral cavity, tongue, teats and above the hoof (coronary band) (Alexandersen et al., 2003). The host disease severity among FMD is, however, varied. The pathogen can be maintained in an African buffalo (*Syncerus caffer*) herd for 20 years with mild or subclinical signs, while it can cause high mortality in mountain gazelles (*Gazella gazella*) and Saiga antelopes (*Saiga tatarica*) (Arzt et al., 2011; Weaver et al., 2013). An FMD outbreak has been reported in gaur in Asia, and the virus was transmitted to other wild ungulates in national parks and villages in India. This outbreak killed several wild ungulates and the authors suggested continuously vaccinating the domestic cattle population to control the disease in wildlife (Chandranaik et al., 2015).

Vaccination against viral diseases has been successful for ungulate diseases. Rinderpest was one of the most important emerging infectious diseases to affect domestic animals. Rinderpest is now globally eradicated, only the second infection after smallpox for this to be achieved. Prior to its eradication, the disease led to devastating outbreaks among domestic cattle, buffalo and wild ungulates (Roeder et al., 2013). For example, this viral infection had a great impact on wildlife in Kenya between 1993 and 1997, causing the sudden death in highly susceptible species including wild buffalo (*Syncerus coffer*), eland (*Taurotagus oryx*) and lesser kudu (*Tragelaphus imberbis*) (Kock et al., 1999).

Vector-borne diseases pose a significant challenge to both livestock production and wildlife health. Several factors related to vector-borne transmission cause these challenges, such as an increase in vector density due to climate change (Caminade et al., 2019; Ogden & Lindsay, 2016), animal and vector movement (Fèvre et al., 2006) and a greater host range for most vector-borne diseases (e.g. three times more than non-vector-borne viruses) (Kreuder Johnson et al., 2015). These factors make controlling vectors, stopping outbreaks and mitigating disease a challenge (de La Rocque et al., 2011). For example, lumpy skin disease, a viral cattle disease which is endemic in Africa and transmitted by blood-sucking arthropods, has spread to Europe, the Middle East, and Central Asia, and was recently reported in Southeast Asia in 2020 for the first time (Ratyotha et al., 2022). One risk is that there is a wide range of widely distributed vector species in the outbreak areas, making the virus extensively spread once infected animals are introduced into the naive and susceptible population (Gelaye & Lamien, 2019).

Healthy wild ungulates and livestock can naturally be exposed to pathogens through biological vectors (e.g. ticks, mosquitoes) and mechanical vectors (e.g. transport by arthropod bodies) without showing clinical signs. A tick survey in Thailand found PCR-positive ticks infected by *Rickettsia, Anaplasma, Coxiella,* and *Francisella* bacteria collected from wild ungulates, including Sambar deer (*Cervus unicolor*), Barking deer (*Muntiacus muntjak*), and Wild boar (*Sus scrofa*) (Sumrandee et al., 2016). The impact of infection on these species is not known. Anaplasmosis has a prevalence of approximately 20% in cattle and 40% in domestic water buffalo but no obvious clinical signs (Nguyen et al., 2020; Sumrandee et al., 2016), while lumpy skin disease clinical signs show obvious nodules on the skin and mucous membrane with high fevers (Sprygin et al., 2019). Therefore, their impact on animal health varies by infection and host species, ranging from very little evidence of infection, through to lower mortality (e.g. ≤ 1-5%) for infections like lumpy skin disease in cattle (Sprygin et al., 2019) to high mortality (e.g. up to 70-90%) as observed in some Bluetongue outbreaks in sheep, goats and deer (WOAH, 2021a).

Natural habitat loss is one crucial driver of increasing human-wildlife interaction (Hayman, 2016) and one of the predominant drivers of infection emergence due to changes in species distribution overlap and habitat sharing (Daszak et al., 2001; Wiethoelter et al., 2015). Expanding livestock production, especially free grazing livestock, has influenced vegetation structure, wildlife habitat (Schieltz & Rubenstein, 2016) and increased the risk of infectious diseases transmission at the interface areas in several regions (Jori et al., 2021). Chaiyarat and Srikosamatara (2009) found that grazing livestock in protected forests may impact food availability and disease transmission for herbivores that share that habitat. Therefore, habitat management between wildlife and free grazing livestock should be considered for sustainable development in livestock farming and conservation and is essential in disease transmission prevention among these populations.

1.3 Livestock farming system in Thailand

Livestock production is an essential agricultural sector for Thai food supplies and the national economy. It has contributed approximately 1.5 - 2% of the gross domestic product (https://www.nesdc.go.th) to the agricultural sector for the past decade. However, globally livestock production has also led to environmental impacts and public health concerns, such as deforestation for feed crops, greenhouse gas emissions, water pollution, and potentially zoonotic disease outbreaks, particularly from intensive farming systems (González et al., 2020; Hayek, 2022).

Livestock farming systems can be classified based on different criteria and patterns, for example, based on the land used and agro-ecology (Robinson et al., 2018), or the scale of production, such as smallholder or traditional system, semi-intensive system, and intensive or commercial systems. In Thailand, based on land use and environmental conditions, common ruminant production systems include mixed rainfed humid and mixed irrigated humid systems, which are typically related to smallholders and livelihoods in rural areas (Lambertz et al., 2012; Steinfeld et al., 2006).

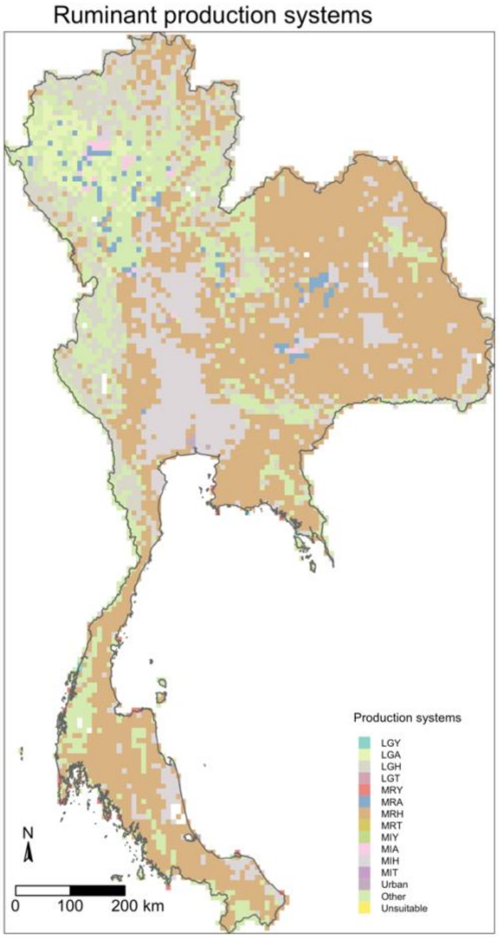


Figure 1.1 Thailand livestock production systems classified by FAO (Robinson et al., 2018). Class abbreviation: Livestock only systems HyperArid (LGY); Livestock only systems Arid (LGA); Livestock only systems Humid (LGH); Livestock only systems Temperate (LGT); Mixed rainfed HyperArid (MRY); MRA Mixed rainfed Arid (MRA); Mixed rainfed Humid (MRH) Mixed rainfed Temperate (MRT); Mixed irrigated HyperArid (MIY); Mixed irrigated Arid (MIA); Mixed irrigated Humid (MIH); Mixed irrigated Temperate (and Tropical Highlands) (MIT).

Within the ruminant production systems, dairy and beef farming are the most important for the Thai food chain, ranging from small- to large-scale production systems. In 2023, the number of beef cattle was around 9 million, and dairy cattle was around 800,000 (https://region6.dld.go.th/webnew/pdf/it6565.pdf). The largest beef and dairy cow farms and highest cattle densities are located in the northeastern and central to western regions. More than half of the beef cattle are Thai native breeds, which have low meat productivity but are resistant to diseases and suited for raising in tropical climates (Bunmee et al., 2018)

Beef production has been developed to improve meat quality and productivity through the whole production chain, from farming to slaughterhouses and meat storage. For example, enhanced disease surveillance systems, tracking of animal movement, and improved farming biosecurity measures have been implemented. However, more studies and research are needed to solve the problems and develop sustainable systems for livestock farming, including relating to land and water availability, greenhouse gas emissions, and emerging disease transmission (Thornton, 2010).

1.4 Bovidae of Thailand including Conservation & Risks

In Thailand, IUCN has listed all the 5 extant species of wild Bovidae as vulnerable [gaur (*Bos gaurus*), Chinese goral (*Naemorhedus griseus*), mainland serow (*Capricornis sumatraensis*)] and endangered [banteng (*Bos javanicus*), and the wild water buffalo (*Bubalus arnee*)] (IUCN, 2020) (Figure 1.2). Although these species are protected under the Reserved and Protected Animals Act, B.C. 2562 of Thai law, their population and genetic diversity levels remain unknown, complicating management actions. Recently, their distribution seems to be limited to the fragmented forests surrounded by agricultural areas and human settlements.

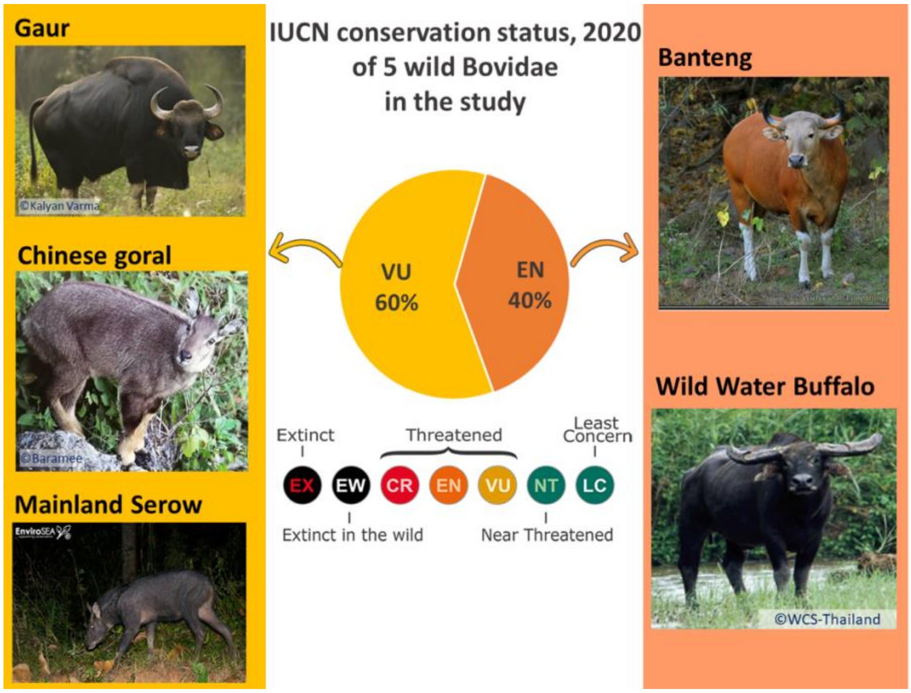


Figure 1.2 IUCN conservation status of the wild Bovidae in Thailand adapted from IUCN (2020). Gaur, Chinese goral, and mainland serow were classified as vulnerable (VU); wild water buffalo and banteng were classified as endangered (EN) species.

Wild bovids play significant ecological roles in tropical forests and grasslands (Hassanin, 2014). They are important seed dispersers, transporting foraged seeds to new areas (Sridhara et al., 2016). Bovidae are grazers and browsers and have been referred to in the literature as ecosystem engineers (Coggan et al., 2018; van der Plas et al., 2016). Several plants have increased seedling survival and germination after passing through the bovid digestive tract and being deposited in the large herbivores' dung (Jaroszewicz & Pirożnikow, 2011). Bovid feeding behaviour also affects plant mortality rates and changes in the plant community and forest structure (Prins & Van Oeveren, 2014). Moreover, their dung provides habitat and food for termites, dung beetles and fungi (Prins & Van Oeveren, 2014; Wurmitzer et al., 2017). Large wild bovids, such as gaur and banteng, are also a major prey of medium to large carnivores such as tigers (*Panthera tigris*), leopards (*Panthera pardus*) and dhole (*Cuon alpinus*) (Andheria et al., 2007; Duangchatrasiri et al., 2019; Simcharoen et al., 2018; Singh et al., 2009). Therefore, the existence and distribution of wild Bovidae are determinants for predators' survival (Duangchatrasiri et al., 2019) and plant community dynamics (Prins & Van Oeveren, 2014).

The habitat requirements for wild bovids are different between species. Gaur can live in various habitats, but they prefer living in semi-evergreen forests covered with dense bamboo. The breeding groups prefer to use lowland and grass patches under 1,000 metres above sea level (masl) while single bulls prefer higher elevation in montane forests (Steinmetz et al., 2008). Banteng prefer dry forest habitats with low elevation, such as dry dipterocarp and mixed-deciduous forest (Steinmetz, 2004). Wild water buffalo also inhabits a mixed deciduous forest but travels closer to streams, rivers, swamp and flat plain areas with low slope and low elevation (Chaiyarat et al., 2004; Choudhury, 2014; Khiowsree et al., 2015). Approximately 2,900 of 4,000 of their largest populations are assembled in Assam Arunachal Pradesh and Chhattisgarh, India (Singh, 2015). Chinese goral (*Narmorhedus griseus*) predominantly live in dry dipterocarp with high altitude mountains 1,400 to 1,900 masl, especially in the rainy season (Chaiyarat et al., 1999).

There are three subspecies of mainland serow (*Capricornis sumatraensis*) including the Sumatran serow (*C. s. sumatraensis*), Chinese serow (*C. s. mildneedwardsii*) and Himalayan serow (*C. s. thar*). Two subspecies were found in Thailand, first, Chinese serow, which is widely distributed over the country, and, second, the Sumatran serow, which is found only in southern forests from Surat Thani province to the border with Malaysia. These two species are elusive and usually found around caves, cliffs and high hills at 200 - 1,000 masl in a mixed and evergreen forest (Phan et al., 2020). Another subspecies, Himalayan serow, can be found in high steep mountains in Nepal and India (Paudel & Kindlmann, 2012) shows the distribution and habitat requirement studies for all the wild Bovidae species.

Table 1.1 Literature review summary wild bovid habitats.

Species	Study area	Study methods	Habitat suitability analysis	References
Bos gaurus	India	Transect survey	Ecological niche factor analysis	Paliwal and Mathur (2012)
		Direct observation, Animal signs surveys,	Distribution, population density	Choudhury (2002)
			Logistic regression	Imam and Kushwaha (2013)
		Radio collar	Minimum Convex Polygon	Sankar et al. (2013)
		Grid-based survey	Linear regression	Ahrestani et al. (2012)
	Nepal, Bhutan, Myanmar	Direct observation, Animal signs surveys	Distribution, population density	Choudhury (2002)
	Thailand	Secondary data, Field survey	Relative abundance	Srikosamatara and Suteethorn (1995), DNP (2010)
		Animal signs survey	Distribution	Steinmetz (2004)
		Animal signs survey	MAXENT	Trisurat et al. (2015), Planisong et al. (2019)
		Direct observation, Camera trapping	Capture-recapture, Relative abundance	Tanasarnpaiboon (2016)
		Transect survey	Animal density, Minimum convex polygon	Laichanthuek et al. (2017)
	Malaysia	Radio collar	Home range, Habitat use	Conry (1989)
	Laos	Animal signs survey	Descriptive	Steinmetz (2004)
	Vietnam	Secondary data, Direct observation,	Population density	Nguyen (2009)
	Myanmar	Animal signs survey	Distribution	Rabinowitz et al. (1995)
Bos javanicus	Thailand	Secondary data, Animal signs survey	Relative abundance	Srikosamatara and Suteethorn (1995)
		Animal sign survey	Descriptive	Steinmetz (2004)
		Field survey	Relative abundance, species richness	DNP (2010)
		Animal signs survey	MAXENT	Trisurat et al. (2015);
		Direct observation, Animal signs survey	Logistic regression model	Chaiyarat et al. (2017)
		Radio collar	MAXENT	Chaiyarat et al. (2019)
	Vietnam	Secondary data, Direct observation,	Population density	Nguyen (2009)
		Animal signs survey	Occupancy	Pedrono et al. (2009)
	Cambodia	Camera trapping	Relative abundance	Gray and Phan (2011)
	Indonesia	Camera trapping	MAXENT	Rahman (2020)
		Forest patrol	Multiple logistic regression	Imron et al. (2016)
	Malaysia	Camera trapping	MAXENT	Lim et al. (2021)
Bubalus arnee	Thailand	Transect survey	Logistic regression	Chaiyarat et al. (2004)
		Field survey	Relative abundance, species richness	DNP (2010)
		Transect survey	MAXENT	Khiowsree et al. (2015)
	Nepal	Population census	Population structure	Heinen and Kandel (2006)
		Field survey	Intersection of habitat suitability criteria	Thapa et al. (2020)
	Sri Lanka	Population census	Population structure	Silva et al. (2012)

Species	Study area	Study methods	Habitat suitability analysis	References
Naemorhedus griseus	India	Transect survey, Interviews	Logistic regression	Singh and Kushwaha (2011)
	Thailand	Animal signs surveys, Direct observation	Home range, Population structure	Chaiyarat et al. (1999)
		Field survey	Relative abundance, species richness	DNP (2010)
		Radio collar	plotting occurrences	Buranapim et al. (2014)
		Animal signs survey,	MAXENT, Multiple logistic regression model	Trisurat et al. (2015)
	China	Animal signs survey	Habitat use	Chen et al. (2012)
Capricornis sumatraensis	Thailand	Field survey	Relative abundance, species richness	DNP (2010)
		Animal signs survey	MAXENT	Trisurat et al. (2015);
	Malaysia	Camera trapping	Animal identification	Ain Ahmad Bakri et al. (2020)
	Thailand	Field survey	Relative abundance, species richness	DNP (2010)
	China	Animal signs survey	Habitat use	Chen et al. (2009)
	Vietnam	Transect survey, Interview	Mann – Whitney U tests	Thuc et al. (2014)
	India	Camera trapping	Occupancy	Tapajit et al. (2012)
	Nepal	Animal signs	Population density, Ivlev's electivity index	Aryal (2009)
		Animal signs, direct observation	Frequency of presence, intactness index	Paudel and Kindlmann (2012)

1.5 What's the ecological niche model, and why do we use this for conservation planning and management

An important task of wildlife research and conservation is to define the distributional ecology of species, how species are related to their environment, climate and other living organisms (Franklin, 2010). Ecological niche models (ENMs) are widely applied to estimate the geographic distribution that is suitable for species using ecological niche dimensions (e.g. environmental conditions) combined with species presence data. This prediction maps the presence of the suitable area for the species distribution (Soberon & Peterson, 2005). In addition to more obvious species niche predictions, this method can be applied for several other purposes, including to predict infectious disease vector distributions based on climate factors (Carvalho et al., 2015; Pearson & Dawson, 2003), to determine species interactions (Wisz et al., 2013) and identify disease transmission risk areas (Peterson, 2006a).

ENM can be approached using the Biotic-Abiotic-Mobility (BAM) (Figure 1.3). This concept explains the relationship of the species' distribution, geographical and climatic factors , and also plays an essential approach to defining when, where and how a disease can be transmitted from the environment or host to host (Peterson & Soberón, 2012). Interactions between species are the major factors to consider, because the infectious disease risk increases more with greater interactions, particularly a direct contact. Therefore, understanding interactions between host, pathogens and environment is important to estimate the risk factors of disease transmission (Peterson, 2014).

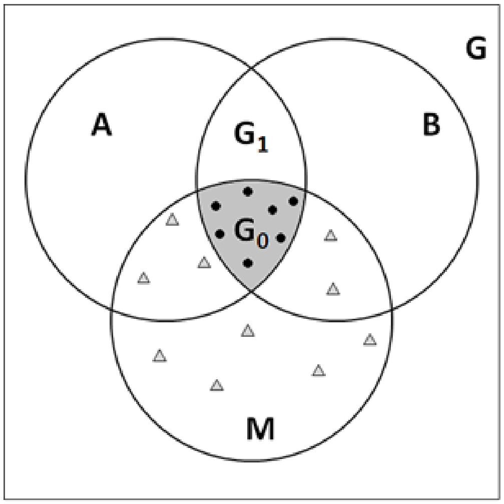


Figure 1.3 The BAM diagram describes the relationship of abiotic, biotic and accessible area (Soberón, 2007; Soberon & Peterson, 2005). G represents the geographical dimensions of the study area. A (Abiotic) represents the areas with suitable abiotic conditions for species to survive, which can be explained as the fundamental niche. B (Biotic) represents the interactions of target species with other species in the study area. M (Mobility) represents the accessible region for species dispersal. This area should differentiate from the potential area because some suitable areas may not be available or accessible by species in an actual situation. G1 represents the suitable biotic and abiotic conditions for species surviving but may not be accessible (e.g. island) or not discovered. G0 represents the potential species distribution area. The black circles represent the source population presence data in suitable areas, and the triangle represents the presence data of sink population distributed in a non-suitable area.

There are two primary types of ENM. Correlative ENMs, also known as climate envelope models, bioclimatic models, or resource selection function models, model a species' observed distribution as a function of environmental conditions. Mechanistic ENMs, also known as process-based models or biophysical models, leverage independently derived information about a species' physiology to develop a model of the environmental conditions conducive to the species' existence (Sillero et al., 2021).

The reliability of these approaches in reflecting real-world species distributions relies on factors like the nature, complexity, and accuracy of the models used, the quality of available environmental data layers, the availability of sufficient and reliable species distribution data, and the impact of various BAM factors. The disparity between the realised niche (where a species is) and the fundamental niche is crucial in this context.

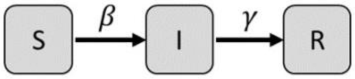
Mapping infectious diseases using the combination of epidemiological and ecological data is useful for predicting risk and analysing the spatiotemporal dynamics of infectious diseases (Ostfeld et al., 2005). Species occurrences and environmental variables integrated with disease parameters have become popular for mapping the high-risk areas (Peterson, 2006b). Environmental factors like climate and geographic data can determine the survival of pathogens outside the host (Mielke & Garabed, 2020) and primarily the survival of the host itself, which is the proximal habitat for pathogens. Migratory bird species detected as a reservoir of West Nile Virus can, for example, be used to develop surveillance plans, whereas their distribution informs us about the potential pathogen distribution (Ain-Najwa et al., 2020; Taieb et al., 2020). Ecological niche models can be used to predict the habitat of a species and its distribution at coarse spatial and temporal scales (Franklin, 2009) while spatial epidemiology (Ostfeld et al., 2005) can be used to estimate the dynamics of disease in the population and project it into the geographic space (Cooch et al., 2012).

Spatially evaluating risk and the impact of infectious diseases in wildlife populations can help the manager focus on target populations and plan mitigation measures. Southeast Asia, including Thailand, is known as a high risk emerging infectious disease hotspot and has a high species richness, with high endemism (Allen et al., 2017; Pimm et al., 2014; Raven et al., 2020). Many livestock infectious diseases have been reported as endemic pathogens in Thailand such as FMD (Arjkumpa et al., 2020), bTB (Singhla et al., 2017) and haemorrhagic septicaemia (Singhla et al., 2020). Although several infectious disease occurrences in livestock have been reported in Thailand, limited epidemiological research has been conducted considering wild Bovidae populations. Modeling the risk of disease transmission benefits disease management planning, pointing to where and how to balance wildlife conservation and livestock production in high-risk areas.

1.6 Dynamical disease model overview

Just as ENMs are useful for predicting species niche’s, mathematical models of infectious diseases can help either understand or project how infectious diseases might behave to help inform public health, veterinary or conservation actions. Different model structures and parameters can be used to compare different scenarios, as well as calculate the effects of different interventions, such as vaccination programs.

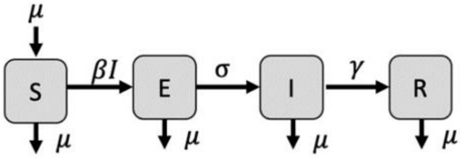
The basic mathematical model for the study of the dynamics of an infectious disease in the population (N) is the SIR model, including three states/compartments: susceptible (S), infectious (I), and recovery/remove (R) (Figure 1.4) (Allen et al., 2012). When infection occurs in the population, susceptible hosts move to infected hosts at transmission rate (β). Then, if an animal has immunity, this can move to the recovery stage at a recovery rate (γ). In a closed population, with no births or deaths. The total population is presented as $N = S+I+R$ (the SIR model without demography) (Keeling & Rohani, 2008).



$$\frac{dS}{dt} = -\beta SI$$

$$\frac{dI}{dt} = \beta SI - \gamma I$$

$$\frac{dR}{dt} = \gamma I$$



$$\frac{dS}{dt} = \mu - \beta SI - \mu S$$

$$\frac{dE}{dt} = \beta SI - \sigma E - \mu E$$

$$\frac{dI}{dt} = \sigma E - \gamma I - \mu I$$

$$\frac{dR}{dt} = \gamma I - \mu R$$

β = transmission rate
S = susceptible
E = exposed
I = infectious
R = recovery /remove
σ = rate of exposed to infectious
μ = birth rate = natural mortality rate/life span

Figure 1.4 The concept of the SIR and $SEIR$ models for building the infectious disease models (Bradhurst et al., 2015; Luz et al., 2010). Each capitalised Latin letter represents a compartment (e.g. I = infected and infectious) and each italicized Greek letter represents a rate of transition between the compartments (e.g. μ = birth and death rates).

In some infectious diseases, such as FMD, susceptible animals are exposed (E) and become infected but not infectious at a transmission rate (β), before moving to the infectious stage (I) rate of infectious (σ), after the incubation or latent period ($1/\sigma$). This model is known as the $SEIR$ model (Figure 1.4). The transmissibility of the pathogen is defined by the Basic Reproduction Number ($R0$); if $R0 > 1$ disease can spread while $R0 < 1$ disease cannot spread (Heesterbeek, 2002).

The benefit of mathematical models is they can be used for informing management decisions. Due to limited resources (e.g. human, time, natural resources), modeling may help predict the possible outcomes, compensate for incomplete data and find solutions for infectious disease prevention and control (Heesterbeek et al., 2015). However, the model presented above is a deterministic model. This means that there is no randomness and so the model will always produce the same output from a given starting condition or initial state. Given the uncertainties often related to populations and infections, a stochastic model which includes randomness is preferred.

A stochastic model may follow the same model SIR or $SEIR$ state variations as above, but allows for random variation in one or more inputs over time, with simulations of multiple runs of the model allowing average behaviour to be determined and behaviours for which is it useful to know event based processes, such as extinctions of a host or an infection. These models take forms such as:

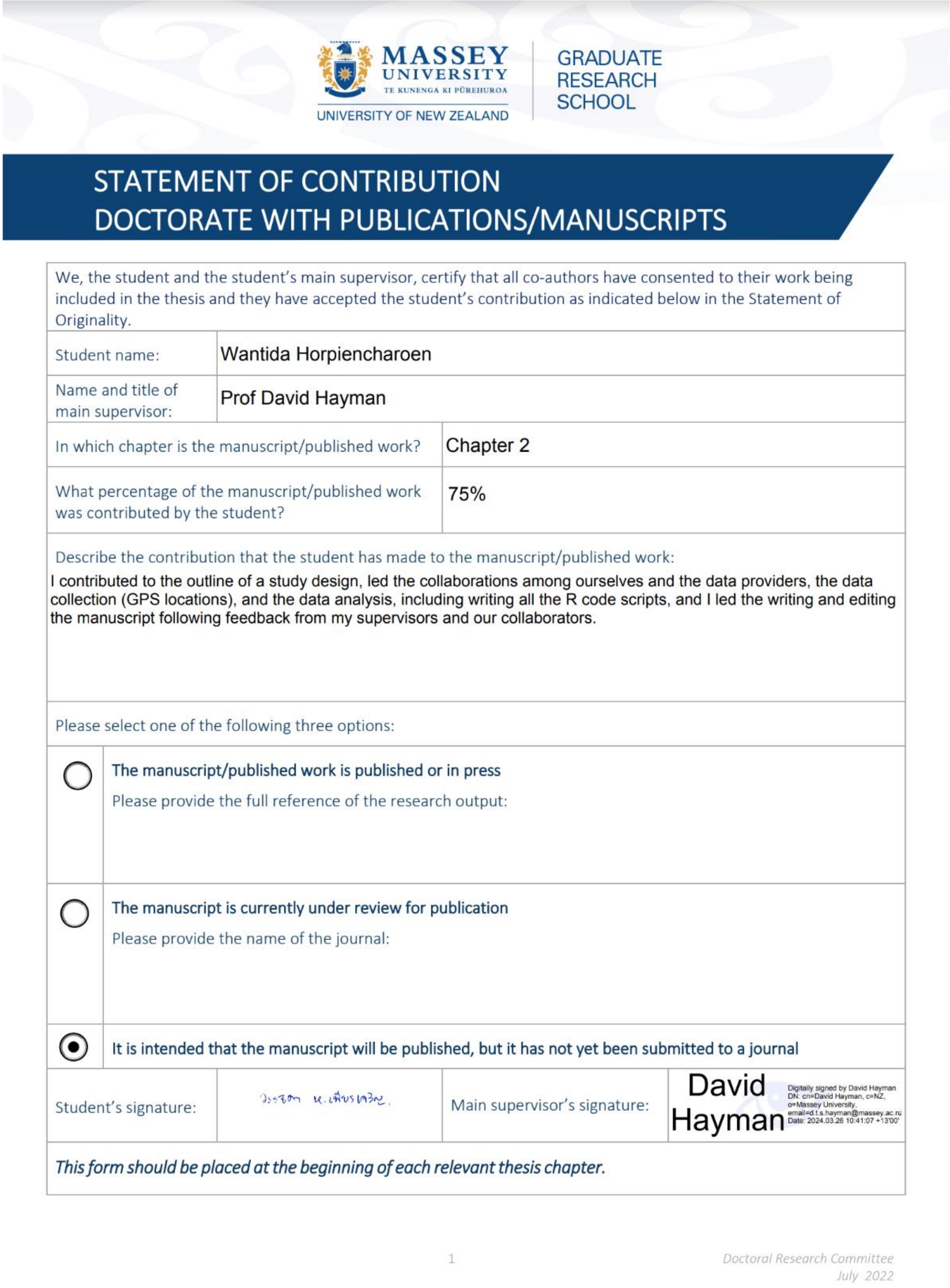
$$N_{birth} = Poisson(\tau * \mu N)$$

Where N_{birth} is the number of births in a time step, modeled as a Poisson distribution, and where an event (here a number of birth) occurs at time step τ and at each step the number of times an event occurs is given by a Poisson distribution with the mean μ (per-animal birth rate) and N (the total number of female adults) determined by equation.

1.7 Layout of this thesis

This thesis will focus on the conservation of Thai wild bovids, focusing on their distributional ecology and population health. It is divided into three main research chapters (Chapter 2 - 4), aligning with the research questions and objectives. The final chapter (Chapter 5) comprises a general discussion, conclusion, and future perspectives on wildlife conservation and infectious disease transmission. Each chapter explores different research questions and methodologies and are organised as peer-reviewed publications with their own introductions, methods, results and discussion sections.

Chapters 2 to 4 address three main research questions: 1) What are the suitable habitats for the remaining wild bovid species in Thailand? 2) What are the consequences of having infected animals in the population? 3) Where are the areas at risk of disease transmission between wild bovids and livestock? Chapters 2 to 4 explore and answer questions 1 to 3, respectively; in Chapter 2, ecological niche modeling is employed to identify suitable habitats, highlighting key environmental variables and significant findings. Chapter 3 utilizes infectious disease modeling (e.g. SI, SIR, SEI) to calculate population dynamics following the introduction of infection into modelled bovid populations. Chapter 4 uses habitat suitability maps from Chapter 2 to map the interface between wild bovids and domestic cattle, defining potential risk areas for disease transmission. The appendices include additional methods, results, and R code (available on GitHub: https://github.com/Wantidah) used for modeling, provided as supplementary materials in the publication. Chapter 5, the final chapter, encompasses a general discussion and conclusion remarks of the chapters 2 to 4 including a framework on wildlife conservation, infectious disease surveillance, prevention and control, then discussed the limitation, study gaps and future perspectives.



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STATEMENT OF CONTRIBUTION DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Wantida Horpiencharoen
Name and title of main supervisor:	Prof David Hayman
In which chapter is the manuscript/published work?	Chapter 2
What percentage of the manuscript/published work was contributed by the student?	75%

Describe the contribution that the student has made to the manuscript/published work:

I contributed to the outline of a study design, led the collaborations among ourselves and the data providers, the data collection (GPS locations), and the data analysis, including writing all the R code scripts, and I led the writing and editing the manuscript following feedback from my supervisors and our collaborators.

Please select one of the following three options:

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Student's signature:	วันทิดา ห.เพียรเจริญ.	Main supervisor's signature:	David Hayman Digitally signed by David Hayman DN: cn=David Hayman, c=NZ, o=Massey University, email=d.t.s.hayman@massey.ac.nz Date: 2024.03.26 10:41:07 +13'00'

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Doctoral Research Committee
July 2022

Chapter 2

Mapping threatened Thai Bovidae species provides opportunities for improved conservation outcomes in Asia

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Abstract

Wild bovids provide important ecosystem functions throughout their native range. In Asia, most are threatened with extinction. Five wild bovids remain in Thailand: gaur (*Bos gaurus*), banteng (*Bos javanicus*), wild water buffalo (*Bubalus arnee*), mainland serow (*Capricornis sumatraensis*) and Chinese goral (*Naemorhedus griseus*). However, their populations and habitats have declined substantially and become fragmented. Here, we aimed to identify potentially suitable habitat for these five threatened bovids using ecological niche models, first throughout the species entire distribution and second within Thailand, and quantified how much suitable area remains within protected areas. We combined species occurrence data (2,732 for gaur, 361 for banteng, 92 for wild water buffalo, 388 for mainland serow, and 135 for Cinese goral) with 28 environmental variables for modelling and used a spatially-restricted Biotic-Abiotic-Mobility framework for two accessible areas: 1) species-specific accessible areas and 2) a single large accessible area. We applied spatially restricted and weighted average ensembles from eight algorithms when generating maps and used out-of-sample predictions to further validate model performance against new data. Gaur, banteng, and wild water buffalo models performed well throughout the entire distribution (≥62%) and in Thailand (≥80%). Mainland serow and Chinese goral performed poorly for the entire distribution and in Thailand (≤36%), though adding a 5 km^2 movement buffer notably improved model performance for mainland serow from 19% to 67% for the entire region and 36% to 86% for Thailand. For gaur and banteng, the best models predicted suitable habitat was mostly within Southeast Asia, with gaur predicted to have large areas in Thailand and India. Banteng suitable habitat was in Cambodia and Thailand, and wild water buffalo suitable habitat was mostly in India. In Thailand, the highest bovid potential richnesses were in the Northern Forest, Western Forest, Eastern Forest and Dong Phayayen-Khao Yai Forest Complexes. We identified unprotected hotspots with >50% of overall suitable habitat located outside protected areas. Wild water buffalo had the smallest proportion of protected habitat (9%) in Thailand. Suitable areas identified in and out of protected areas may guide habitat management and conflict mitigation strategies.

2.1 Introduction

An important task of wildlife research and conservation is to define the distributional ecology of species and to understand how they relate to the environment, climate and other organisms (Franklin, 2009). Ecological niche models (ENM) are applied to predict the geographic distribution suitable for a species by using ecological niche dimensions combined with species' presence data (Soberon & Peterson, 2005). ENM can be approached using the 'Biotic-Abiotic-Mobility' (BAM) framework, which considers the relationship between the species' distribution, geographical and climatic factors and explains the influence of factors on predicted habitat suitability (Peterson & Soberón, 2012). Abiotic (A) factors generally determine the potential distribution (or fundamental niche) of a species, and the intersection of abiotic and biotic (B) factors form the realised niche, or the part of this potential distribution where species actually live (Soberón & Nakamura, 2009). Mobility (M) is the area accessible by species related to their distribution over periods of time (the 'accessible area'; (Barve et al., 2011)). Selecting the extent of species' accessible areas, including buffer zones, impacts model prediction results (Anderson & Raza, 2010; Barve et al., 2011).

Wild Bovidae (Mammalia: Artiodactyla) play significant ecological roles in tropical forests and grasslands (Hassanin, 2014). Bovids are grazers and browsers, modifying plant diversity and abundance within ecosystems (Ripple et al., 2015; Romero et al., 2015). Large wild bovids are also the prey of predators such as tigers (*Panthera tigris*) and leopards (*Panthera pardus*) (Simcharoen et al., 2018). Throughout Asia, wild bovid populations are threatened by poaching (Gray et al., 2018) and habitat loss (Nguyen, 2009), especially in South to Southeast Asia (Giam & Wilcove, 2012). Natural habitats have been disturbed by free-grazing livestock, which can lead to interbreeding (e.g. between domestic and wild water buffalo, (Kaul et al., 2019), increased competition for food and natural resources (Bhandari et al., 2022), and increased risk of disease transmission between wildlife and livestock (Hassell et al., 2017). Moreover, habitat destruction is likely to influence the species' distribution and behaviour adaptation, which could lead to shared natural resources and conflict between humans and wild bovids.

In South and Southeast Asia, there are 27 recognised bovid species (IUCN, 2021), of which seven species are listed as vulnerable, five as endangered and three as critically endangered with extinction. Thailand has five bovid species (gaur; *Bos gaurus*, banteng; *Bos javanicus*, wild water buffalo; *Bubalus arnee*, mainland serow; *Capricornis sumatraensis* and Chinese goral; *Naemorhedus griseus*) remaining in their natural habitat. These species are distributed in other countries from South to Southeast Asia (Figure 2.2) and also have different suitable habitats. For example, gaur can be found in evergreen forest or grassland and range from India, Nepal, across Southeast Asia to Peninsula Malaysia (Duckworth et al., 2016). Mainland serow also has a wide distribution from Nepal to Sumatra in Indonesia through hill forests to shrubland habitats (Phan et al., 2020). Nevertheless, the prediction of the remaining habitat quality and suitability in Thailand and other countries have been conducted only in some protected areas (Chaiyarat et al., 2019; Pintana & Lakamavichian, 2013), but not at the regional or national level.

Species distribution modelling provides an overview of potential habitats for threatened species and aids in conservation planning (Catullo et al., 2008). For instance, previous studies have focused on identifying potentially high-quality habitat connectivity and fragmentation (Crooks et al., 2011) as well as predicting global biodiversity trends (Araújo et al., 2019). In Thailand, there are several studies that have predicted habitat suitability for some of these five wild bovids in local areas (Prayoon et al., 2021), but habitat suitability studies for larger extents across their distribution are lacking.

Here, we built ENM for the five Thai wild bovid species: gaur, banteng, wild water buffalo, mainland serow and Chinese goral at two scales: first, at the regional scale throughout the entire distribution and, second, at the country scale in Thailand. We aim to 1) identify the potential distribution for these five species in South to Southeast Asia, and 2) identify conservation areas in their geographical distribution, with a particular focus on Thailand.

2.2 Materials and methods

Our workflow consisted of two main processes of data preparation and model building (summarised in Figure 2.1) that generated habitat suitability maps for all species and accessible areas used. Data preparation consisted of gathering the species occurrence data and environmental data and selecting the accessible areas. Then, the model building consisted of pre-processing, processing and post-processing steps.

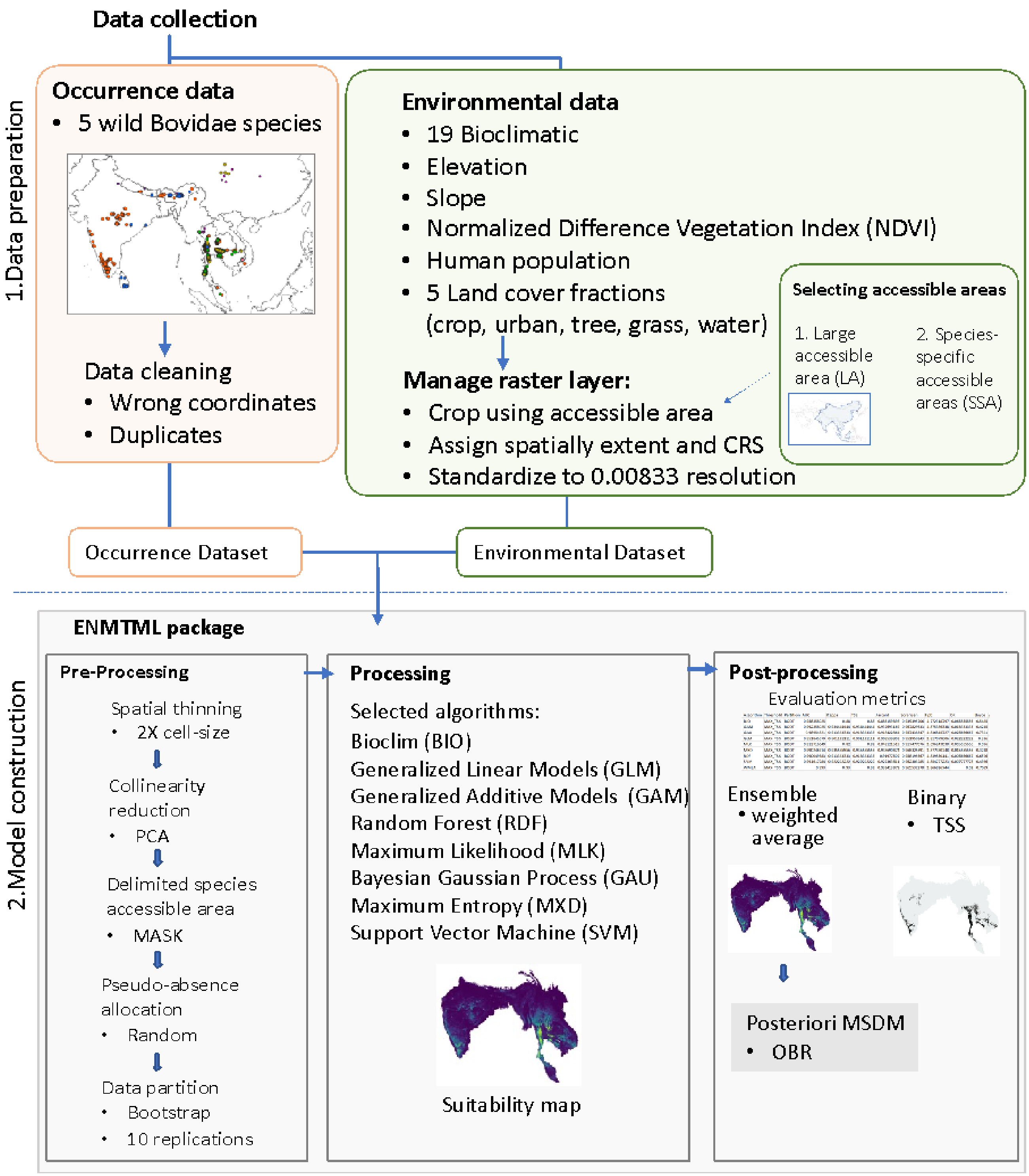

Figure 2.1 The study workflow for ENM modelling was based on the frameworks from Andrade et al. (2020) and Peterson et al. (2011).

2.2.1 Study area

The study area consists of 13 Asian countries: Bhutan, Bangladesh, Cambodia, China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Sri Lanka, Thailand and Vietnam (Figure 2.2), that cover the distribution of gaur, banteng, wild water buffalo, mainland serow and Chinese goral based on the literature (Table 1.1).

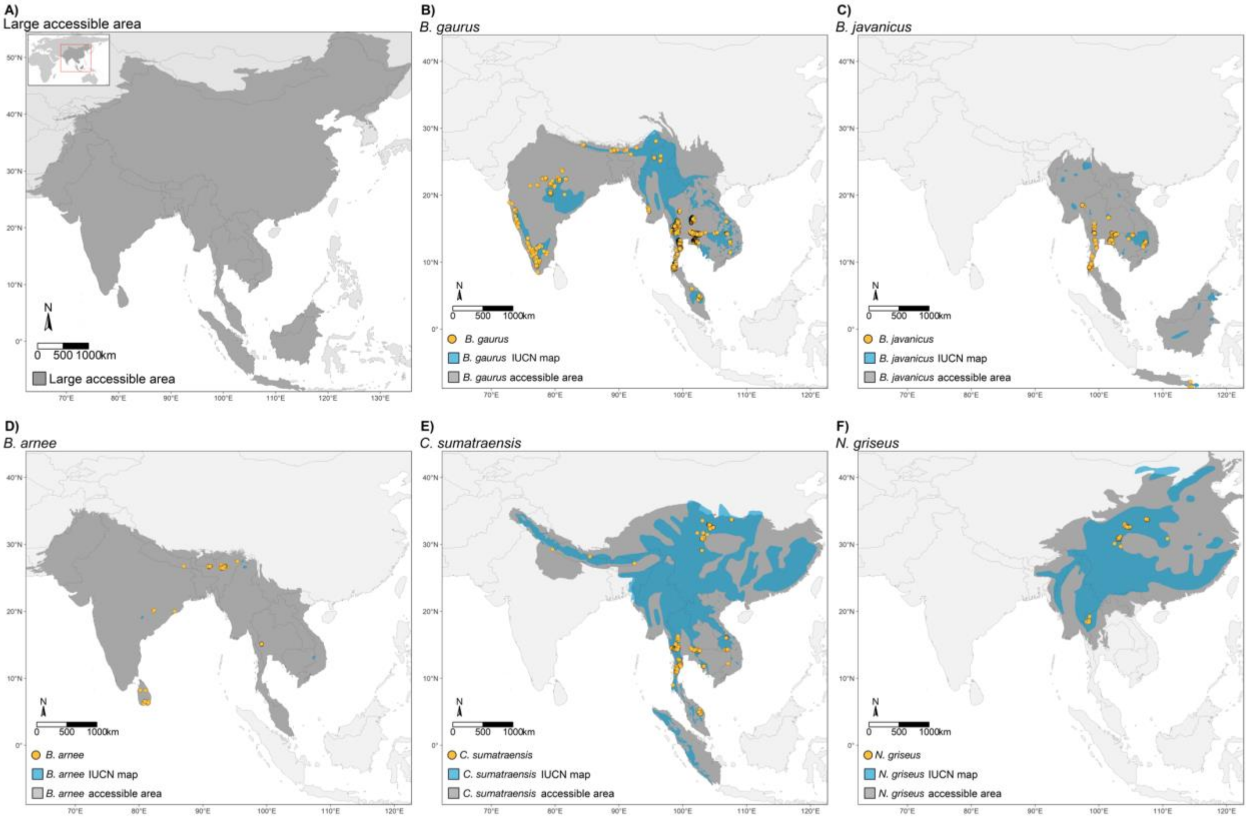

Figure 2.2 Species occurrence data before thinning (yellow circles), IUCN polygons (blue areas) and study areas (grey areas) used in model building for five wild bovid species. First, a common large 'accessible area' (A) was used for all species for model building, and then species-specific accessible areas (B-F) for individual species.

2.2.2 Species Occurrence data

Raw species occurrence data came from several different sources. The data were collected using various field study methodologies, including observation of animal signs (e.g. footprint and dung; 23,396 points) during forest patrols, direct observation during wildlife surveys (444 points), camera trapping (5,483 points), and radio-collar signals (4,341 points), comprising data collected from 23 organizations Table 2.1. We used species occurrence data from GPS records collected between January 2000 and June 2021 from researchers, government, NGOs (World Wildlife Fund, Wildlife Conservation Society, Freeland (Ash et al., 2021)), Panthera, Fauna & Flora International, Friends of Wildlife and RIMBA) and open data sources, including GBIF (https://www.gbif.org/) and eMammal (https://emammal.si.edu/). The data coverage by country can be found in Table 2.1 and details of the data collection sites see the Appendix 1 Table S1.7.

Table 2.1 Number of species occurrences. The raw data and data after spatial thinning are shown by species and data collection methods.

	Raw data					Thinned data				
Species	Camera trap	Direct Observation	Radio collar	Track/Sign	Total	Camera trap	Direct Observation	Radio collar	Track/Sign	Total
Gaur *Bos gaurus*	3,055	286	0	22,436	25,777	257	247	0	2,228	2,732
Banteng *Bos javanicus*	483	16	4,341	911	5,751	64	16	34	247	361
Wild water buffalo *Bubalus arnee*	1	100	0	49	150	0	85	0	7	92
Mainland serow *Capricornis sumatraensis*	1,653	16	0	0	1,669	373	15	0	0	388
Chinese goral *Naemorhedus griseus*	291	26	0	0	3,17	125	10	0	0	135
Total	5,483	444	4,341	23,396	33,664	818	373	34	2,482	3,708

Table 2.2 The number of raw and after spatial thinning occurrence points is shown by species and country.

Raw data

Country	*Bos gaurus*	*Bos javanicus*	*Bubalus arnee*	*Capricornis sumatraensis*	*Naemorhedus griseus*	Total
Bangladesh	X	X	X	?	X	0
Bhutan	1	X	?	?	X	1
Cambodia	44	355	?	38	X	437
China	?	?	X	109	301	410
India	286	X	78	2	?	366
Indonesia	X	6	X	?	X	6
Laos	2	1	X	11	X	14
Malaysia	1,067	?	X	603	X	1,671
Myanmar	114	5	?	99	?	218
Nepal	4	X	1	2	X	7
Sri Lanka	X	X	21	X	X	21
Thailand	24,258	5,383	50	805	16	30,512
Vietnam	1	?	?	?	?	1
Grand Total	**25,777**	**5,751**	**150**	**1,669**	**317**	33,664

Thinning data

Country	*Bos gaurus*	*Bos javanicus*	*Bubalus arnee*	*Capricornis sumatraensis*	*Naemorhedus griseus*	Total
Bangladesh	X	X	X	?	X	
Bhutan	1	X	?	?	X	1
Cambodia	14	48	?	28	X	90
China	?	?	X	64	130	194
India	244	X	64	2	?	310
Indonesia	X	6	X	?	X	6
Laos	2	1	X	8	X	11
Malaysia	26	1	X	49	X	76
Myanmar	53	2	?	51	?	106
Nepal	4	X	1	1	X	6
Sri Lanka	X	X	20	X	X	20
Thailand	2,387	303	7	185	5	2,887
Vietnam	1	?	?	?	?	1
Grand Total	**2,732**	**361**	**92**	**388**	**135**	3,708

Colour definitions

Number	Species presence with occurrence data
?	Species presence without occurrence data
X	No species presence

2.2.3 Environmental variables

Hypothesised environmental variables were selected based on species' habitat and distribution related literature Table 1.1. We used 28 variables (Appendix 1 Table S1.1) for model construction, including 19 bioclimatic variables (Booth et al., 2014) (average for 1970 - 2000) from WorldClim v2 (Fick & Hijmans, 2017), elevation (Shuttle Radar Topography Mission-SRTM) from WorldClim (Fick & Hijmans, 2017), slope (Amatulli et al., 2020), five land cover fractions (grass, tree, urban, water and crop) (Buchhorn et al., 2019), human population density (Stevens et al., 2015) and greenness through the normalized difference vegetation index (NDVI) (Didan, 2015). All layers were processed using the geographic coordinates system (Datum WGS84) and ~1 km^2 spatial resolution. We transformed the human population density using logarithm base 10 to adjust for skewness. We rescaled the NDVI layer by multiplying all values with a scale factor (0.0001), based on the Moderate Resolution Imaging Spectroradiometer (MODIS) User's guidelines (Didan et al., 2015).

2.2.4 Accessible areas

The accessible area refers to the parts of the world that have been accessible to species via dispersal over time (Barve et al., 2011). The extent of the accessible area and the inclusion of a buffer zone have an important effect on ENM performance (Anderson & Raza, 2010; Barve et al., 2011). We used two accessible area sizes to delimitate our modelling extent (Figure 2.2). The first larger accessible area (hereon LA) includes most of the Asian continent and its ecoregions, and all species distributions are included as a common extent. The second accessible area was more restricted and cropped based on individual species-specific distributions (hereon SSA) from literature reviews (Table 1.1), IUCN polygons or 'ranges' (IUCN, 2020) and the terrestrial ecoregions where they occur.

For creating the extent, we downloaded the current IUCN range maps for each species, then intersected those on ecoregions (Olson et al., 2001), then combined the results with selected ecoregions based on biogeographic knowledge of the species distributions and habitat preference from the literature reviews. For example, gaur habitat typically contains moist evergreen, semi-evergreen, and dry evergreen forests (Steinmetz et al., 2008; Tanasarnpaiboon, 2016), so we included these regions in our accessible areas. Further details on ecoregions included in accessible areas are in Appendix 1 Table S1.2. To reduce overprediction and make our predictions closer to realised niche estimates, we used an occurrences-based threshold (OBR) method with ensemble models from (Mendes et al., 2020) for creating the spatially restricted ENM (hereon MSDM). OBR is an *a posteriori* method that restricts the suitable areas of our final ensemble models based on presence and the largest nearest neighbour distance among pairs of occurrences. Overall, we built four combinations between two accessible areas with and without

MSDM methods for each species, including 1) No MSDM-SSA (species-specific accessible areas, without MSDM); 2) No MSDM-LA (large accessible area, without MSDM); 3) MSDM-SSA (species-specific accessible areas, with MSDM); 4) MSDM-LA (large accessible area, with MSDM).

2.2.5 Model building

We processed the species occurrence files and environmental datasets in R 4.0.1 (R Core Team, 2020). We developed reproducible ecological niche models with optimized processing times using the ENMTML package (Andrade et al., 2020), following three main steps: 1) pre-processing, 2) processing and 3) post-processing.

In pre-processing, we performed occurrence thinning using 2 times the cell-size (1 km^2) (Velazco et al., 2019) to reduce clustering of species records and sampling bias. We used principal component (PC) analysis (PCA) to reduce the collinearity of the predictors. We assigned species' accessible areas to determine the species' distributions using a mask function. We used random sampling to create pseudo-absence background points in a 1:1 ratio with presence points (Barbet-Massin et al., 2012). The occurrence and pseudo-absence data was divided into two sets for fitting the model (75%) and evaluating the fitted models (25%), using the bootstrapping partition method with 10 replications for each algorithm.

In the processing step, eight algorithms were used to build the ENMs, namely: BIOCLIM (Booth et al., 2014), Generalized Linear Models (McCullagh & Nelder, 1989), Generalized Additive Models (Hastie, 2018), Random Forest (Liaw & Wiener, 2002), Support Vector Machine (Karatzoglou et al., 2004), Maximum Entropy default (Phillips et al., 2006), Maximum Likelihood (Royle et al., 2012) and Bayesian Gaussian Process (Golding, 2014). All models used the default settings from the ENMTML package, which included the functions from different packages (e.g. dismo, maxnet) based on the algorithms that use to fit the models. The data type used for each algorithm is in Appendix 1 Table S1.3.

In the post-processing step, we created ensemble models using the weighted average (WMEAN) method based on the True Skill Statistic (TSS) values for building final habitat suitability and binary maps. The benefits of ensemble models are 1) robust decision-making (Ahmad et al., 2020); 2) reducing uncertainty (Marmion et al., 2009); and 3) a combination of several models into one model prediction (Kindt, 2018). We used TSS to calculate threshold values to convert habitat suitability maps into binary suitability maps (0 = unsuitable and 1 = suitable). We used TSS and area under the curve (AUC) for evaluating model performance. The TSS threshold is calculated using the maximum summed specificity and sensitivity and is not based on prevalence, where an equal TSS score for given models means similar performance (Allouche et al., 2006). Therefore, we selected the final models from the best TSS of weighted average ensemble models. We assessed the model's accuracy by plotting a new dataset of species occurrences obtained from camera traps and human observations (https://www.gbif.org/) on the binary maps. Because, for example, gaur have been recorded to walk up to 6.3 km a day (mean 1.6 km (Rizal et al., 2020)), we created a 5 km buffer zone measured from the edges of the suitable pixels to include occurrences within the travel distance of wild bovids' movement (Ahrestani & Karanth, 2014; Gardner et al., 2014). The percentage of points inside and outside the suitable areas and the buffer zone was calculated for each species. We present all the results, then only models with high prediction accuracy (greater than 80%,(Zhang et al., 2015)) are selected for further analyses. The total suitable areas of the best TSS binary map models were calculated using the zonal function in the raster R package (Hijmans, 2023). Then, we summed the pixels of the best TSS binary maps to generate the map of species number.

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2.2.6 Protected area analyses

The source for our protected areas map was the World Database of Protected Area (WDPA) (UNEP-WCMC & IUCN, 2021). We classified protected areas based on IUCN protected areas from WPDA into 8 categories, including categories 1 to 6 as IUCN management categories I to VI; category 7 as ‘not applicable’, which includes ‘not reported’, ‘not applicable’ and ‘not assigned' protected areas; and category 8 as non-protected areas, which are the remaining areas that have not been classified as IUCN categories 1 to 7 (UNEP-WCMC and IUCN, 2021). Then, we used the zonal function in the Raster package (Hijmans et al., 2015) to calculate overlapping areas between the suitable areas and protected areas for each species.

We calculated the percentage of suitable areas in WDPA polygons using the exact_extract function in exactextractr package (Baston et al., 2021) for extracting the suitable areas (values = 1) from binary map rasters in each WDPA polygon. Then, we classified each PA into 5 different suitability categories based on the percentage of suitable habitat in the PA: low suitability (0 - 20%); low - medium suitability (>20 - 40%); medium suitability (>40 - 60%); high suitability (>60 - 80%) and very high suitability (≥80%), and selected only the PAs that have the proportion of suitable area larger than species home range in the result. We have provided the code for creating the models in a GitHub repository.

2.3 Results

We compiled 33,664 occurrence records (Table 2.1, Appendix 1 Table S1.7). After filtering and spatial thinning, we used 3,708 points for modelling: 2,732 for gaur, 361 for banteng, 92 for wild water buffalo, 388 for mainland serow, and 135 for Chinese goral. The majority of the thinning occurrences (77%) were collected in Thailand, India and other countries in mainland SEA; see Table 2.2 for details on the data coverage by country.

The PCA reduced the 28 environmental variables into 12 PCs that explained 95% of the environmental variance in the variables for the LA models for all species. The PCs for SSA models explained more than 96% of the total variance and the PC number varied by species, comprising 13 PCs (wild water buffalo), 11 PCs (gaur, mainland serow), and 10 PCs (banteng, Chinese goral). The bioclimatic variables were important variables in all species models. For LA models, the first two axes (PC1 and PC2) have high contributions from the annual mean temperature (bio01), mean temperature of the coldest month (bio06), mean temperature of the driest quarter (bio09) and mean temperature of the warmest quarter (bio10). The first two axes of SSA models showed high positive contributions from mean temperature of the coldest month (gaur), minimum temperature of coldest month (banteng, mainland serow), annual mean temperature (wild water buffalo, mainland serow), and precipitation of the wettest quarter (Chinese goral). We found NDVI, elevation, slope and human population density have less effect on explaining the variability for the first two PCs for all species. The correlations between PCs and individual environmental variables, PC biplots and percentage of explained variance are summarised in Appendix 1, Table S1.4 and Figure S1.1.

2.3.1 Ecological niche models

Overall, all ensemble models showed high performance both for TSS and the area under the curve (AUC) with the highest performing models over 0.8 for all species (Table 2.3). Models with species-specific accessible areas were not always the best performing models, but most ensemble models performed above 0.7 TSS. The habitat suitability prediction maps using the best model ensembles are in Appendix 1 (Figure S1.2 (SSA), Figure S1.3 (LA), Figure S1.4 (selected the best model of SSA and LA), Figure S1.5 and Figure S1.6 (the binary maps which were used for calculating the suitable area)). The performance of spatially restricted ensembles was higher in comparison with the No MSDM models, as the TSS was improved for banteng, Chinese goral and wild water buffalo. The lowest performing model for wild water buffalo was the No MSDM-SSA (TSS = 0.57). The best model for gaur was No MSDM-LA, banteng and Chinese goral is MSDM-LA, wild water buffalo is MSDM-SSA, and mainland serow is No MSDM-SSA. We found that all species have small predicted suitable habitats. Moreover, all species models predicted less than 50% of the suitable areas inside PAs. The total of the suitable areas in km^2 for each species and country are shown in Figure 2.3 and suitable areas calculated from the best model are in Appendix 1, Table S1.5 .

Our model's out-of-sample predictions with new species occurrences demonstrated a higher prediction accuracy within Thailand than the entire distribution, and this was further improved by including 5 km buffer zones, with the exception of Chinese goral, which exhibited poor accuracy across all scales (Table 2.4 and Figure 2.4). Implementing a buffer zone improves the accuracy of all four remaining species. For large herbivore species gaur, banteng and wild water buffalo, the model cropped to Thailand showed a higher accuracy (>80%) compared to the entire distribution (~60-80%). We selected only model predictions with a high accuracy percentage, greater than 80%, for further analyses. Out-of-sample points that lay outside suitable areas showed a mean distance to the nearest suitable area of around 1 – 6 km (Table 2.5), which is within the possible movement range of these species. As a result, three species, including gaur, banteng, and wild water buffalo, were retained, while two species, mainland serow and Chinese goral, were excluded from the rest of the study. Furthermore, we cropped the entire distribution to focus only on the result within Thailand as the number of data collection and model predictions is higher compared to the entire species distribution. The result of the entire distribution for all species can be found in the Appendix 1, Figure S1.2 and Figure S1.3.

Table 2.3 True Skill Statistics (TSS) and Area Under the Curve (AUC) values of the weighted average ensemble, and the threshold values for binary maps for five species classified by accessible area type and MSDM method.Best performing models for each accessible area by TSS are shown in **Boldface**.

	Large accessible area						Species specific accessible area					
	No MSDM[a]			MSDM (OBR)[b]			No MSDM[a]			MSDM (OBR)[b]		
	TSS		AUC	TSS		AUC	TSS		AUC	TSS		AUC
Species	Score	Threshold	Score	Score	Threshold	Score	Score	Threshold	Score	Score	Threshold	Score
Gaur *Bos gaurus*	**0.92**	0.49	0.99	0.92	0.44	0.99	**0.88**	0.39	0.98	0.88	0.41	0.98
Banteng *Bos javanicus*	0.93	0.55	0.99	**0.94**	0.41	1	0.85	0.33	0.96	**0.83**	0.42	0.97
Wild water buffalo *Bubalus arnee*	0.67	0.47	0.88	**0.72**	0.6	0.9	0.57	0.58	0.83	**0.85**	0.44	0.95
Mainland serow *Capricornis sumatraensis*	**0.87**	0.55	0.97	0.76	0.47	0.94	**0.93**	0.57	0.98	0.93	0.52	0.98
Chinese goral *Naemorhedus griseus*	0.91	0.29	0.98	**0.91**	0.59	0.98	0.87	0.47	0.96	**0.9**	0.39	0.97

[a] spatially restricted ENM
[b] occurrences-based threshold

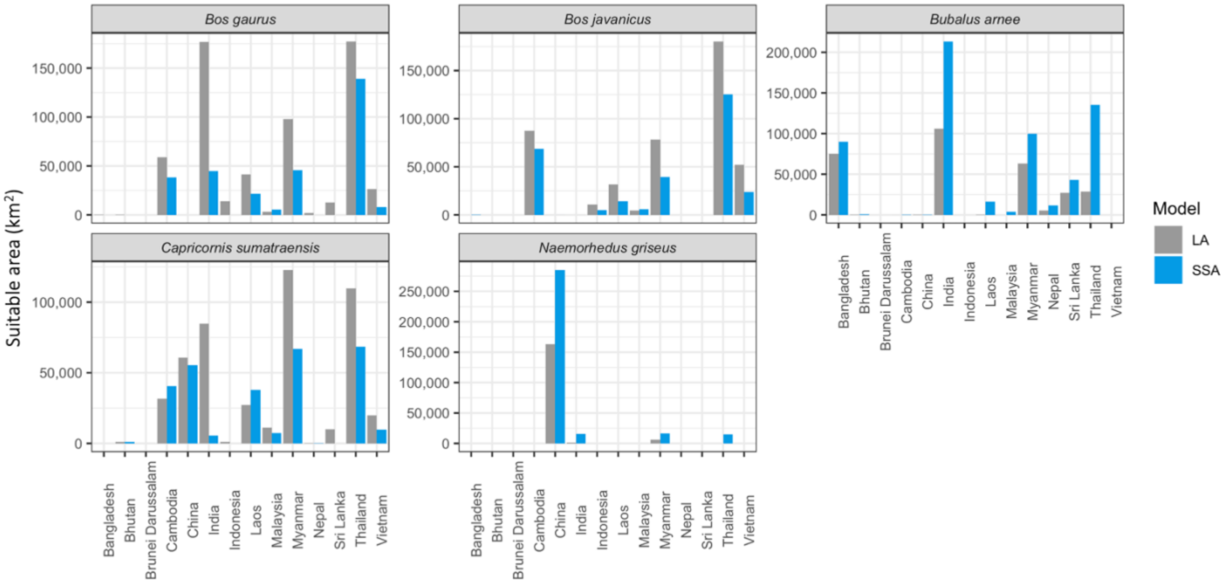

Figure 2.3 Total of the suitable area in km^2 for each species and countries. Blue is the species-specific accessible area (SSA) and grey is the large accessible area models (LA) (see details in Appendix 1 Table S1.5).

Table 2.4 Comparison of the accuracy of the selected best models in predicting out-of-sample data for the entire accessible areas range and Thailand.

		No buffer			Buffer			
Entire accessible areas	Total	Unsuitable	Suitable	Accuracy %	Unsuitable	Suitable	Buffer 5 km	Accuracy %
Gaur (*B. gaurus*)	221	85	136	62	23	136	62	90
Banteng (*B. javanicus*)	12	4	8	67	2	8	2	83
Wild water buffalo (*B. arnee*)	35	4	31	89	0	31	4	100
Mainland serow (*C. sumatraensis*)	21	17	4	19	7	4	10	67
Chinese goral (*N. griseus*)	10	9	1	10	7	1	2	30

		No buffer			Buffer			
Thailand	Total	Unsuitable	Suitable	Accuracy %	Unsuitable	Suitable	Buffer 5 km	Accuracy %
Gaur (*B. gaurus*)	52	8	44	85	2	44	6	96
Banteng (*B. javanicus*)	10	2	8	80	0	8	2	100
Wild water buffalo (*B. arnee*)	1	0	1	100	0	1	1	100
Mainland serow (*C. sumatraensis*)	14	9	5	36	2	4	8	86
Chinese goral (*N. griseus*)	2	2	0	0	2	0	0	0

[a] The best models for gaur is No MSDM-LA, banteng is MSDM-LA, wild water buffalo and Chinese goral is MSDM-SSA and mainland serow is No MSDM-SSA.

Table 2.5 Nearest distance from out of sample points to suitable area

		Distance (km)		
Species	point	Min	Mean	Max
Gaur	52	0.0047	1.54	22.4
Banteng	10	0.0323	4.72	39.9
Wild water buffalo	1	0.811	0.811	0.811
Mainland Serow	14	0.00668	6.07	38.1
Chinese goral	2	0.147	1.54	2.93

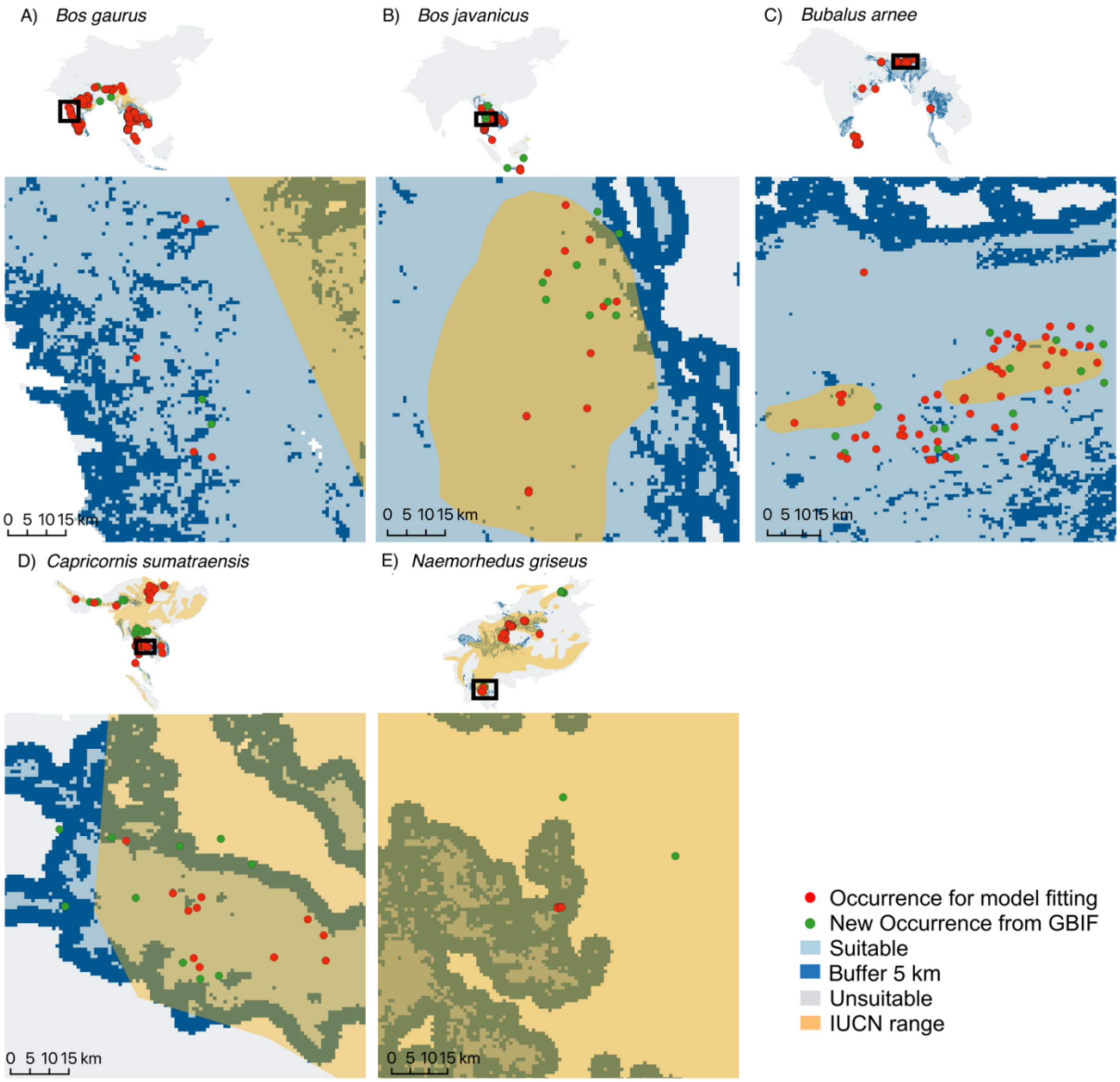

Figure 2.4 Model prediction testing for five bovid species (A-E) by calculating the percentage of the out of sample points that fall inside the model predicted suitable areas (blue). The model fitting datasets (red) were mainly within the suitable areas compared to the new occurrence dataset (green). IUCN ranges show greater areas than the predictions for mainland serow and Chinese goral. Some of the occurrence data were distributed outside both the model predicted suitable area and IUCN range.

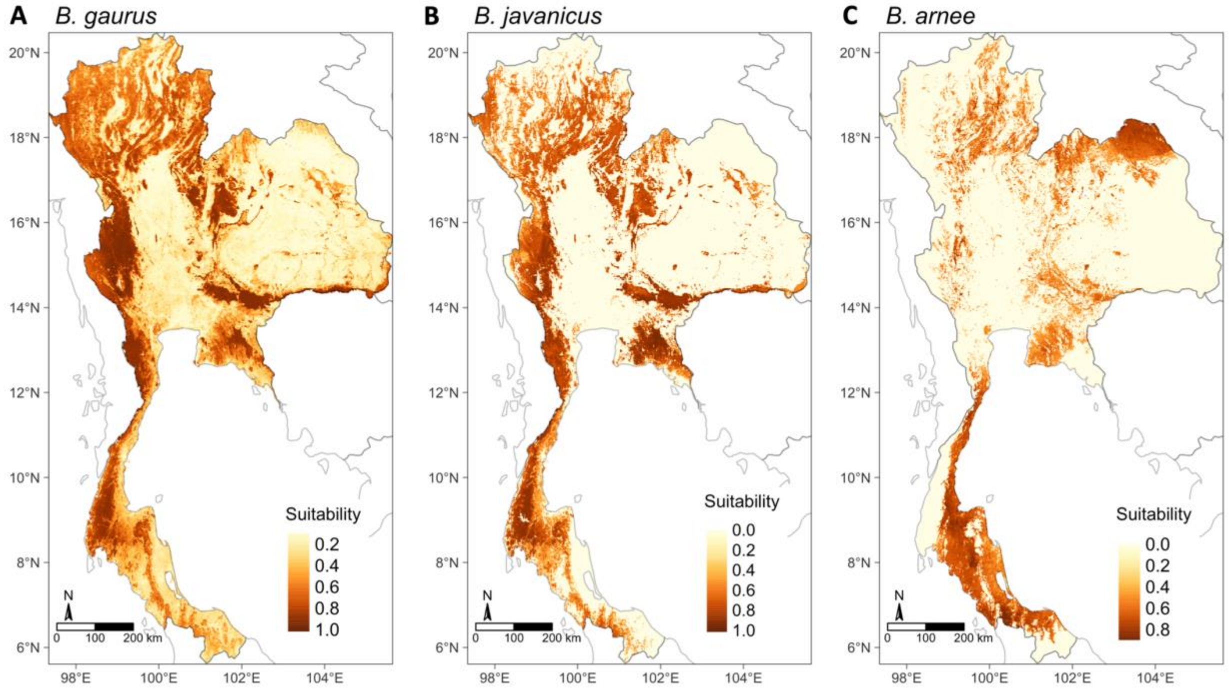

Figure 2.5 Habitat suitability prediction maps of three wild bovids species in Thailand: gaur (*B. gaurus*), banteng (*B. javanicus*) and wild water buffalo (*B. arnee*) species (A-C) using the best model from the weighted average ensemble. The value ranges from 0-1: yellow represents low suitability and dark brown represents high suitability. Interactive maps are provided in the online supplementary material (link).

2.3.2 Identifying priority areas for conservation

Most suitable habitats in protected areas are located in IUCN category Ia (Strict nature reserve), Ib (Wilderness area) and II (National park) areas for the best TSS models for all species, while IUCN category V (Protected landscape or seascape) has the least. Overall, more than half of the species' suitable habitat is not under any form of protection defined by the WDPA (Appendix 1 Table S1.6). The proportion of the suitable area in each WDPA of the best models from SSA and LA for each species are presented in Appendix 1 Figure S1.7 and Figure S1.8.

In Thailand, we identified a high percentage (≥80%) of suitable area of Thailand for gaur in 122 PAs (74,268 km^2; 15% of Thailand), banteng in 102 PAs (59,528 km^2; 12% of Thailand), and wild water buffalo in 3 PAs (559 km^2; 0.1 % of Thailand). A high proportion of the suitable area for gaur and banteng is in Thungyai Naresuan, Kaengkrachan and Huai Kha Khaeng, and for wild water buffalo in Phu Wua and Dong Yai (Figure 2.6 and Figure 2.7). The hotspots for five species can be found in Appendix 1 Figure S1.9.

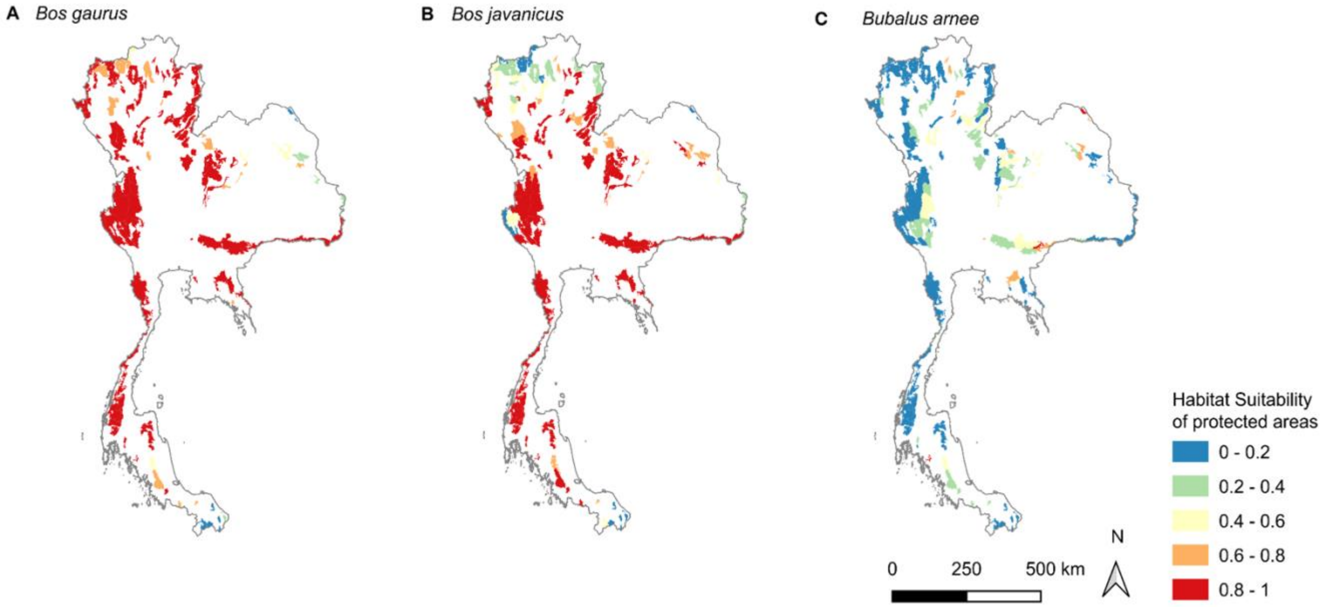

Figure 2.6 The proportion of predicted suitable areas within protected areas of three wild bovids species in Thailand. Proportions range from 0 (all unsuitable) to 1 (all suitable), with suitability determined by thresholds from species best performing models. (A) gaur (*Bos gaurus*), (B) banteng (*Bos javanicus*) and (C) wild water buffalo (*Bubalus arnee*).

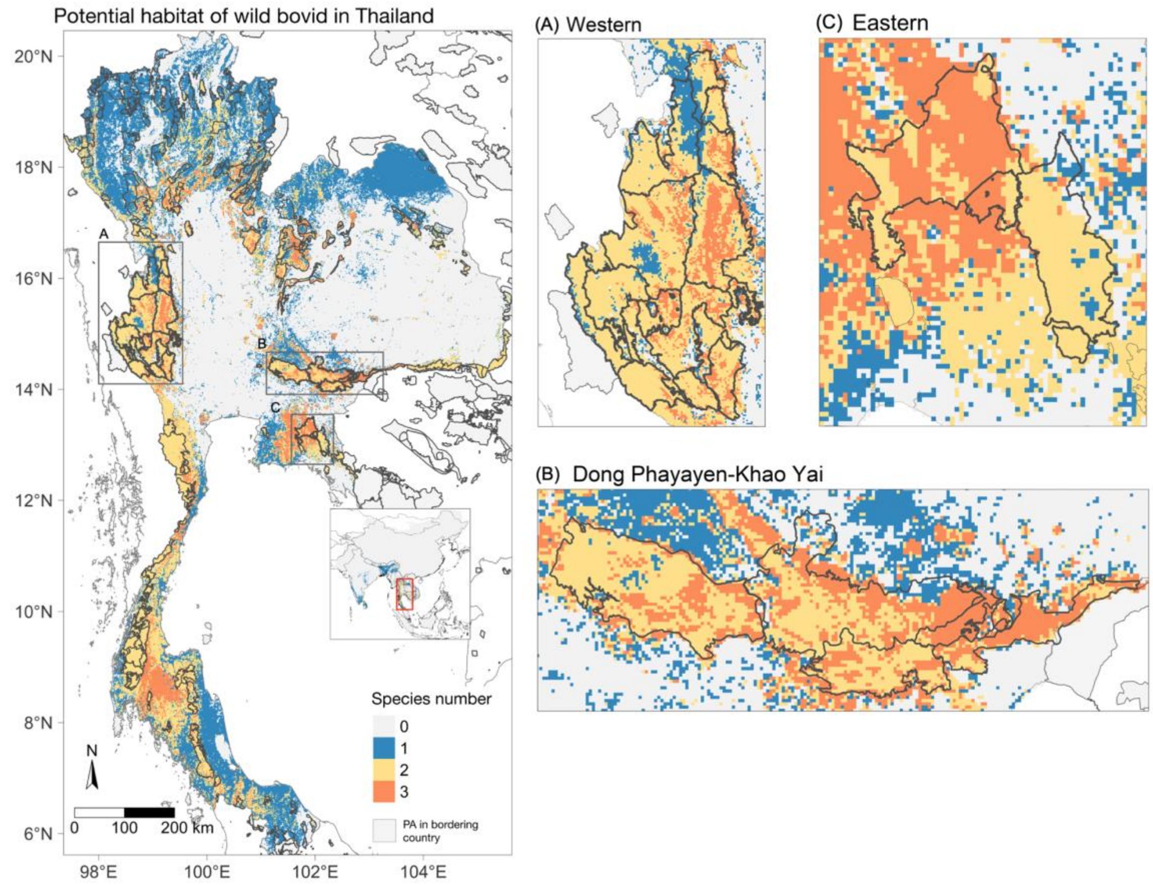

Figure 2.7 Estimated species richness of three wild bovids in Thailand. The species are gaur, banteng, and wild water buffalo. Frames A-C focus on (A) Western Forest Complex (WEFCOM), (B) Dong Phayayen-Khao Yai Forest Complex (DPKY-FC) and (C) Eastern Forest Complex, where there are overlapping predicted suitable areas of all species (n=3). Western, Dong Phayayen-Khao Yai and Eastern forests have suitable areas for gaur, banteng and wild water buffalo both inside PAs and in the surrounding areas.

We found that the highest percentage of suitable area was comprised of mixed deciduous forest for all species, followed by evergreen forest for gaur and banteng, and dry dipterocarp forest for wild water buffalo. Western, Dong Payayen-Khao Yai and Eastern forests have suitable areas for gaur, banteng and wild water buffalo for both inside PAs and also in the surrounding areas. We found a percentage of non-forest areas identified from the total suitable for all species: wild water buffalo (71%), banteng (33%), and gaur (24%). For more details of forest types by suitable areas, see Table 2.6 and Figure 2.8.

Table 2.6 The suitable areas of five bovid species classified by forest types in Thailand.

	Gaur (*Bos gaurus*)		Banteng (*Bos javanicus*)		Wild water buffalo (*Bubalus arnee*)		Mainland serow (*Capricornis sumatraensis*)		Chinese goral (*Naemorhedus griseus*)	
Forest types	km^2	%	km^2	%	km^2	%	km^2	%	km^2	%
Bamboo Forest	390	0.22	348	0.19	178	0.13	250	0.37	2	0.02
Beach Forest	3	-	8	-	26	0.02	1	-	-	-
Dry Dipterocarp Forest	11,119	6.26	12,876	7.13	7,365	5.43	1,415	2.07	3,546	23.91
Dry Evergreen Forest	20,730	11.68	19,209	10.63	5,944	4.38	13,893	20.3	1,027	6.93
Freshwater Swamp Forest	66	0.04	134	0.07	24	0.02	-	-	-	-
Mangrove Forest	609	0.34	1,072	0.59	1,028	0.76	121	0.18	-	-
Mixed Deciduous Forest	66,132	37.25	59,211	32.77	18,837	13.88	25,243	36.88	7,347	49.54
Moist Evergreen Forest	14,802	8.34	15,729	8.7	1,975	1.46	12,213	17.84	-	-
Montane Forest	16,693	9.4	8,497	4.7	812	0.6	7,532	11	1,878	12.66
Peat Swamp Forest	49	0.03	2	-	201	0.15	-	-	-	-
Pine Forest	634	0.36	185	0.1	87	0.06	78	0.11	15	0.1
Savanna	548	0.31	348	0.19	108	0.08	312	0.46	7	0.05
Secondary Forest	2,017	1.14	1,856	1.03	1,189	0.88	602	0.88	153	1.03
Teak Plantation	846	0.48	1,045	0.58	919	0.68	60	0.09	12	0.08
Vegetation on Pen Rock Platform	201	0.11	208	0.11	118	0.09	90	0.13	2	0.01
Other Plantations	37	0.02	42	0.02	29	0.02	9	0.01	-	-
Non-forest Area	42,649	24.02	59,923	33.16	96,883	71.38	6,631	9.69	842	5.68
Total	177,526	100	180,693	100	135,725	100	68,452	100	14,831	100

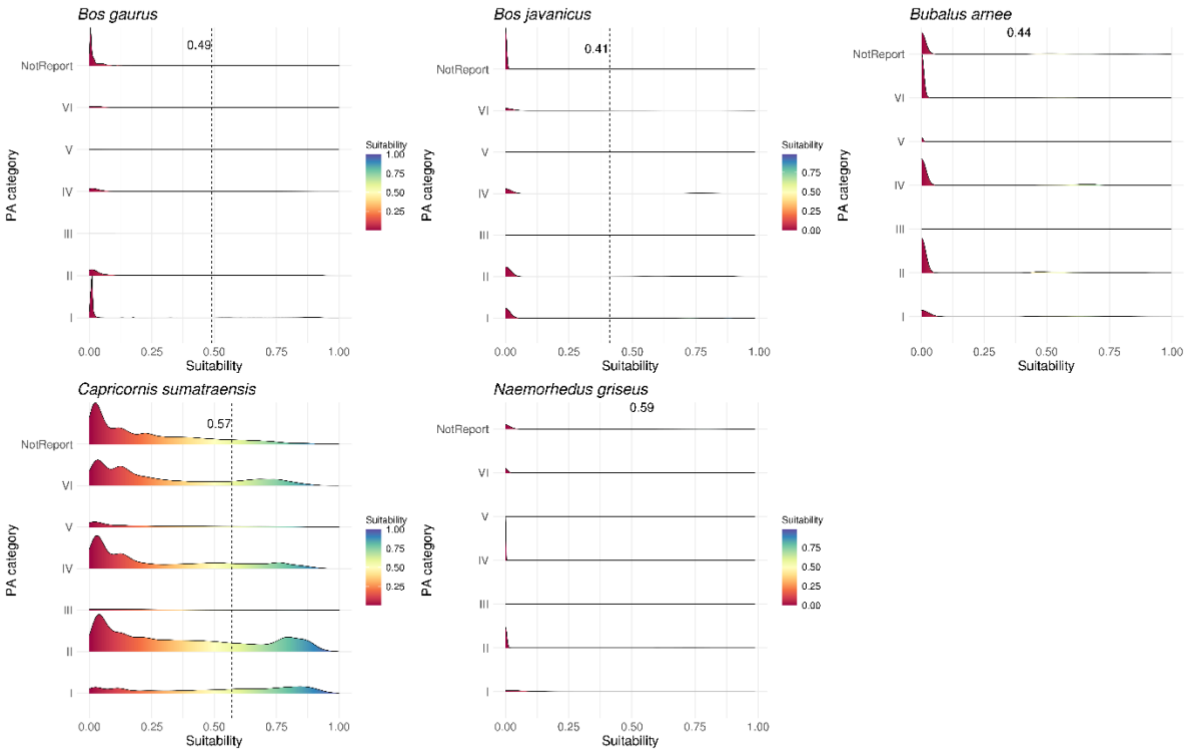

Figure 2.8 Density of suitable areas by forest types within Thailand for five species (A-E). The values range from 0 (low suitability - blue) to 1 (high suitability - red). The dashed lines show the true skill statistics threshold values calculated for the best performing models for each species.

2.4 Discussion

We modelled the potential distribution for five threatened wild bovid species present in Thailand, distributed in East, South and Southeast Asia. Our aim was to build predictive models to identify conservation areas, and potential species richness maps in their entire geographical distribution. However, the model predictions were more accurate for Thailand, where most data were collected for all the species except for Chinese goal (Table 2.4), therefore, we focused our analysis on Thailand. Our models were able to predict the presence of out of sample observations well for three species, gaur, banteng, and wild water buffalo throughout the entire distribution (≥62%), but not mainland serow or Chinese goral (≤19%). We identified that suitable areas were fragmented and often (all >50%) located outside PAs. Those suitable areas outside PAs could possibly be managed as corridors or buffer zones to connect currently fragmented bovid populations inside PAs, thereby enhancing long-term wild bovid conservation success (Karanth, 2016; Penjor et al., 2021). When considering the minimum likely areas of continuous, connected suitable habitat, needed to maintain populations in PAs in Thailand, some suitable habitat might be suitable but excluded here because we only considered suitable patches greater in area than home ranges, yet smaller patches might be connected enough if animals can move between them. Future analyses should consider the necessary required areas and the movement of animals between patches or habitat and their connectivity. We recommend incorporating fragmentation analyses at finer scale resolutions into specific location analyses in future studies to understand the habitat fragmentation and prioritise the vulnerable areas to support effective habitat management (Hesselbarth et al., 2019).

Our study found that most suitable areas for gaur were aligned with IUCN range assessments (Duckworth et al., 2016) and other studies that have confirmed species presences in Thailand (Prayoon et al., 2021), Myanmar (Hein et al., 2020), the Western Ghats in southwestern India and Manas WS in the Himalayan foothills (Choudhury, 2002). Our study predicted larger gaur suitable habitats in Thailand inside (~82,400 km^2) and outside (95,000 km^2) PAs than Prayoon et al. (Prayoon et al., 2021), who predicted 39,508 km^2 of total suitable habitat. Choudhury (2002) predicted larger gaur distributions in the Western Ghats, Central and North-eastern India than our predictions. These differences might be due to the changes in the percentage of the forest cover and habitat destruction over the past two decades, which has reduced the suitable areas. Our predictions also used NDVI and land coverage fractions (Table S3) for predicting greenness, which may be useful for predicting the vegetation quality and availability for ungulates (Borowik et al., 2013). However, NDVI is difficult to differentiate vegetation variations (Didan et al., 2015; Martinez & Labib, 2023), such as between specific agricultural areas, grassland, and dense forest canopy. This may include vegetation types other than the species' preferred habitat in suitable areas and predicted larger suitable areas in non-forest areas and non-PAs in our study, compared to Prayoon et al’s study. Other studies suggest that gaur does use crop plantations or man-made grasslands, which may increase the suitable areas in our prediction, even if these are not their natural habitats and lead to conflict between humans and gaur (Chaiyarat et al., 2021).

Our best model predicted larger suitable areas (446,075 km^2) for banteng than the IUCN-SSC report released in 2010 (~ 209,000 km^2) (IUCN-SSC AWCS Group, 2010). We found a high percentage of predicted suitable areas in Eastern Plains Landscape (ELP) and Chhaeb WS in Cambodia; the former supports the likely largest banteng population globally (Gray et al., 2012). However, our results showed low habitat suitability in Sundaic Southeast Asia, with just 2% of the total suitable area in Indonesia (mainly in Alas Purwo NP, Java) and 2% of the total suitable area in Malaysia. Banteng populations and habitats in Southeast Asian islands (Borneo, Java, and Bali) are threatened due to hunting for horn and meat consumption and habitat loss (Dewi et al., 2020). In Thailand, we found high suitability similar to previous studies in Eastern (Menkham et al., 2019) and Western forest complexes (Jornburom et al., 2020), including reintroduction areas in Salak Pra WS (Chaiyarat et al., 2019) and where recent recolonisation by natural population movement has occurred in Mae Wong NP (Phoonjampa et al., 2021).

Wild water buffalo has been domesticated and bred as livestock, making it hard to distinguish between the free-grazing domestic buffalo and wild water buffalo as domesticated animals may replace wild animals in suitable habitats and cause high suitable area prediction outside PAs, especially in overlapping habitats (Zhang et al., 2020). We estimate the highest percentages of suitable area in Kaziranga NP in India, which currently has the largest population of wild water buffalo (Kaul et al., 2019). Grasslands and flood plain areas of Manas NP (500 km^2) and Kaziranga NP (>850 km^2) in India contain the most suitable habitat and are the main population strongholds for wild water buffalo (Choudhury, 2014). In Thailand, this type of habitat can be found in many places, but it is not often represented in protected areas. Wild water buffalo are only found in Huai Kha Kheang WS parts of the Western Forest Complex. Our model predicts that only 43% of Huai Kha Kheang Wildlife Sanctuary is suitable for this species, primarily because the floodplains are mainly situated close to the main river in the middle of the PA. Additionally, the population has remained constant for decades, which could be attributed to a single population group or constraints within suitable habitats.

The three selected species showed overlapping suitable areas in the Western Forest Complex, Eastern Forest Complex, and Dong Phayayen-Khao Yai Forest Complexes (DPKY-FC). These forest complexes encompass extensive areas of high wildlife biodiversity and diverse forest types, including several contiguous PAs situated at the borders of Cambodia and Myanmar. The Western Forest Complex is the largest conservation area in Thailand where these wild bovids still exist. The DPKY-FC maintains a high population of gaur as it is mainly covered by evergreen forest. The Eastern Forest Complex sustains a large population of banteng because most of the vegetation consists of deciduous and dipterocarp forest. Gaur uses a diversity of types of habitats and prefers denser canopy at higher elevation than banteng, which tends to inhabit in dry and open habitats such as dry dipterocarp and deciduous forests (Gray & Phan, 2011; Steinmetz, 2004). Wild water buffalo also shares overlapping areas with these two species, despite its distribution being found exclusively in Huai Kha Khaeng Wildlife Sanctuary. We recommend protecting these important suitable habitats to ensure the protection of wild bovids. This may involve implementing active patrolling to reduce illegal intrusions, snare removal and habitat management based on their diet diversity (McShea et al., 2019). Additionally, one option to maintain wild water buffalo populations is to reintroduce them into their historical range, from which they have been extirpated. This method could be evaluated by combining predicted suitable areas with several important factors such as vegetation types, forage biomass, carrying capacity and hunting pressure (Bora et al., 2024).

In this study, we included all subspecies data points in our model ensembles as we aim to extrapolate and predict the entire range of species' habitat suitability, but this may increase uncertainty (Dormann, 2007). The five bovids have multiple subspecies, including 3 subspecies of gaur (Duckworth et al., 2016), banteng (Gardner et al., 2016), wild water buffalo (Kaul et al.,

2019) and mainland serow (Mori et al., 2019), and 2 subspecies of Chinese goral (Duckworth et al., 2008). Subspecies may vary in niche, climate and biological interactions that could affect the model predictions. The low habitat suitability of our study in Borneo for banteng could be because climatic and geographic conditions differ for *B.j. lowi* compared to those in mainland Asia, affecting model transferability across different regions (Zhu et al., 2021). Equally, Mori et al. (Mori et al., 2019) suggest that Chinese goral (*N. griseus*) should be reclassified within Brown goral (*N. goral*) together and Burmese goral (*N. evansi*) that together with *N. griseus* should be split to become an individual species. Future analyses must consider these taxonomic reclassifications. However, we modelled species level habitat suitability, rather than the subspecies, as we assume that there is less likely to be habitat and environmental condition variation at the subspecies level for these bovids (Smith et al., 2019).

We found that using the MSDM OBR technique showed a better predicted suitable area of the ecological niche, closer to the real distribution for species with more restricted ranges like banteng, wild water buffalo and Chinese goral, with higher performance TSS values compared to No MSDM models. We recommend restricting the accessible area for predicting wild water buffalo potential habitat to reduce overprediction caused by overlapping areas with domestic water buffalo.

We also used ensemble approaches, to obtain better predictive performance than from any single model type, but further analyses could also look at individual model results using different parameters, such as differing pseudo-absence background point ratios. The equal ratio of presence to pseudo-absence (1:1 ratio) has been used in several types of model like general linear models, artificial neural networks, and Maxent models, and it is also recommended for use in ensemble models when dealing with small sample sizes (Liu et al., 2019).

We acknowledge sampling deficiencies across the regions. We had fewer occurrences in Vietnam, Laos, Myanmar and Indonesia compared to Thailand, from which a large number of our data points came (30,512 points in Thailand, 3,152 points outside Thailand, Table 2.3). Occurrence data based on data accessibility may have sampling bias, particularly with clustered points for gaur, banteng, and mainland serow. We minimised these biases through spatial thinning (Aiello-Lammens et al., 2015). Since we found large amounts of suitable areas outside of Thailand, we suggest that future studies should focus on monitoring bovid populations in other countries, especially in India and Myanmar. However, because of this and the model performance, we focused on Thailand. For both banteng and wild water buffalo we also observed that there was higher suitability predicted by our models for areas of montane forest type (5% for banteng) and high elevation (over 1,300 m) and slope (9 degrees) than we consider likely to be highly suitable for these species. In our raw data the highest elevation for banteng is 800 m and for wild water buffalo 684 m. We examined the data and observed that the most important predictors are bioclimatic variables, rather than topographic variables [elevation, slope etc.], which showed lower percentage of contribution to the model building (see Appendix 1 Table S1.4, Figure S1.1 (D) and Figure S 1.10).

We are aware of the limitations of using the WDPA dataset, as a previous study has found the lower of the proportion in WDPA protected areas compared to China's National Nature Reserves (CNNR) (You et al., 2018). However, we used the WDPA dataset as it provides data for the entire distribution at a resolution that is appropriate for our analysis and for the consistency of modelling and interpreting the results. Moreover, for Thailand, our main area of study, the WDPA database's forest areas and categories are mostly consistent with Thai protected areas (e.g., national parks, wildlife sanctuaries, non-hunting areas) and this database has been used for conducting species distribution modelling (Pomoim et al., 2022) and evaluating the effectiveness of protected areas in Thailand (Singh et al., 2021).

Missing data has likely impacted some results. The model TSS values for endangered banteng and Chinese goral are over 0.8, yet our models predict no suitable areas in parts of Indonesia (east and central Kalimantan; (Dewi et al., 2020)) for banteng, and in China (e.g. Beijing and northeast Inner Mongolia; (J. Yang et al., 2019)) for Chinese goral from which these species have been reported. This would likely be improved if more spatial data were available for these species. Recent surveys of gaur and banteng in China suggest gaur are present, but banteng is extinct (Ding et al., 2018). Our models have not predicted highly suitable areas for gaur in China, though there are suitable areas in the north of Myanmar close to South Yunnan, whereas for banteng our findings are similar, with very low predicted suitable areas for banteng in China (5 – 20 km^2; Table S1.5)—a notably small area compared to the entire country. However, we predicted the largest suitable areas for Chinese goral (~ 285,000 km^2) and mainland serow (~ 60,000 km^2) in China, which are within the range of those reported (Jiang, 2024). We used a new dataset of species occurrences to assess our model's performance with a 5 km buffer zone, aiming to enhance modelling accuracy. Given these species have quite large home ranges and daily movements, adding a buffer to represent this movement unsurprisingly lead to better model predictions for all species, but most notably for mainland serow, changing the out of sample prediction from 19% to 67% for the entire region and 36% to 86% for Thailand. The buffer zone may indicate the utilisation of unsuitable areas of the species near forested regions, such as secondary forests, agricultural areas, or water resources, which possibly extend these buffer areas from the protected aeras to enhance the wildlife protection.

Our final model excluded two out of five species, the Chinese goral and mainland serow, and I cropped the entire species ranges to focus only on Thailand due to relatively poor model accuracy and performance for these species and habitat suitability outside Thailand. To improve model accuracy and performance, we may need more species occurrence data and updated species distribution maps, which can be used to mask areas and reduce overprediction. The occurrence data can be collected through various wildlife population survey methods, such as camera trapping, GPS locations, distance sampling, population censuses, and sourced from online databases like GBIF and iNaturalist. We encourage continued research and data collection on species habitat suitability and distribution, as land use and environmental changes may affect population distribution dynamics, behavior, and suitable habitats.

The spatial restriction method, OBR, can be sensitive to the distribution of occurrence data, because it keeps predicted suitable areas close to the occurrence locations. This may lead to the exclusion of potential suitable areas driven by a lack of occurrence data in those areas. For example, the wild water buffalo No MSDM predicted potentially suitable habitat around the Sre Pok Wildlife Sanctuary in Cambodia where the species is distributed (Gray et al., 2012), but after the spatial restriction (MSDM), this potential habitat was excluded as we lack occurrence data in Cambodia. Although our study showed slightly different TSS values between two different accessible area extents, we encourage testing the different accessible areas as it affects the model results (Anderson & Raza, 2010). Moreover, model performance varied with accessible area sizes and spatial restrictions, emphasising the need for careful accessible area definition in ecological modelling (Barve et al., 2011). Further, future analyses may try to better account for the current presence of species by accounting for factors such as hunting using other proxies, such as other human-disturbance metrics like distance from roads (Lim et al., 2021).

2.5 Conclusion

Our study provided an overview of the suitable remaining habitat for threatened bovid species at a regional scale using high-resolution environmental variables and species occurrence data from multiple observation methods. Our predictions showed that the suitable areas are small and fragmented for all species, and more than 50% of suitable areas are outside of protected areas. Those suitable areas outside PAs could possibly become efficient conservation areas, such as forest corridors or buffer zones to connect fragmented bovid populations and enhance long-term habitat conservation. Our predictions may inform conservation actions to avoid further defaunation of wild bovidae such as the management of human-wildlife conflicts and habitat quality for long-term species survival.

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STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Wantida Horpiencharoen
Name and title of main supervisor:	Prof David Hayman
In which chapter is the manuscript/published work?	Chapter 3
What percentage of the manuscript/published work was contributed by the student?	75%

Describe the contribution that the student has made to the manuscript/published work:

I have contributed to the outline of a study design, led the data analysis, including building the infectious disease models and collecting the parameter values and writing the R code scripts, and I lead the writing of the manuscript and along with editing the manuscript following feedback from my supervisors.

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Chapter 3

Impact of Infectious Diseases on Wild Bovidae Populations in Thailand: Insights from Population Modelling and Disease Dynamics

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Abstract

The wildlife and livestock interface is vital for wildlife conservation and habitat management. Infectious diseases maintained by domestic species may impact threatened species such as Asian bovids, as they share natural resources and habitats. To predict the population impact of infectious diseases with different traits, we used stochastic mathematical models to simulate the population dynamics over 100 years for 100 times a model gaur (*Bos gaurus*) population with and without disease. We simulated repeated introductions from a reservoir, such as domestic cattle. We selected six bovine infectious diseases; anthrax, bovine tuberculosis, haemorrhagic septicaemia, lumpy skin disease, foot and mouth disease and brucellosis, all of which have caused outbreaks in wildlife populations. From a starting population of 300, the disease-free population increased by an average of 228% over 100 years. Brucellosis with frequency-dependent transmission showed the highest average population declines (-97%), with population extinction occurring 16% of the time. Foot and mouth disease with frequency-dependent transmission showed the lowest impact, with an average population increase of 200%. Overall, acute infections with very high or low fatality had the lowest impact, whereas chronic infections produced the greatest population decline. These results may help disease management and surveillance strategies support wildlife conservation.

3.1 Introduction

Livestock encroachment into wildlife habitats can drive disease transmission between wildlife and domestic livestock, which is a vital issue for both human public health and wildlife conservation. An effect of agricultural expansion and land-use change is to bring wildlife and livestock close to each other and increase the contact frequency and time between domestic and wildlife populations (Byrne et al., 2022; Hassell et al., 2017; Hayman, 2016). This increased contact may increase the risk of disease transmission as they can share the same natural resources (e.g. grassland and water) (Jori et al., 2021).

Infectious diseases can cause dramatic declines in wildlife populations, as demonstrated by chytridiomycosis, which has been implicated in the likely extinction of over 200 amphibian species (Skerratt et al., 2007). Most infectious bovid pathogens are capable of infecting both domestic and wild species. For example, bighorn sheep populations declined from ovine respiratory disease (*Mycoplasma ovipneumoniae*) acquired when sharing the grazing areas with domestic sheep (Carpenter et al., 2014). Similarly, bovine brucellosis has been transmitted from domesticated yak to wild yak in China (Shi et al., 2016), and between bison, elk and domestic cattle in the USA (Cotterill et al., 2020). Brucellosis affects these bison and elk populations both indirectly and directly as the seropositive animals may be culled for management and directly as the pathogen affects animal reproductive systems (Schumaker et al., 2012) Schumaker et al., 2012. Critically, the impact of infectious diseases is determined by disease-specific traits, such as infection fatality rates (Hayman et al., 2022).

There are five wild bovids species (gaur, banteng, wild water buffalo, mainland serow and Chinese goral) that remain in Thailand. They are experiencing dramatic population declines from habitat destruction, illegal hunting (Jenks et al., 2012), and resource competition with domestic livestock (Chaiyarat & Srikosamatara, 2009). Infectious diseases transmitted from contact with domestic cattle could cause further declines. Several diseases are circulating in Thai cattle, including endemic diseases like bovine tuberculosis (bTB) from *Mycobacterium bovis* (Singhla & Boonyayatra, 2022), and new infectious diseases, such as the recent lumpy skin disease (LSD) (Punyapornwithaya et al., 2022).

Infectious disease modelling provides a tool to understand disease dynamics better and predict the potential consequences of infection in a population, helping disease prevention and control programs (Kirkeby et al., 2020), particularly as collecting field data or conducting experiments on some pathogens and hosts is extremely challenging. Models have, for example, been used to determine the potential impact of disease on endangered species, such as canine distemper in the Amur tiger (Gilbert et al., 2020). Although models contain uncertainty and may not cover all factors, predictions can guide the policies and help decision-making (Singer et al., 2011).

Here, we use mathematical models to explore the potential consequences of six major bovine infectious diseases on endangered Thai wild bovid populations. Our aim is to estimate the potential population changes after the disease is introduced in the population from a reservoir, such as domestic cattle. The diseases are anthrax, haemorrhagic septicaemia (HS), bTB, LSD, foot and mouth disease (FMD) and bovine brucellosis, which all infect a range of bovid species, are distributed worldwide, including Thailand, and have different characteristics. Our study predominantly focuses on the gaur (*Bos gaurus*) population as their populations are well described plus, of five species of Thai wild bovids, they have the greatest opportunity to interact with domestic livestock and humans since they are the most likely to share space and resources (e.g. agricultural areas, watering holes) (Chaiyarat et al., 2021; Chockcharoen et al., 2020). We hypothesised that acute infections with very low and very high infection fatality rates would have less impact on populations than those with moderate mortality or chronic diseases, the latter high fatality case because they ‘burn out’ by removing infectious individuals rapidly (Hayman et al., 2022). The study aims to help infectious disease surveillance and monitoring prioritisation strategies in wildlife and livestock for wild bovid conservation.

3.2 Material and methods

3.2.1 Model construction

Population dynamic models

We selected gaur populations as a model system because they are widespread across Thailand, overlap with livestock and people, and demographic data are available (Chaiyarat et al., 2021; Prayoon et al., 2021). Further, their demography is similar to other threatened wild bovids (Figure S2.1 in Appendix 2). The demographic parameters for the remaining four bovid species used in simulations are provided in Table 3.1 because they exhibit variations in population sizes, social behaviours, and distribution, making them interesting for further infectious disease modelling of population impact.

We assumed demographic parameters were otherwise constant. If N is the total animal population, N_a is the adult population, N_{sa} is the subadult population, N_c is the calf population and μ is the annual birth rate. Only adult females were assumed to add new calves to the population, which enter the susceptible class at a birth rate $\mu_b N_a$. Animals can leave their compartments at the natural death rate (μ_a, μ_{sa} or μ_c) or ageing from calf to subadult (δ_c) and from subadult to adult (δ_{sa}). The natural death rate was estimated based on the mortality rate of wild ungulates and gaur in captivity (Ahrestani et al., 2011). The initial population was 300 animals, based on the gaur population size in the Khao Pheang Ma non-hunting area (8 km^2) in Thailand (Duengkae et al., 2022; Laichanthuek et al., 2017). Thus, the population dynamic model equations at time *t* can be as following:

$$
\begin{aligned}
N_t &= N_c + N_{sa} + N_a \\
\frac{dN_c}{dt} &= \mu_b N_a + \delta_c N_c - \mu_c N_c \\
\frac{dN_{sa}}{dt} &= \delta_c N_c - \delta_{sa} N_{sa} - \mu_{sa} N_{sa} \\
\frac{dN_a}{dt} &= \delta_{sa} N_{sa} - \mu_a N_a
\end{aligned}
$$

(Equation 1)

Table 3.1 Parameters and variables.

		Species							
Symbol	**Description**	**Gaur**	**Banteng**	**Buffalo**	**Serow**	**Goral**		**Units**	**References**
N	Starting total population	300	470	69	120 (assume)	292 (assume)		animal	
μ_b	Birth rate	0.34	0.35	0.40	0.70	0.50		year^{-1}	Duengkae et al. (2022); Laichanthuek et al. (2017); Srikosamatara and Suteethorn (1995)
μ_c	Calf death rate	0.27	0.26	0.27	0.50	0.45		year^{-1}	Ahrestani et al. (2011); Choquent (1993); McCullough (1979)
μ_{sa}	Subadult death rate	0.15	0.26	0.15	0.15	0.28		year^{-1}	Ahrestani et al. (2011); Gardner et al. (2014); Heinen (1993); Tang et al. (2019)
μ_a	Adult death rate	0.17	0.15	0.20	0.28	0.18		year^{-1}	Ahrestani et al. (2011); Gardner et al. (2014); Heinen (1993); (Tang et al., 2019)
δ_c	Calf ageing	0.0027	0.0027	0.0027	0.0027	0.0027		day^{-1}	Jones et al. (2009)
δ_{sa}	Subadult ageing	0.0009	0.0009	0.0009	0.0009	0.0009		day^{-1}	Jones et al. (2009)
		Disease							
		Anthrax	**bTB**	**HS**	**LSD**	**FMD**	**Brucellosis**		
β	Disease transmission rate	$0.01- 3x10^{-5}$	$1.4x10^{-3}$	0.330	0.008-0.032	0.115-0.026	$5.5x10^{-3}$ - $5.5x10^{-6}$	day^{-1}	Cabezas et al. (2020); Cross and Getz (2006); Deepak (2020); (Dobson & Meagher, 1996); Magori-Cohen et al. (2012); (Saad-Roy et al., 2017); Wongsathapornchai et al. (2008)
σ	1/Incubation period	0.14	$6.7x10^{-3}$	-	0.14	0.13	0.07	day^{-1}	Cross and Getz (2006); Hugh-Jones and Tinline (1976); Magori-Cohen et al. (2012); Sun et al. (2020); WHO (2008); WOAH (2021c)
γ	1/Infectious period	1	-	0.33	0.03	0.20	0.0014	day^{-1}	Hobbs et al. (2015); Mardones et al. (2010); Mat et al. (2021); Sinkie and Narasimha (2016)
ρ_c	Disease-induced fatality in calf	1	0	0.53 - 5.84	0.05	0.10	0.10	day^{-1}	Baptista et al. (2017); Das et al. (2021); Govindaraj et al. (2021); Jolles et al. (2005); Njeru et al. (2021); Sinkie (2016)
ρ_{sa}	Disease-induced fatality in subadult	1	0	0.53 - 5.84	0.03	0.05	0.05	day^{-1}	Baptista et al. (2017); Das et al. (2021); Govindaraj et al. (2021); Jolles et al. (2005); Njeru et al. (2021); Sinkie (2016)
ρ_a	Disease-induced fatality in adult	1	0.11	0.53 - 5.84	0.01	0.03	0.03	day^{-1}	Baptista et al. (2017); Das et al. (2021); Govindaraj et al. (2021); Jolles et al. (2005); Njeru et al. (2021); Sinkie (2016)
α	Infected female will produce infected calf	0	-	-	-	0.50	0.9	day^{-1}	Dobson and Meagher, 1996
μ_{bI}	Birth rate for infectious individuals	-	$6.8x10^{-4}$	-	$8x10^{-4}$	$8x10^{-4}$	$5x10^{-4}$	day^{-1}	Abdulqa et al. (2016); Dobson and Meagher (1996); Jolles et al. (2005)
ω_c	Losing of immunity for calf	-	-	$5.6x10^{-3}$	$5.6x10^{-3}$	$8.3x10^{-3}$	$5.6x10^{-3}$	day^{-1}	Hobbs et al. (2015); Jolles et al. (2021); Tuppurainen and Oura (2012); Verma and Jaiswal (1998)
ω_{sa}	Losing of immunity for subadult	-	-	$5.6x10^{-3}$	$5.6x10^{-3}$	$8.3x10^{-3}$	$5.6x10^{-3}$	day^{-1}	Hobbs et al., 2015; A. Jolles et al., 2021; Tuppurainen and Oura, 2012; Verma and Jaiswal, 1998
ω_a	Losing of immunity for adult	-	-	$5.6x10^{-3}$	$5.6x10^{-3}$	$1.8x10^{-3}$	$5.6x10^{-3}$	day^{-1}	Hobbs et al., 2015; A. Jolles et al., 2021; Tuppurainen and Oura, 2012; Verma and Jaiswal, 1998
ω_m	Waning of maternal immunity	-	-	-	-	$6.9x10^{-3}$	$5.6x10^{-3}$	day^{-1}	Hobbs et al. (2015); Jolles et al. (2021)
ϵ	External force of infection rate	$2x10^{-5}$	$2x10^{-5}$	$2x10^{-5}$	$2x10^{-5}$	$2x10^{-5}$	$2x10^{-5}$	day^{-1}	Hayman et al. (2022)

[To interpret the parameters, any rate r can be converted to probability $P(t)$ using $1 - exp^{-rt}$, where t is the time period, e.g. for $\epsilon, P(t) = 1 - exp^{-\epsilon t} = 1 - exp^{-2x10^{-5} * 365} = 0.007$, or if the total S in the population is 300, ≈ 2 events per year. The dashed line (-) means no parameters were used in the models.]

Infectious disease models

We used the same age-structured population as the baseline model (Equation 1) and incorporated compartments with different parameter values for building the disease models.

We modelled the diseases based on Susceptible-Infected-Recovered (SIR) models and modified them based on the disease parameters of domestic animals (e.g. dairy cattle, domesticated buffalo) and wildlife from the previous studies and background knowledge. Table 3.2 presents the diseases and model structures we used, and a flow diagram is in the Appendix 2. For the compartments used in the models, S denotes the number of susceptible animals, E denotes the number of exposed animals, I denotes the number of infected animals, R denotes the number of recovered animals, and M denotes the number of calves with maternally derived immunity.

We selected six infectious diseases which have been reported to cause outbreaks in wild ungulates and livestock populations in several places, including Thailand, which are: anthrax (*Bacillus anthracis*) with an SI structure, bovine tuberculosis (bTB-*Mycobacterium bovis*) with an SEI structure, haemorrhagic septicaemia (HS-*Pasteurella multocida*) with an $SIRS$ structure, lumpy skin disease (LSD) with an $SEIRS$ structure, and both foot and mouth disease (FMD) and brucellosis (*Brucella abortus*) with an $SIERMS/E$ structure. These infections have a range of key parameters of interest. They include infectious diseases with very short (effectively no) incubation periods (e.g. HS) to long incubation periods (e.g. bTB), and very high mortality (e.g. anthrax) to low mortality (e.g. LSD, FMD).

Table 3.2 Diseases, pathogens, and the structures

Disease	Pathogens	Model structure
Anthrax	*Bacillus anthracis*	$S \rightarrow I$
Bovine TB	*Mycobacterium bovis*	$S \rightarrow E \rightarrow I$
Haemorrhagic septicaemia	*Pasteurella multocida*	$S \rightarrow I \rightarrow R \rightarrow S$
Lumpy Skin Disease	*Capripoxvirus*	$S \rightarrow E \rightarrow I \rightarrow R \rightarrow S$
Foot and Mouth Disease	*Aphthovirus*	$S \rightarrow E \rightarrow I \rightarrow R \rightarrow M \rightarrow S$ or E
Bovine brucellosis	*Brucella abortus*	$S \rightarrow E \rightarrow I \rightarrow R \rightarrow M \rightarrow S$ or E

Mode of transmission

Different transmission types can provide different model results (McCallum et al., 2001). Here, we considered two disease transmission modes; 1) density-dependent (DD) and 2) frequency-dependent (FD). DD transmission is assumed when the contact rate is proportionate to the population density, while FD transmission is assumed when the contact rate is independent of the population density (McCallum et al., 2001; Smith et al., 2009). We assumed the transmission modes for each pathogen and then compared them by introducing both transmission modes because, for some infections, there is no clear evidence of which type suits the pathogen's transmissions and these represent extreme situations of population change for both transmission modes (Hayman et al., 2022).

Transmission is often likely a mix of both DD and FD in many cases such as FMD and bTB (Beck-Johnson et al., 2023; Ciaravino et al., 2018). For the transmission rate (β), we used parameter values based on the reference studies with the reported FD or DD transmission (Table 3.1), which differs among infectious diseases. However, to test the sensitivity of the results to these assumptions, we also rescaled the β rate to all models to examine the consistency of the results between FD and DD using Equations 2:

$$\beta_{DD} = \frac{\beta_{FD}}{N}$$

$$\beta_{FD} = \beta_{DD}\ x\ N$$

(Equation 2)

Infection reintroduction

To model the repeated introduction of an infection from a reservoir such as domestic cattle (e.g. for FMD) or the environment (e.g. anthrax), we repeatedly reintroduced infection into our population at rate ϵ independently of any infection in the population. This reintroduction means the impact of infections are not simply estimated by the basic reproductive number (R_0), the average number of secondary cases caused by a primary case in a completely susceptible population.

Anthrax (*Bacillus anthracis)*

To model anthrax, we initially assumed the transmission is FD. We used an SI model (Friedman & Yakubu, 2013; Saad-Roy et al., 2017) with the transmission rate for FD at 0.01, then rescaled to FD using Equation 2. We assumed that S animals are exposed to infected animals and then become infectious (I) at rate β. All infected animals (I) die (100% mortality) (Sinkie, 2016) at disease-induced death rate (ρ) and the infectious rate (γ), $\gamma\rho I$.

Bovine tuberculosis (bTB - *Mycobacterium bovis*)

Bovine TB is a chronic and zoonotic infection in livestock and wildlife worldwide (Cross & Getz, 2006). We first assumed DD transmission and used an SEI structure for modelling. The flow of the model starts from S, which are exposed to I animals and become exposed (E) at transmission rate (β); then E animals enter the I compartment at the incubation rate (σ). As we assume lifelong infection without recovery (Cross & Getz, 2006); I animals either die with an age-specific disease-induced fatality rate (ρ) or natural death rate (μ). S and E adults give birth with the normal birth rate $\mu_b(S_a + E_a)$ but I adults are assumed to have a lower fecundity rate (reduced by 27%, (Jolles et al., 2005)) at $\mu_{bI}I_a$. Bovine TB has a long incubation period from several months up to 7 years (Barlow et al., 1997), so here we used 5 months based on the mean incubation period in the African buffalo (Cross & Getz, 2006). We also assumed there's no vertical or pseudo-vertical (e.g. in utero or calf rearing) transmission as it is uncommon in bTb (Menzies & Neill, 2000; Phillips et al., 2003).

Haemorrhagic septicaemia (HS - *Pasteurella multocida*)

HS is a fatal septicemic disease in cattle and buffalo. We assume DD transmission based on a previous HS modelling study (Deepak, 2020). We used an $SIRS$ model and excluded an E class as the disease can show acute clinical signs with a short incubation period of $\sim$ 18 – 20 hours (De Alwis, 1992) animals become I at the transmission rate (β). I animals may die from HS at the disease-induced fatality rate (ρ) or survive and become recovered (R) at infectious rate ($1/\gamma$). We calculated the fatality rate in the cattle population to range from 0.53% to 5.84%. This was determined by dividing the number of deaths from HS (0.21%, assumed from the percentage of deaths from bovine respiratory disease, (Baptista et al., 2017) by the minimum (3.59%) and maximum (40%) prevalence of seropositive animals from *P. multocida* infected herds (Khan et al., 2006; Nobrega et al., 2021). Therefore, we used two infection fatality rates (0.53 and 5.83%), since case fatality is underestimate as a large proportion of animals are infected but do not develop clinical signs of diseases. R animals reenter S when they lose immunity at the immunity loss rate (ω). We used the proportion of susceptible animals (0.6) to calculate R_0 and therefore the β rate using the equation: $R_0 = (1/(1-I)) = 1/S$.

Lumpy skin disease (LSD - Lumpy skin disease virus, *Capripoxvirus*)

We used an $SEIRS$ structure for LSD. We inserted E and R compartments as the disease has an incubation period of between 7 and 14 days and a recovery period of around 4 - 6 months. We initially assumed the transmission is DD as the cattle density could be one of the risk factors to increase the transmission rate within-herd. However, we used both FD and DD β values because the published work has reported differences in incidence rates associated with different transmission modes (Magori-Cohen et al., 2012). We assumed different birth rates for I females (μ_{bI}) from the natural birth rate, because LSD can reduce the fertility rate by 10% (Abdulqa et al., 2016). Also, we applied the highest fatality rate in calves (5%) and lower mortality rates to subadults (3%) and adults (1%) (Das et al., 2021).

Foot and mouth disease (FMD - Foot-and-mouth disease virus, *Aphthovirus*) & Bovine Brucellosis (*Brucella abortus*)

We initially assumed the transmission was FD for both FMD and brucellosis. An $SEIRMS/E$ model was applied for FMD and brucellosis. We considered the $SEIR$ model appropriate for both diseases. Recovered FMD and brucellosis cows can pass immunity to their offspring. Therefore, we added a maternally-derived immunity (M) compartment, which refers to the calves born with maternally-derived immunity from recovered mothers (R_a). We assumed that if recovered adults (R_a) calve at the birth rate (μ_b), a calf will receive maternal immunity and stay in M compartment for 6 months (Laubscher & Hoffman, 2012) before immunity wanes and they become susceptible again (S_m) at a loss of immunity rate (ω_m). S_m calves can either become an exposed calf (E_c) if contact with I or enter a susceptible subadult (S_{sa}) compartment at a loss of immunity rate plus calf ageing rate: $1/\delta_c = 1/(\delta_m + \omega_m)$ or $1/\delta_m = 1/(\delta_c - \omega_m)$ if they have no contact with I to ensure that animals spend the same average time in the calf age class ($_c$).

Vertical transmission from mothers to calves can be a consequence of infection among infected mothers with different probabilities for FMD (~ 0.5) and brucellosis (~ 0.9). Infectious adults are assumed to produce an infectious calf (I_c) entering I at the birth rate $\mu_b I$. The proportion of infected females producing infected calf denotes α. So, an infected female can produce an infected calf at a rate $\alpha\mu_{bI}I_a$ and produce a susceptible calf at a rate $(1-\alpha)\mu_{bI}I_a$.

The mathematical ordinary differential equations for the calf population (X_c) are:

$$\frac{dS_c}{dt} = \underbrace{\mu_b(S_a + E_a) + (1-\alpha)\mu_b I_a}_{\text{birth}} - \underbrace{\beta_c S_c(I_c + I_{sa} + I_a)}_{\text{transmission rate}} - \underbrace{\delta_c S_c}_{\text{ageing rate}} - \underbrace{\mu_c S_c}_{\text{natural death}} + \underbrace{\omega_c R_c}_{\mathit{recovery\ rate}} - \underbrace{\epsilon S_c}_{\text{force of infection}}$$

$$\frac{dE_c}{dt} = \beta_c S_c(I_c + I_{sa} + I_a) + \beta_c S_m(I_c + I_{sa} + I_a) - \sigma_c E_c - \delta_c E_c - \mu_c E_c + \epsilon S_c$$

$$\frac{dI_c}{dt} = \sigma_c E_c - (1-\rho_c)\gamma_c I_c - \rho_c\gamma_c I_c - \delta_c I_c - \mu_c I_c + \alpha\mu_{bI} I_a$$

$$\frac{dR_c}{dt} = (1-\rho_c)\gamma_c I_c - \omega_c R_c - \delta_c R_c - \mu_c R_c$$

$$\frac{dM}{dt} = \mu_b R_a - \omega_M M - \mu_c M$$

$$\frac{dS_m}{dt} = \omega_M M - \delta_m S_m - \beta_m S_m(I_c + I_{sa} + I_a)$$

(Equation 3)

The system of ordinary differential equations and all other disease model equations and diagrams can be found in the Appendix 2. Note that all equations are subsets or variants of Equation 3.

3.2.2 Model simulations

Due to the small population size of gaur and other endangered bovids, we were interested in how infections might lead to their decline. Additionally, as we aimed to allow infections to go extinct in populations if they could not be sustained, we used stochastic models to simulate population dynamics in different scenarios, briefly, categorising them into non-infection and infection diseases. We chose stochastic models for this study because they effectively capture the stochastic nature of wildlife populations using random values. This randomness introduces variations in population changes, which significantly affects a small population sizes and long-term simulations (Wei et al., 2017). First, we built the population dynamics model without infectious disease classes and parameters as a baseline model (Hayman et al., 2022). Then, we introduced an infectious adult ($I_a = 1$) to the susceptible (S) population. We assumed that I would infect S at a transmission rate, β, and enter the next compartment based on the model structure. Demography (birth rate, natural death rate and ageing rate), the external force of infection (ϵ), and disease-induced fatality (ρ) were included in all disease models. The stochastic simulation was performed using the Poisson distribution to calculate the probability of events by multiplying the rate parameters i with a time step through Gillespie's τ-leap algorithm (τ = 1) (Equation 4).

$$Prob_i = Poisson(\tau * rate_i * X) \qquad \text{(Equation 4)}$$

Where X is a state (e.g. S, I, R). All models were simulated for 100 years, and the stochastic models were simulated 100 times to generate the mean and to understand the uncertainty. We modelled the population change for 100 years, as long-term simulations of at least 10 years or three generations of species is recommended to explore population trends, and short-term time series may lead to misleading conclusions (White, 2018).

The parameter values used for modelling were collected from the literature review and observational data (Table 3.2).

3.2.3 Measuring impact

We compared the difference in total population (N) between no infection and disease models by calculating the average percentage of the population change using the total population at the start ($N_{t=0}$) minus the total population at the end, ($N_{t=100}$) of the simulation time, divided by $N_{t=0}$ and converted this to a percentage, then divided by 100 times of simulations, using the following equation:

$$\bar{x} = \left(\sum_{i=1}^{100} \frac{N_t - N_{t=0}}{N_{t=0}} / 100 \right) \times 100$$

(Equation 5)

We used a principal component analysis (PCA) to find which parameters contributed most to the percentage of the total population change. We selected four disease parameters (transmission rate, incubation rate, infectious rate and fatality rate) and then coloured the values based on the percentage of the total population change. We performed PCA in R software using the PCATools package (Blighe & Lun, 2019). The highest percentage of the first two axes contributed most to the population percentage changes.

3.2.4 Code availability

We used R Core Team (2022) to simulate all the models and for further analysis. The R code for reproducing the analyses is available at a GitHub repository https://github.com/Wantidah/InfectiousModel.

3.3 Results

3.3.1 Disease free model

We developed stochastic models for a gaur population, including a baseline model without infection and six infectious disease models. The baseline model of the gaur population demonstrated significant population growth, increasing from 300 to an average of 685 (range 113 - 1469) additional animals, which is approximately a 228% (38 - 489%) increase. The average adult and subadult populations consistently increased, while the calf population slightly decreased from 95 to 82 animals (19 - 279) on average (Figure 3.1: A&I). This gave us a disease-free population to model the impact of disease introduction into.

The population dynamics of the four other wild bovid species in Thailand show similar trends to the gaur population (Appendix 2, Figure S2.1), so we assumed there will be similar trends for the other two large bovids (banteng, wild water buffalo) that have similar herd sizes, population demography (e.g. age-structure, birth rate, death rate) and social behaviours to gaur (Srikosamatara, 1993).

However, the population dynamics may differ from the medium-sized bovids (Chinese goral and mainland serow) that live in smaller groups or even pairs and can be isolated from each other (Chen et al., 2019).

3.3.2 Disease impacts

Brucellosis had the greatest impact on population decline, while FMD had the lowest impact. Our PCA quantitatively shows that pathogens with longer incubation periods, chronic infection and medium to low fatality lead to greater population growth in smaller populations of endangered bovids than a high fatality or high transmission rate alone (Figure S2.17 and Figure S2.18). The first axis, PC1, has 43.25% and the second axis PC2 has 31.61% of the variance explained. The greatest contribution to the percentage population change in the first axis was the infectious rate (55%), and for the second axis is the incubation period (74%).

Using different parameter values, fatality rates and modes of transmission yielded different effects on the modelled populations for HS, FMD, LSD and brucellosis. FD brucellosis had the largest population impact, yet DD brucellosis suppressed population growth but led to a stable population. In contrast, FD transmission of HS, LSD and FMD showed a continued population increase. Anthrax and bTB showed only a slight difference in the average population change between the two transmission modes. Simply rescaling the β with modelling FD or DD transmission had limited changes, which demonstrated consistency in the population change within the same infectious disease. Rescaling the β also reduced the probability of local extinction in the gaur population (N = 0) for FD brucellosis. Figure 3.2 and Figure 3.3 present the results of rescaling.

LSD, FMD and brucellosis highlighting differences in population trends between FD and DD transmissions. We selected some important model results in Figure 3.1, and all modelling results and diagrams for infectious diseases and population changes can be found in the Appendix 2, Figure S2.2 - Figure S2.16 and Table S2.1.

Anthrax

There is no substantial impact on the population after introducing anthrax into the population, with a similar population change observed between FD and DD models (Figure 3.1 (B, J) and Appendix 2, Figure S2.3). Both transmission rates showed an increase in population, with a 57% increase for FD and 51% for rescaled DD model (Figure 3.3). No massive deaths were found, only 1 – 3 infectious animals were predicted for each outbreak for both transmission modes, consistent with the low transmission rate (β = 0.01) applied and a rare case of animal-to-animal transmission.

Bovine tuberculosis

There was uncertainty regarding the mode of transmission in bTB models, however, (Cross & Getz, 2006) showed limited qualitative differences in model outcomes when they used FD or DD transmission. Here, we saw similar results in that overall, the populations tended to decline gradually through the simulation period with a 88 – 89% decline from the initial population (Figure 3.1 (C, K) and Figure 3.3). Rescaling the β transmission parameter also led to limited qualitative differences in population trends, but we did see differences in predicted classes; for example, this increased or decreased the number of infected individuals over time (i.e., higher or lower prevalence) (see Appendix 2, Figure 2.5 and Figure 2.6).

Haemorrhagic septicaemia

For HS, we found that the impact of infection was less dependent on the mode of transmission than case fatality. A ten-fold increase in fatality rate led to a decline in the total population change (Figure S2.8 and Figure S2.9).

Lumpy skin disease

For LSD, we found that the two published transmission parameter values (0.008 and 0.032) led to differing outcomes that also depended on the mode of transmission Magori-Cohen et al. (2012). Whilst rescaling the parameters did not lead to qualitative differences, the use of the parameter values estimated from direct density-dependent transmission within herds from Magori-Cohen et al. (2012) led to a population decline. However, the estimate from the indirect transmission (presumably via mechanical transmission from flies) did not and the modelled population still grew by 155% with FD LSD (Figure S2.11).

Foot and mouth disease

The least impact was seen in the FMD model with FD transmission, which predicted the total population growing by 200%, around 28% less than the disease-free population. Frequency-dependent FMD transmission with a β transmission rate of 0.115 and the rescaled DD parameter 3e-4 similarly had limited impact on the population growth with an increasing population over time (Figure 3.1 (D – F)). Increasing β in the DD model, however, decreased the total population by -80% at β = 21, which had a greater impact on the population change from 130% at β = 3e-4. FMD also showed a periodic pattern with outbreaks around every 3 - 5 years (Figure 3.1 (G, O)). Increasing the β rate from 0.11 to 21 in FD FMD models led to similar dynamics close to DD transmission (Figure S2.13 and Figure S2.14).

Bovine Brucellosis

Brucellosis with FD transmission led to a 97% decrease in the average population change (Figure 3.1 (H, P), Figure 3.2 (H)) and was most likely to drive the population to local extinction with 16% of the total simulations leading to extinction, mostly occurring from year 80-100 (Figure S2.15).

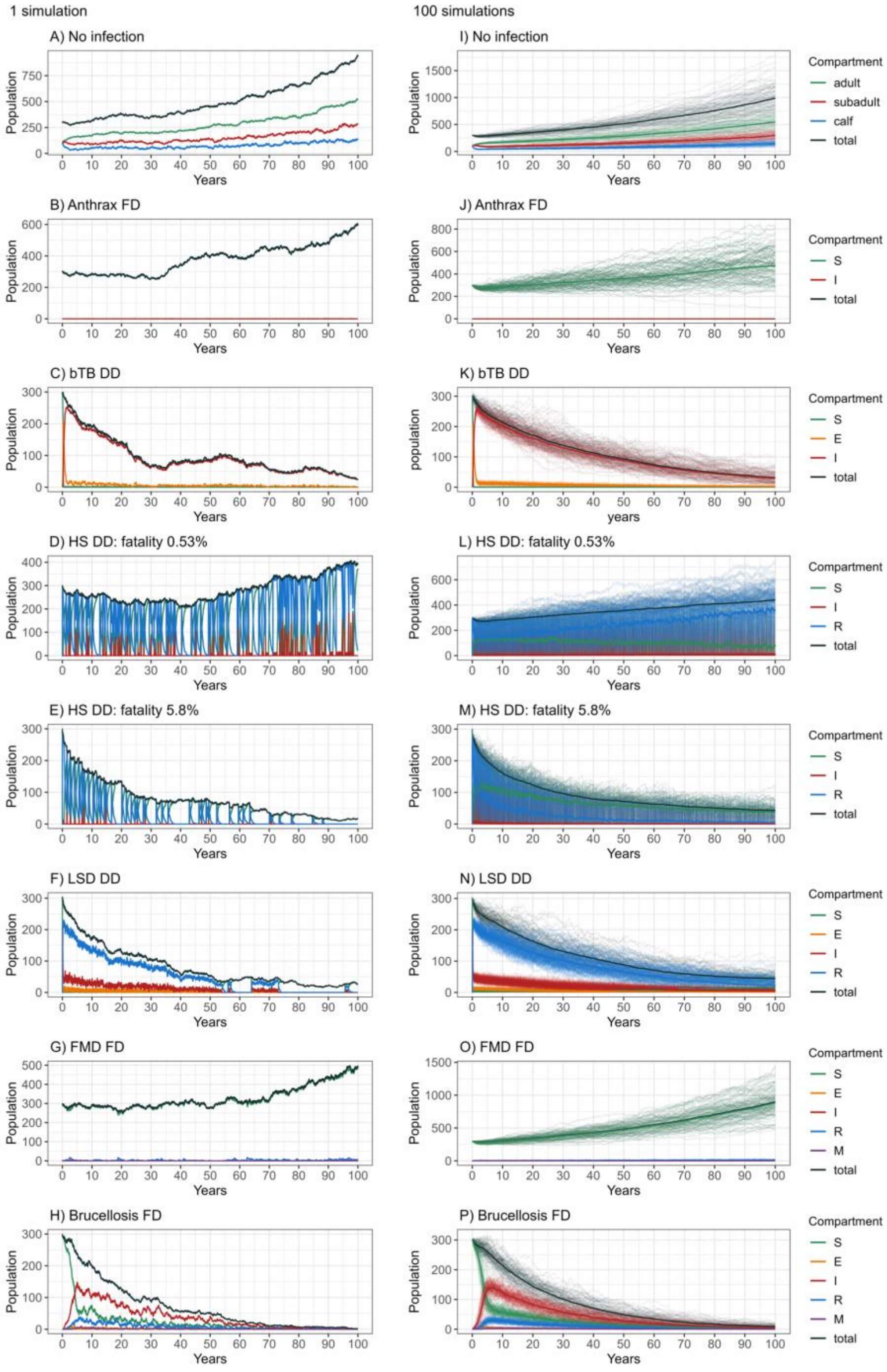

Figure 3.1 Modelled gaur population dynamics with and without disease : A – H are single example stochastic simulations for 100 years; I – P are 100 stochastic simulations for 100 years. Mean values are in solid lines. A and I are no infection models and the others are the infectious disease models where bTB is bovine tuberculosis; HS haemorrhagic septicaemia; LSD lumpy skin disease; and FMD foot and mouth disease. The entire model results, including all disease parameters used in the simulations, can be found in the Appendix 2.

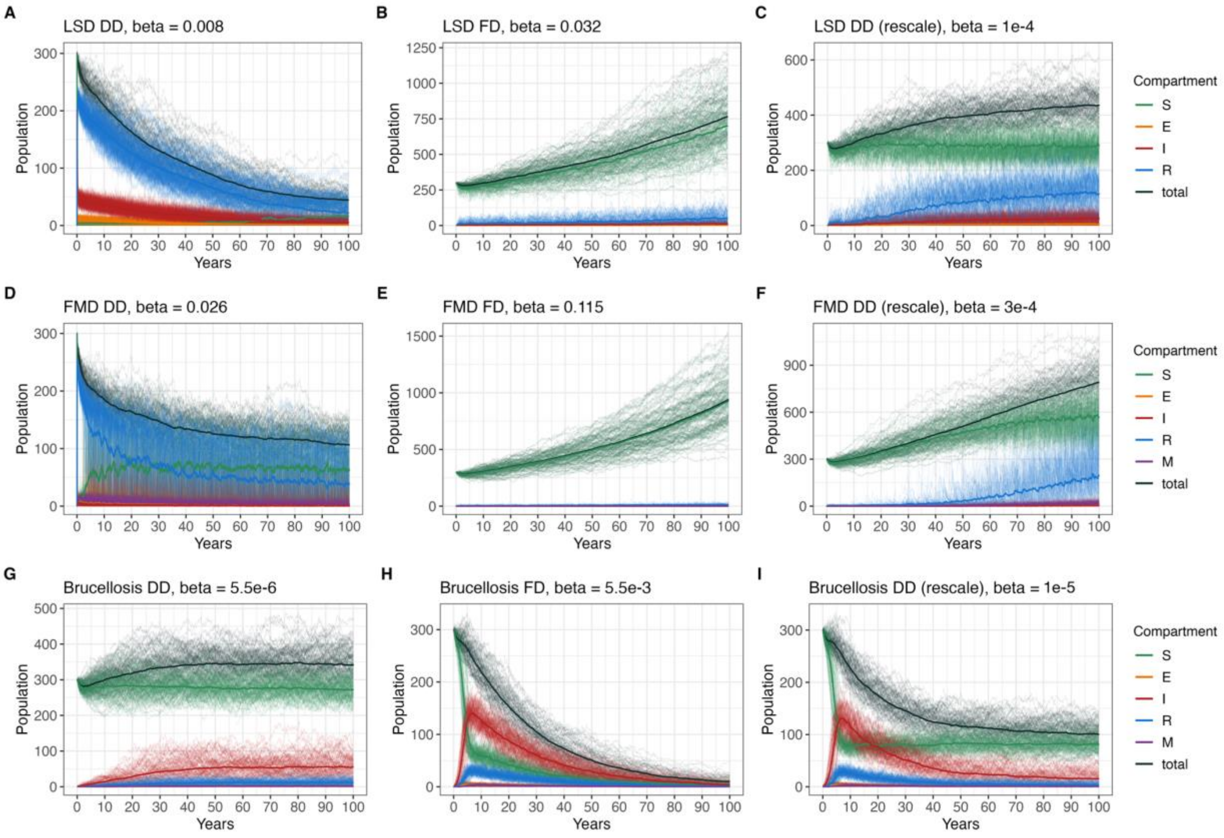

Figure 3.2 Population dynamics for LSD, FMD and brucellosis with different transmission modes and rescaled β transmission coefficient values to isolate the effect of the mode of transmission. A, D, G (left) are DD models; B, E, H (centre) are FD models, and C, F, I (right) are DD models with rescaled β transmission of FD parameters. Rescaling LSD (A-B) and FMD (D-E) parameters have limited impact over the period modelled, but rescaling the brucellosis β shows a reduction in FD transmission.

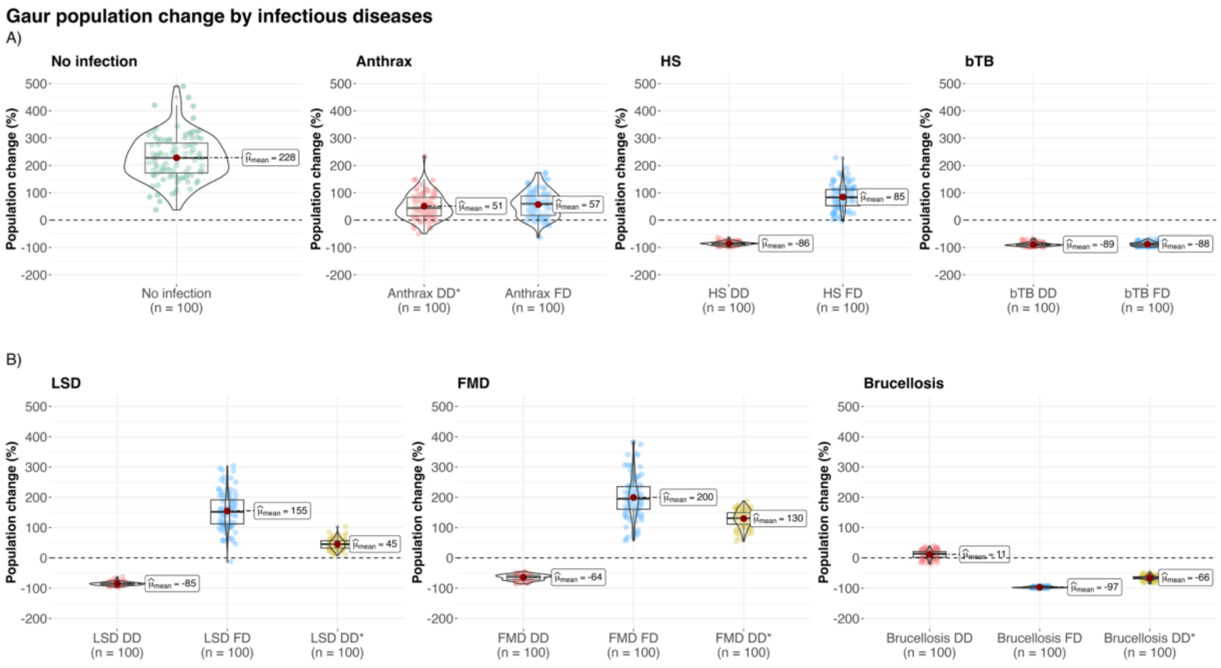

Figure 3.3 Overall modelled gaur population changes for each infection. Shown are the 100 results after 100 years of 100 stochastic simulations. The x-axis is the type of disease transmission and y axis is the population change in percentage. A (top) compares no infection, FD and DD for anthrax, HS and bTB; B (bottom) compares FD and DD transmission and DD* that uses the rescaled β transmission from the FD model with DD transmission for LSD, FMD, and brucellosis.

3.4 Discussion

Interactions between wildlife and livestock can facilitate the transmission of emerging infectious diseases (Wiethoelter et al., 2015), making this interface an essential zone of concern to public health, animal production and wildlife conservation. We identified the potential consequences and severity of six bovine infectious diseases present in Thailand (anthrax, HS, bTB, LSD, FMD and brucellosis) in a model wild bovid population, using different infectious disease model compartments based on the current literature (Table 3.1). Brucellosis had the greatest population impacts and FMD the lowest, despite the same model structures being used for these two pathogens. Overall, our base model predicted population growth with varying impacts of diseases, and our analyses matched our expectation that those acute infections with very high fatality rates (anthrax and HS) have less impact than chronic infections with lower infectious rates (bTB, brucellosis), as infected individuals are rapidly removed from populations (Hayman et al., 2022). Therefore, our analyses suggest that pathogens with longer incubation periods, chronic infection and low to medium fatality rates have a greater negative impact on population growth in small populations of endangered bovids (Figure 2.5, Figure 2.6 and Figure S2.15). This is most likely because these traits allow infections to persist, allowing long-term infection effects on demographic structures (e.g. reduced birth rate, increased death rate).

We used 100% fatality rates in all infected animals as the worst-case scenario for the anthrax model, which led to limited impact over the 100 years, likely because of this rapid removal of infected individuals (I), despite repeated reintroduction of infection (Hayman et al., 2022). We first considered anthrax transmission between infected and susceptible animals as FD transmission, assuming contact rate is more influential than host density (Saad-Roy et al., 2017). However, the transmission mode could also be DD, based on the density of spores in the contaminated environment (e.g. infected carcass, soil) (Friedman & Yakubu, 2013), and the cattle density that could contribute to between-species (Otieno et al., 2021). Thus, we modelled repeated introductions through ϵ to cover the external force of infections, including the risk of disease transmission from cattle, other than within-herd transmission.

Bovine tuberculosis causes chronic, fatal infection and reduces pregnancy rates and, therefore, the population growth of wild bovids (Jolles et al., 2005; Joly & Messier, 2005). There is no current evidence of bTB infection driven population declines in Asian wild bovids, however our study found that, regardless of both transmission modes, the long-term effect of bTB would be to reduce the expected total population by around 88 – 89%. This is similar to findings by Jolles et al. (2005), who showed that bTB persisted in African buffalo populations and reduced adult buffalo numbers primarily through mortality of animals more than 4.5 years old. The transmission coefficient (β) was noted as one of the most important parameters for bTB in African buffalo (Cross & Getz, 2006). In our work, we found consistent population dynamics between FD and DD transmission, defined by similar trends and percentages of population change, when converting β between the original value (from several studies) and the rescaled values (Figure 3.3, Figure 2.5 and Figure 2.6). This is likely due to the duration of the infection, which might increase the probability of contact with infectious animals in the population and the number of transmissions.

For HS, many animals are infected but do not develop clinical signs, making it difficult to detect an infected animal. Further, variable clinical signs make positive cases difficult to detect, therefore the case fatality rate is normally substantially higher than the actual infection fatality rate. In our study, we calculated the fatality rate using the prevalence of seropositive animals (max = 40%) from reported studies of cattle populations, and this substantially decreased the case fatality from 90% to around 6% of animals (Nobrega et al., 2021; Singhla et al., 2020). Our model shows that changing the mortality from 0.53% to 5.8% affects the total population numbers more than changing the transmission modes, by more strongly reducing the population sizes (Figure S2.8 – Figure S2.9). HS antibodies were found in free-ranging buffalo in Asia so this population might be a reservoir, but this needs further investigation (De Alwis, 1992). HS is endemic in Thailand (Singhla et al., 2020), and mortality in wild ungulates has been reported historically (Robinson et al., 2019), so the mortality and infection status of HS should be considered in the mitigation plans for endangered species (e.g. wild water buffalo and banteng).

Both FMD and LSD with FD transmission showed the least impact on populations, with both having acute, short infections with lower overall mortality (Jori & Etter, 2016; Tuppurainen & Oura, 2012). FMDV in particular, is highly contagious among cattle with a very high β coefficient compared to the other diseases (Beck-Johnson et al., 2023). Yet, although Beck-Johnson et al. (2023) found little effect of FMD with either transmission modes within-herds, our results showed that DD transmission led to greater population declines as did rescaling the parameter used for FD models (Figure S2.13 and Figure S2.14). The reason for the latter observation is not clear but might be because the dynamics with reintroduction allow more infection to persist and so suppress the population (Figure 3.2). Note that with reported wild bovid herd sizes, acute transmission is unlikely to allow FMDV to persist, but reintroductions from cattle reservoirs (modelled through ϵ) are likely A. (Jolles et al., 2021). Our result for FMD DD transmission also showed cyclic patterns in outbreaks consistent with seasonal patterns of outbreaks observed in Thailand (Chanchaidechachai et al., 2022).

We found that brucellosis with FD transmission and its reported β rate might cause extinction 16% of the time, whereas DD transmission may suppress population growth, but not enough to cause population declines, even with the published FD rate rescaled and used in a DD model. Brucellosis has caused population declines among African buffalo, especially when there is co-infection with tuberculosis (Gorsich et al., 2018). However, brucellosis only caused limited population growth impacts in American bison, even though the disease persisted in the population over time (Dobson & Meagher, 1996; National Academies of Sciences et al., 2017). In Dobson and Meagher's study (Dobson & Meagher, 1996), their FD brucellosis models showed bison populations would increase in numbers, whereas our models predicted a decrease, perhaps because our model species' population size and structure differed from their study. Notably, *Brucella* can infect multiple species, and the transmission source may not be obvious when multiple species interact. For example, brucellosis outbreaks in Yellowstone National Park, USA, were not from wild bison as first thought, with elk the likely primary host (Godfroid, 2018). Understanding the potential transmission among and from other wild Asian ungulates may be necessary to fully understand potential brucellosis impacts.

We assumed a single, closed (no migration) population with constant natural birth and death rates. Therefore, our models explore the intrinsic population dynamics without considering the influence of other positive (e.g. conservation) or negative factors (e.g. habitat destruction, competition). Furthermore, it is unclear what population changes occur during migration (Ahrestani & Karanth, 2014), so a closed population model can only simulate within-herd dynamics and reflect the population impacts in a small population, such as in small protected areas (Duengkae et al., 2022; Prayoon et al., 2021).

Selecting the appropriate transmission mode for modelling is challenging (Luis et al., 2018). The infectious disease parameter values themselves are mostly estimated from livestock outbreak data, which can vary among the regions. Rarely is infection 'natural' without intervention through disease control (Beck-Johnson et al., 2023). Although the transmission type for some pathogens have been recorded as FD or DD in previous studies, these were mainly conducted under farm husbandry or experimental conditions in captive or closed systems. These conditions significantly allow animal density to affect contact rates. However, our study focused on wildlife populations that are distributed in areas in which the frequency of contact could have more influence. Moreover, some infectious diseases can display aspects of FD and DD depending on the conditions, such as within – or between herd transmission, herd size, density, contact with other reservoirs and contact mode (indirect, direct). For example, the bTB transmission rate can be increased correlated to herd size if the area is stable because the density of animals is increased (Alvarez et al., 2014). Also, the transmission mode for anthrax spores from animal to animal is FD, but from the environment to an animal is based on the density of the spores in the areas. We, therefore, took the strategy of assuming the most extreme scenarios, fully FD and DD, and used both for modelling.

Our models also added the external force of infection (ϵ), which represents the re-introduction of pathogens. ϵ is assumed to include transmission from other sources of infection other than just infectious animals, such as transmission due to environmental factors (e.g. soil, carcasses) or vectors (e.g. blood-sucking fly) to susceptible animals (Hayman et al., 2022). This transmission can theoretically cause population extinctions if agents have high case fatality rates. Here, we chose a relatively high reintroduction rate ($\sim$2 per year into the initial population), which likely represents a worst-case scenario. However, to improve this study, we encourage adding the specific environmental factors for each disease and incorporating spatial analyses (Pepin et al., 2022; Rohani et al., 2009).

Further studies might also consider adding the potential reservoir hosts and their dynamics into the models by building two or more host models to examine the transmission route among the potential hosts (Aranaz et al., 2004; Godfroid et al., 2013; Mohamed, 2020; Roche et al., 2021; Royce & Fu, 2020). Modelling coinfection is another important point as there are interactions between infections such as FMDV and HS, which seen as a secondary infection in FMD outbreaks (Chandranaik et al., 2015), or between brucellosis and bTB (Gorsich et al., 2018). However, our analyses provide an approach to understanding the *relative* likely impact of common endemic and emerging diseases with different traits and is a tool for understanding gaps in disease surveillance and control systems by using the prediction modelling before implementing actions. Another further analysis is a sensitivity analysis that can be applied to identify the degree of influence of the disease parameters on the model output, in this case, population change. It also suggests which state of disease transmission should prompt action and aids in selecting optimal control measures (Nadeem Anjam et al., 2024).

Strengthening disease surveillance and mitigation programs may be further achieved by targeting virulent diseases through passive and active surveillance data, such as collecting the frequency of infections, number and species of wild ungulates, behaviour and time spent together between wild and domestic livestock (particularly in the high-risk areas) (Bengis et al., 2002; Silk et al., 2019). It may be useful for disease mitigation to largely focus on domestic animal disease control and preventing transmission to wildlife as an amenable approach (Bengis et al., 2002). Moreover, conserving wildlife habitat can reduce the probability of contact and the risk of disease transmission between wildlife and domestic livestock (Caron et al., 2013; Hayman, 2016). Limiting the contact between wildlife and livestock could reduce species extinction (Pedersen et al., 2007).

With applications in wildlife conservation, a reproducible modelling framework is advantageous for targeting pathogens that threaten other wildlife populations with similar assumptions. Although our infectious disease modelling focused on the traits of pathogens in one species population, our method and framework may be applicable to other wildlife populations by incorporating their population demographics and disease parameters. This framework is also beneficial for endangered species, enabling the simulation of various scenarios and the identification of potential disease threats, along with estimating the recovery period after introducing the infection.

3.5 Conclusion

Our study has provided a prediction of the potential consequence of disease in wild bovid populations considering six important bovine infectious diseases; anthrax, HS, bTB, LSD, FMD and brucellosis. The baseline population model shows a natural population growth of ∼228%, suggesting maintaining healthy vulnerable populations could allow them to reestablish and overcome current levels of extinction threats while diseases and other factors may regulate population growth. The inclusion of different disease traits has consequences on the population numbers depending on the transmission, incubation, fatality and infectious rates. Brucellosis and bTB models show the greatest, long-term impact among all the models, whereas FMD and LSD showed the least impact, suggesting common but more chronic or ’slow’ infections with relatively high mortality may pose the greatest threat to smaller, threatened bovid populations.

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STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Wantida Horpiencharoen
Name and title of main supervisor:	Prof David Hayman
In which chapter is the manuscript/published work?	Chapter 4
What percentage of the manuscript/published work was contributed by the student?	75%

Describe the contribution that the student has made to the manuscript/published work:

I contributed to the study design, led the data analysis, including developing the risk maps and writing the R code scripts, and I led the writing and editing of the manuscript.

Please select one of the following three options:

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Chapter 4

Spatial risk of disease transmission of wild bovids and livestock in Thailand

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Abstract

The livestock-wildlife interface is one of the most essential issues threatening wildlife conservation and public health. Identifying interface areas can help to prioritise disease surveillance and implement mitigation measures and control programs for targeting threatened wildlife. We predicted interface areas which were assumed to be areas at risk of infectious disease transmission based on the spatial overlap between three Thai wild bovids (including gaur, banteng and wild water buffalo) habitat suitability and domestic cattle. We assumed that domestic cattle are the reservoir of bovine infectious disease and that high cattle density is a proxy for a higher risk of disease transmission. Our study indicated that the highest risk areas for the native species are at the forest edges where overlap exists between high habitat suitability and high cattle density. Wild water buffalo showed the largest proportion of high risk areas (8%) while gaur and banteng showed similar risk areas (4%) in Thailand. The largest proportion of risk areas overlapping with protected areas was Namtok Sam Lan PAs at 89% for gaur, 84% for banteng and 65% for wild water buffalo. Kuiburi NP has the largest risk area around 274 km^2 (around 28% of the total protected area) for gaur and banteng whereas wild water buffalo has the largest risk area overlapping with Huai Thabthan-Had Samran around 126 km^2 (10% of the PA). Kaengkrachan Forest Complex showed the second largest risk area from 249 km^2 for gaur and 273 km^2 for banteng (8-9% of the PA). Our results address how habitat suitability might be

helpful for infectious disease prevention and control strategies focused on native fauna and One Health. Furthermore, this work may also support the wild bovid habitat conservation initiatives and land use planning by informing decision-making about balancing wildlife habitats and livestock farming.

4.1 Introduction

Wild Bovidae (Mammalia: Artiodactyla) are distributed worldwide and play crucial ecosystem roles because they determine the forest structure, transport micronutrients, and disperse plant seeds (Ripple et al., 2015; Romero et al., 2015) across forests and are also important prey species of predators (Simcharoen et al., 2018). In Asia, wild bovid populations are threatened by multiple factors, including habitat loss and hunting, especially in South to Southeast Asia (Tilker et al., 2019). Natural habitat loss often comes with increased free-grazing livestock interaction, which can lead to problems as varied as resource competition, reduced wildlife population abundance (Bhandari et al., 2022), interbreeding between domestic and wild water buffalo (Bhattarai et al., 2023), and infectious disease transmission (Hassell et al., 2017).

Among the twenty-seven recognized wild bovid species as of 2020 (IUCN), five species remain in Thailand, including gaur (*Bos gaurus*), banteng (*Bos javanicus*), wild water buffalo (*Bubalus arnee*), mainland serow (*Capricornis sumatraensis*) and Chinese goral (*Naemorhedus griseus*). Their habitat and populations have been threatened by human activities such as deforestation and hunting (Carr et al., 2023; Harrison et al., 2016; Nguyen, 2009). Wild bovids, especially the large herbivores (e.g. gaur, banteng and wild water buffalo), gradually adapt their distribution and behaviour to land use change. For example, gaur has been found close to agricultural areas and forest edges where they forage on crop plantations (e.g. grass, cassava) (Chaiyarat et al., 2021). Banteng is also well-adapted to secondary forests near villages and logging sites (Journeaux et al., 2018). These wild bovids are, therefore, able to share natural resources with free-grazing domestic bovids, which can potentially cause disease transmission via direct and indirect contact with the sources of infections (e.g. infectious cattle, host, environmental reservoirs (Bacigalupo et al., 2020).

The livestock-wildlife interface is one important issue threatening wildlife conservation and global public health because 72% of emerging diseases originate from wildlife to humans and/or livestock (Jones et al., 2008). Bovine infectious diseases, such as bovine tuberculosis, brucellosis and foot and mouth disease, can be transmitted and circulated in domestic and wild bovid populations (Caron et al., 2013). These diseases and their impact on wildlife and livestock population health have been studied in Europe (Martin et al., 2011), North America (Miller et al., 2013) and Africa (Garine-Wichatitsky et al., 2013), but less so in Asia, including Thailand.

Several factors can drive disease transmission between livestock and wildlife populations, such as the expanding livestock production (Morand, 2020), the shrinking of wildlife habitat (Wilkinson et al., 2018), and changes in wildlife distribution, demography and behaviour (Eby et al., 2023). Among these factors, high host density is potentially a determinant risk factor that can lead to successful disease transmission as it may translate to a higher probability of between- and among-host species interactions, contact and pathogen exposure (Habib et al., 2011; Sirdar et al., 2021). The movement and spatial overlap of wildlife and livestock can lead to increased infectious disease transmission risk. Areas where there is potential for interaction between a new susceptible host and a reservoir can increase the chance of disease transmission through increasing contact rates and time (Clifford et al., 2009). For wild and domesticated species, these areas are usually the transition areas between two or more land use types, such as the edges of forest and agricultural areas, which are likely to have more species activities leading to a greater chance of interaction and so disease transmission among wildlife and livestock (Miguel et al., 2013). Previous studies indicated the presence of some infectious diseases, such as Babesiosis and leptospirosis (Simking et al., 2014; Yatbantoong & Chaiyarat, 2019) in the domestic cattle at the edge of the forests, making these domestic animals a potential reservoir of disease transmission to the wild bovids.

Bovine infectious diseases can circulate between livestock and wild ungulates with varying levels of virulence (Caron et al., 2013). Certain pathogens can circulate within either livestock or wildlife populations without causing visible clinical signs but have a significant impact on other species. For example, foot and mouth disease (FMD) might not affect African buffalo, but can lead to mortality in gaur (Chandranaik et al., 2015). Similarly, haemorrhagic septicaemia (*Pasteurella multocida*) might be identified within the farm environment as non-pathogenic with limited mortality except under certain circumstances but can cause mass mortality in saiga (Robinson et al., 2019). Chronic diseases like bovine tuberculosis and brucellosis with long incubation and relatively low fatality rates could potentially have long-term consequences by reducing populations due to disease, while FMD, which has a higher transmission rate with short incubation periods or even highly fatal infections such as anthrax, may have lower impacts on populations (Horpiencharoen et al., 2024).

Moreover, in the past twenty years, there have been numerous transboundary emerging disease outbreaks among domestic animals in Thailand. For example, there have been outbreaks of lumpy skin disease among cattle (Arjkumpa et al., 2022), African horse sickness among horses (King et al., 2020), and African swine fever among pigs (Thanapongtharm et al., 2022). Hence, it is crucial to investigate where there are high risk areas to prevent disease transmission to wild populations, considering their susceptibility to similar pathogens shared by livestock. Targeting the potential risks of disease transmission in wildlife and livestock interface areas can support the implementation of surveillance and control measures that may help prevent cross-species transmission (Kelly et al., 2017).

In this study, we aim to 1) identify the potential risk of disease transmission of wild bovids and livestock in Thailand and 2) provide suggestions for disease surveillance and conflict mitigation measures in the wildlife-livestock interface areas of Thailand. The outputs could be used to prioritise local surveillance and mitigation measures for optimising resource allocation.

4.2 Methods

4.2.1. Study area

Thailand is located on the Indochina Peninsula, part of mainland Southeast Asia. Thailand borders four countries, Myanmar, Laos, Cambodia and Malaysia, with the Gulf of Thailand on the southeast connected to the Pacific Ocean and the southwest connected to the Andaman Sea. The total country area is around 514,000 km², with agricultural land covering 41% and forested areas comprising around 32% of the country area. Most agricultural areas consist of rice fields (51%) and crop plantations (34%), while livestock farming covers only around 0.6% of the total agricultural area or around 0.3% of the total country (land use data source: https://agri-map-online.moac.go.th/). There is high cattle production in the central west, which includes free-range cattle and buffalo in some rural areas. These free-ranging livestock have encroached into wildlife habitats and share the same resources. Moreover, there is shared land use, for example, domestic buffalo may use rice fields.

4.2.2. Population

This study focuses on wildlife and livestock populations, and we calculate the largest potential for wildlife-livestock interface areas. We selected the remaining wild bovid species in Thailand because they are widely distributed and likely to share the same resources and pathogens as livestock, especially the large bovids (gaur, banteng and wild water buffalo) distribution, which tends to overlap with free-ranging cattle and agricultural areas. For the livestock population, we used the cattle population estimates as cattle production is all over the country, with varied production scales and systems from intensive farming to free grazing. We assume that domestic cattle can be a pathogen reservoir and transmit diseases to the wild bovid population, and our focus is on livestock transmitting infection to wild species, though the alternative is possible. Therefore, for our analysis, a high cattle density is assumed to have a higher risk transmission risk and a lower cattle density have a lower risk, as reported in previous studies (Khanyari et al., 2021; Miguel et al., 2013).

4.2.3 Identifying the potential risk

Briefly, we identified the risk area using two types of datasets: 1) wild bovid distribution and 2) cattle density. Then, we overlaid these together and calculated the overlapping areas in 1-km^2 cells as a sampling unit.

Wild bovid potential distribution

We assumed wild bovid distributions correlate with their suitable habitat we previously predicted by ecological niche models (Figure 2.5 in Chapter 2). Ecological niche models used 28 as predictor environmental variables using 8 algorithms. We conducted the ensemble models using the weighted mean method and used True Skill Statistics as a threshold to convert the ensemble models to binary values (1 = suitable areas and 0 = unsuitable). Full methods can be found in Chapter 2. Our occurrence data is limited based on small sample sizes, and we took a conservative approach and focused on the species with best performing models. For that, we selected only ecological niche model ensembles performing with over 80% accuracy in out of sample occurrences testing. Models that performed poorly (less than 80% accuracy) were excluded from the posterior analysis. We found our models were able to predict the presence of out of sample observations well (over 80% accuracy) for three species out of five bovids of Thailand: gaur (*B. gaurus*), banteng (*B. javanicus*), and wild water buffalo (*B. arnee*). We excluded Mainland serow (*C. sumatraensis*) or Chinese goral (*N. griseus*) from the analyses because the models did not perform well (Figure 2.4 and Table 2.4 in Chapter 2).

Cattle density

We downloaded cattle density data from Global Livestock of the World 2015, GLW 4 (link). This data gives values of cattle density at an original spatial resolution of 10 km^2. We cropped the raster layer to Thailand limits and disaggregated the raster to 1 km^2 per cell to make it compatible with the habitat suitability raster using the raster package (Hijmans, 2023). Then, we rescaled the density values to 0 - 1 using this equation:

$$X_2 = \frac{X_1 - X_{minimum}}{X_{maximum} - X_{mimimum}}$$

Where X is the value in the cattle density cell.

Then, we used the mean of cattle density (0.14 cattle/km^2) in Thailand calculated from the GLW 4 raster as a cut-off value for converting the cattle density raster into the binary values of high and low. The raster cells containing values greater than the mean were converted to 1 (high density), and the values lower than the mean were converted to 0 (low density).

We assumed that higher cattle density correlates with a greater risk of infectious diseases. Therefore, we counted the number of outbreaks in low and high cattle density areas to test this assumption. We divided the total number of outbreak events by the total area of cattle density for each category to check whether the higher number of outbreaks in high – density areas was not simply due to larger areas, as the following calculation:

$$\frac{Number\ of\ outbreak\ in\ \ high\ (or\ low)\ cattle\ density}{Total\ area\ of\ high\ (or\ low)\ cattle\ density}$$

The results found a higher incidence of outbreak events in high cattle density areas compared to low cattle density areas. Thus, we used cattle density as the major risk factor to identify the potential disease transmission areas (more details in the results, Table 4.2).

The potential risk areas

In this study, the potential high risk areas refer to the interface areas between wildlife and livestock that potentially share the resources (e.g. water bodies, grassland, mineral lick) and have a higher risk of disease transmission due to the increased opportunity of direct and indirect contact with disease reservoirs and environment, compared to other areas (Barasona et al., 2014; Khanyari et al., 2021; Miguel et al., 2013).

To define the risk areas, we overlapped the cattle density raster with the species' binary maps and calculated the percentages of the potential risk areas in Thailand. Then, we intersected the risk areas with the national protected areas (PA) (UNEP-WCMC & IUCN, 2021) to calculate the risk areas inside and outside PAs and also classified the risk areas by land use types to prioritise where to implement the disease surveillance. Lastly, we counted the occurrence of disease outbreaks reported by the Department of Livestock Development, Thailand, within the interface areas to explore the distribution of highly frequent diseases in the high risk areas (see below). All spatial analyses were programmed in R 4.3.1 (R Core Team, 2023). The code is available at a public repository (https://github.com/Wantidah/BovidRiskMaps). Data is available upon reasonable request.

Disease occurrence data

We used the national database of livestock disease outbreak reports from 2013 to 2021 generated by the Department of Livestock Development, Thailand. The data collection starts when an outbreak in livestock is reported by local authorities or farm owners. Then epidemiological data are recorded, including the date of the index case, animal type, clinical signs, and number of animals infected, followed by collecting the samples for laboratory diagnosis. If a diagnosis is made and the causative pathogen and disease known, the authorities will record this in the database. If the authorities cannot find the causing pathogen, they will add the tentative diagnosis from the clinical signs. Each outbreak will be reported as confirmed if the causative pathogen is identified by laboratory diagnostics. However, if there is no laboratory result, the authority will fill in the tentative diagnosis according to animal clinical signs. The GPS location of the outbreak refers to the centroid of the sub-district (average area of districts of Thailand = 87 km^2, range: 0.88 - 2,387 km^2) where the outbreak occurred.

Here we selected five globally or regionally common bovine infectious diseases considered important for livestock health: 1) foot and mouth disease (FMD), 2) haemorrhagic septicaemia (HS - *Pasteurella multocida*), 3) bovine tuberculosis (*Mycobacterium bovis* - bTB), 4) lumpy skin disease (LSD) and 5) bovine brucellosis (*Brucella abortus*) from the national database. We selected outbreaks from these five diseases in cattle, then cleaned the outbreak events by excluding incorrect coordinates falling outside Thailand using R. Lastly, we counted the number of outbreaks within overlapping areas for each species and cattle population densities using the 'extract' function in the raster R package (Hijmans, 2023).

4.3 Results

The high-risk areas with high wild bovid habitat suitability and high cattle density are mostly found in the central-western through the southern part of Thailand for the three species (Figure 4.1, Figure 4.2). The districts that showed the highest percentages of the risk areas are Nakhon Si Thammarat (south), Ratchaburi and Prachuap Khiri Khan) for all three species. Wild water buffalo showed the largest of the total interface areas, covering ~44,000 km^2 (8% of Thailand), due to their potential habitat suitability predicted across the country. However, in the actual species distribution, only one population remains in the Huai Kha Khaeng Wildlife Sanctuary. Banteng and guar showed similar potential habitat suitability species, which also resulted in the closest number of interface areas, ~22,000 km^2 (4% of Thailand) (Table 4.1).

The highest percentage of risk areas inside the PA were identified in Namtok Sam Lan (also known as Phra Budda Chai) National Park (NP) (45 km^2) in Saraburi Province, covering approximately 89% for gaur, 83% for banteng and 65% for buffalo. The second highest percentage for gaur and banteng is Namtok Huai Yang (160 km^2) NP in Prachuap Khiri Khan, covering 60% (~100 km^2) of the total PA, and for wild water buffalo is Huai Thabthan-Had Samran (498 km^2) representing 25% (125 km^2) of the total PA. However, for gaur and banteng, the largest risk area is located in the same PA—Kuiburi NP (970 km^2), representing 273 km^2 (28% of the PA). This is followed by the Kaengkrachan forest complex, representing 249 km^2 for gaur (8% of the PA) and 261 km^2 for banteng (9% of the PA). These two protected areas are in close proximity, with high-risk areas situated along the western forest edge, connected to agricultural areas with high cattle density, while the western side is connected to the Myanmar forest (Table 4.1). Moreover, the large intact forests like the Western, Eastern and Dong Payayen - Khoa Yai forest complex illustrated high habitat suitability with low cattle density within the PA but showed high risk at the border of the forests, while the fragmented forests in the north illustrated the potential high risk of disease transmission with high cattle density and low habitat suitability.

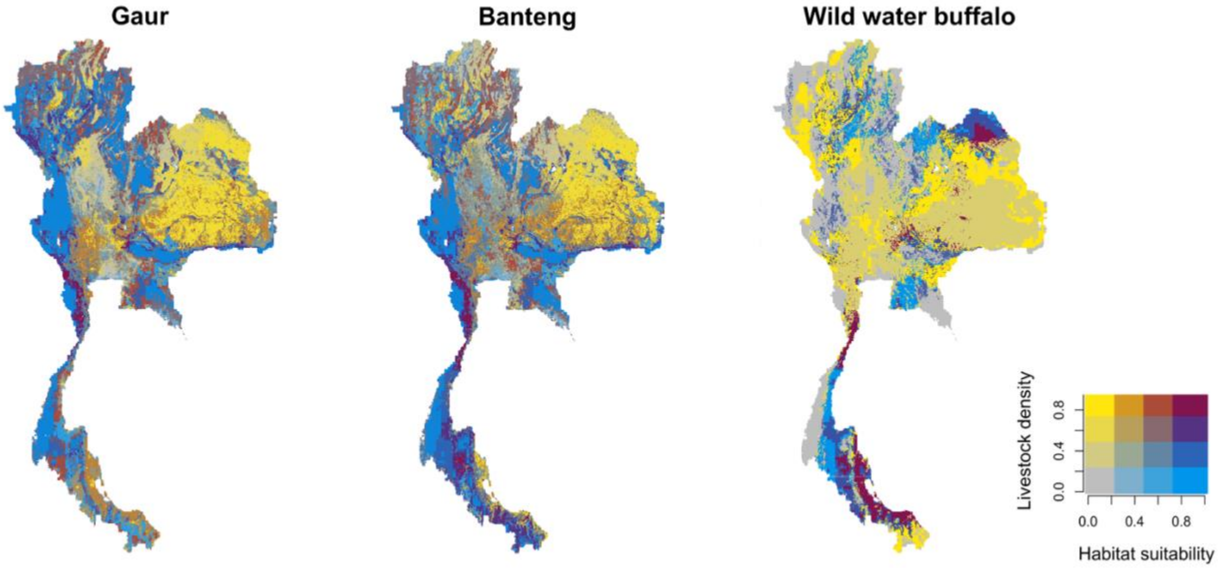

Figure 4.1 Bivariate maps of the potential risk area between the habitat suitability (blue) and cattle density (yellow) reveal the interface areas between three wild bovid species and domestic cattle populations in Thailand. High-risk areas are represented in dark red, while low-risk areas are represented in grey.

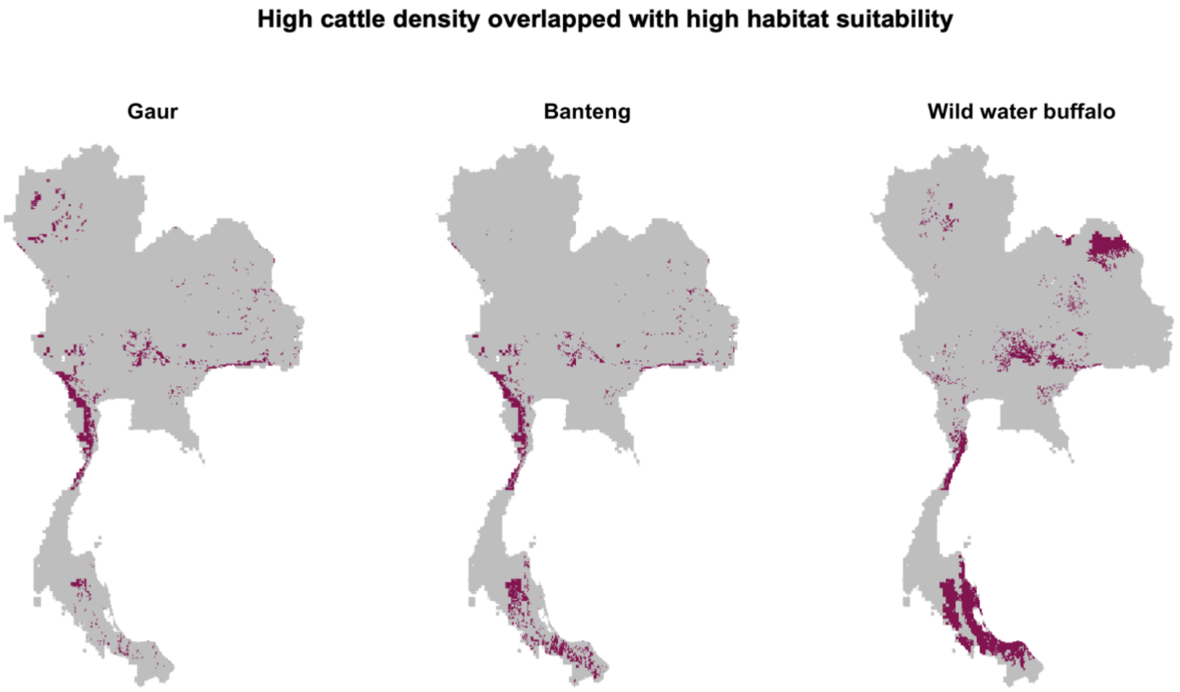

Figure 4.2 The potential high-risk areas for disease transmission between three wild bovid species and cattle populations in Thailand. High-risk areas are represented in dark red, extracted from the interface areas inFigure 4.1.

Table 4.1 The percentage of interface areas overlapped with protected areas by three wild bovid species.

	Interface area with livestock (km^2)			
Species	inside PA	outside PA	total	**Percentage (%) of overlap area in Thailand**
Gaur	2,018	18,367	20,385	3.9
Banteng	2,089	20,477	22,566	4.4
Wild water buffalo	747	43,642	44,389	8.7

According to the national disease surveillance, the total number of outbreak events is 7,522 events for five bovine infectious diseases from 2013 to 2021. LSD (6,913) has the most outbreak events among the others, followed by FMD (563) and brucellosis (39), while HS and bTB have only 5 and 2 events, respectively (Table 4.2 and Figure 4.3). This is because there the first LSD outbreak occurred in cattle herds in Thailand in 2021, leading to a large number of events reported across the country in a short period, while the other infections, which have lower records, are endemic in this area.

The cattle density demonstrated correlations with the number of infectious disease outbreaks, and this correlation is proportional to the area size. We observed that in high cattle density areas (190,076 km^2), there were higher outbreak events, totalling around 6,894 events (0.036 events per km^2), 18 times more than low cattle density areas (324,335 km^2), which had 640 events (0.002 events per km^2). The results of outbreak events by cattle density areas are presented in Table 4.2.

Table 4.2 The occurrence of outbreak events classified by infectious disease and cattle density from 2013 to 2021.

	Cattle density		
Infectious disease	Low (<=mean)	High (>mean)	Total
bTB	2	0	2
HS	3	2	5
LSD	445	6,473	6,918
FMD	175	395	563
Brucellosis	15	24	39
Total	640	6,894	7,534
Area of Thailand (km^2)	324,335	190,076	514,410
Total outbreak event per area (km^2)	0.0020	0.0363	0.0146

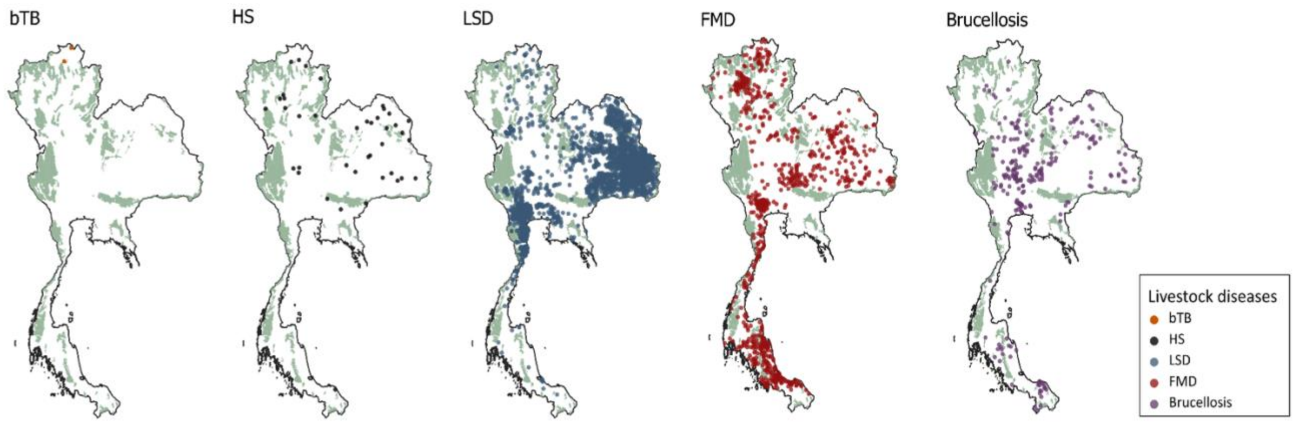

Figure 4.3 Occurrence of bovine infectious disease outbreaks in Thailand from 2013 to 2021 and protected area distribution (PA). The maps show that the outbreaks occurred across Thailand, particularly in proximity to protected and forest areas that overlap with suitable habitats for wild bovids.

Table 4.3 The reported outbreak events of bovine infectious disease occurrences in the high risk areas.

		Within high cattle density - high habitat suitability		
Bovine Infectious Diseases	**All occurrences**	**Gaur**	**Banteng**	**Wild water buffalo**
Tuberculosis	2	0	0	0
HS	5	0	0	1
LSD	6,918	166	108	442
FMD	563	32	51	190
Brucellosis	39	1	3	14
Total	7,534	199	162	647
High risk areas (km^2)		20,385	22,566	44,389
Thailand	514,410			
Total outbreak event per risk area (km^2)	0.015	0.010	0.008	0.015

We found that the density of outbreak events in cattle within the potential high risk area of gaur (0.01) and especially for wild water buffalo (0.015) were similar to the average density calculated for the country (0.0146) (Table 4.3). Wild water buffalo showed the highest events

(647) within the risk areas as they have the largest potential habitat areas across the country while gaur (199) and banteng (162) show close results to each other. Similar to Table 4.2, the greatest numbers of disease events within high risk areas was for LSD and FMD in all species and the other diseases presented only small numbers.

Moreover, according to the land use types, the most extensive interface areas were found in close unknown forests (meaning they did not match any of the other forest definitions), followed by the cropland for three species. The closed evergreen forests also contain risk areas for gaur and banteng. The open deciduous forest had no interface areas detected (Figure 4.4).

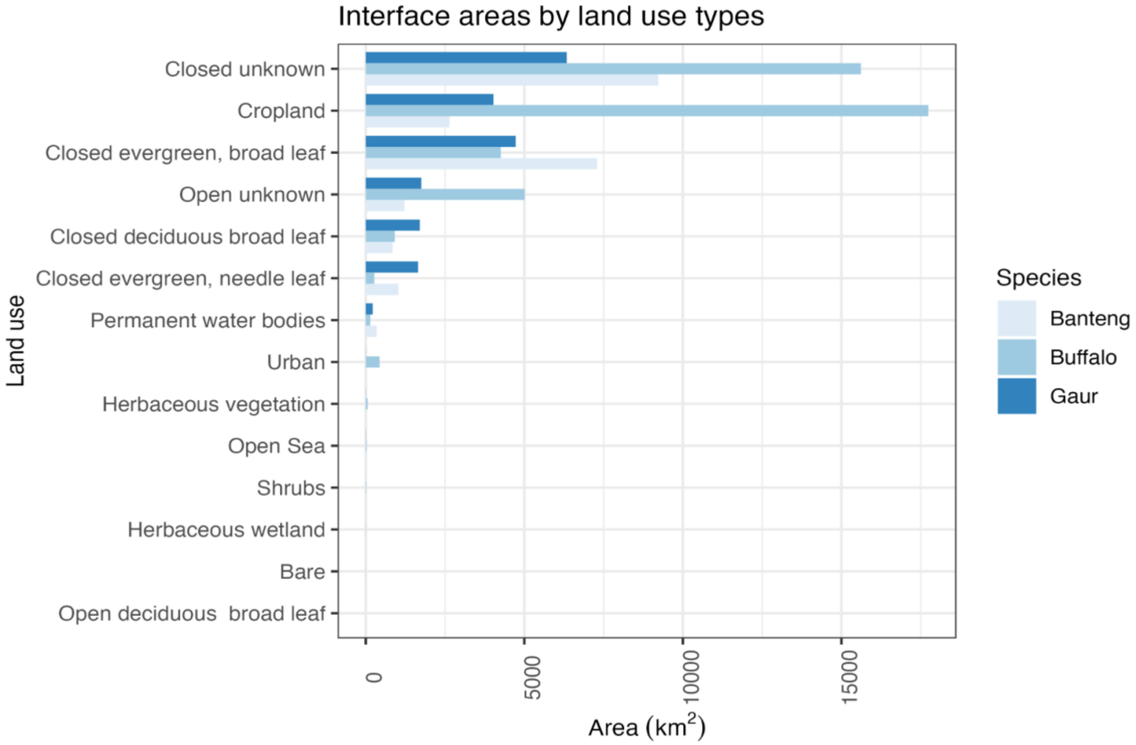

Figure 4.4 Interface areas of three wild bovid species are categorised based on land use types.

4.4 Discussion

We examined potential risk areas of disease transmission between wild bovids and livestock and provided the preliminary focus area that should be considered for disease surveillance in Thailand. Total risk areas in Thailand are between 4% (gaur and banteng) to 9% (wild water buffalo) of the country, with the most risky area being from the central west (Ratchaburi) to the south (Nakhon Si Thammarat). The highest risk proportion inside PAs was at Namtok Sam Lan National Park (NP) in the central, and the largest risk areas were Kuiburi NP and

Kaengkrachan NP in the western forest, related to the highest cattle density in Thailand. Gaur and banteng have similar risk areas mostly around the edge of forests, while wild water buffalo have risk widely across the country because models predicted extensive amounts of suitable areas in the central down to the southern part that coincide with the high cattle density areas.

Although the wild water buffalo showed the largest areas of predicted suitable habitat among all three bovid species, it is also the most endangered. This is due to its current distribution being confined solely to the Huai Kha Khaeng Wildlife Sanctuary, with the population remaining stable and not exceeding 69 individuals for decades (Chaiyarat et al., 2004; Khiowsree et al., 2015). Consequently, this population is highly susceptible to endemic infectious diseases that could rapidly lead to serious decline or even local extinction. For instance, diseases like HS can cause a high fatality rate of up to 80% in domestic buffalo (Deepak et al., 2020). The highly contagious and fatal nature of diseases like rinderpest and FMD may be contributing factors to population disappearances in Nepal and India (Choudhury, 2014). An outbreak could also lead to local extinction in a single fragmented population, as the recovery process is prolonged and potentially results in a lack of gene flow (McKnight et al., 2017), especially with the independent mother origin of Thai wild water buffalo (Sarataphan et al., 2017). In contrast to wild water buffalo, gaur and banteng have more opportunities for contact with domestic cattle and humans, while wild water buffalo may encounter livestock and humans encroaching into the protected areas and suitable habitat. Gaur and banteng can share habitats, making the interface areas similar to each other. But, gaur uses a wider range of habitat types (e.g., evergreen, deciduous dipterocarp, mixed deciduous forests) than banteng, which is restricted to dry and open forests (e.g., dry dipterocarp, mixed deciduous forest) (Prayurasiddhi, 1997; Steinmetz, 2004). These two species show evidence of contact with livestock and humans due to their ability to adapt and tolerate human activities, resulting in conflicts in overlapping areas (Chaiyarat et al., 2023; Chaiyarat et al., 2021; Journeaux et al., 2018). However, their habitat suitability decreases when the distance is closer to human settlement and the presence of domestic cattle grazing (Jornburom et al., 2020).

Our study identified the potential high-risk areas in the northeastern and southern parts, which have the highest cattle density but low or even an absence of the actual species distribution in some areas. This caveat is observed in the ecological niche modelling of wild water buffalo, where high habitat suitability represents potential distribution and may not necessarily correspond to the actual species distribution. Nevertheless, this caveat could be mitigated by collecting and regularly updating occurrences of these bovid species, as well as data on livestock density and distribution, or by restricting the analyses to areas with sufficient data.

Urbanisation and expansion of agricultural areas increase the opportunity for contact between domestic livestock and wildlife. Contact rate, the probability of transmission and the location shifts of animals at each time step, are the major factors that need to be considered for the spatial disease transmission model (Böhm et al., 2009). The direct contact between wildlife and livestock is unlikely but indirect contact in the same space at different times via shared resources (e.g. water, grassland, supplement) with domestic animals potentially causes a chance of wildlife exposure to pathogens and disease transmission (Bacigalupo et al., 2020; Yang et al., 2021). However, to succeed in cross-species infection, several factors should converge to drive pathogens through the natural barriers before having a pathogenic infection into a new host (Plowright et al., 2017). We found that the highest interfaced areas were identified in cropland and unclassified forests, which potentially be shared among free-ranging livestock and wild bovids. Thailand also experienced significant land cover changes (Wang et al., 2022) primarily driven by the increase of crop plantations and urbanisation with concurrent population growth, which leads to changing wildlife and livestock interactions and risk of disease transmission as per the previous studies (Shah et al., 2019).

Host density is one of the main risk factors in wildlife and livestock disease transmission (Daszak et al., 2000; Smith et al., 2009) (Daszak et al., 2000; Smith et al., 2009). We used host density and distribution as the main risk factors to identify and prioritise the potential risk areas of wildlife and livestock disease transmission that have been used in the other studies (Miller et al., 2017; Morgan et al., 2006; Yang et al., 2021). The advantage is knowing the target place for implementing the disease surveillance system, but the disadvantages can arise from the complexity of disease transmission dynamics, which depend on factors such as host species movement (Morgan et al., 2006), contact pattern (Craft, 2015), high adaptability of wildlife behaviour, transmission modes (e.g. density or frequency-dependent) (Pruvot et al., 2020; Smith et al., 2009) and population size (Lambert et al., 2018).

Understanding the underlying factors that contribute to disease outbreaks in a specific potential risk area is essential for planning effective disease mitigation and control strategies. Multidisciplinary approaches incorporating key elements like pathogens, hosts, and environmental factors (supplementary Table S3.1) also help policymakers develop disease control and mitigation measures. Pathogen spillover events are complicated, with a convergence of risk factors, which are difficult to approach. Integrating a complex system of human, animal and environmental will benefit prevention or at least mitigate the loss of the next spill-over event (Vora et al., 2023).

Mitigation strategies will likely vary according to local socioeconomic conditions, but among the preventive actions are using vaccination of livestock or even wild species, targeted reduction of infected individual animals, herds or farms (ideally with compensation), along with reducing livestock herd sizes and densities, transport of livestock among farms, and contacts between farmed animals and wild species (Carrasco-Garcia et al., 2016; Kuiken & Cromie, 2022). Contact reduction might be through measures such as altering land use at the local level, or with “natural” (e.g. plant-based) or artificial (e.g. metal) fencing or barriers and zoning of forests, livestock and human settlements to minimise the contact (Jori & Etter, 2016; Miller et al., 2013), which may lead to induce pathogen spillover (Plowright et al., 2021). Longer term strategies might include societal transitions to lower meat-based, more plant-based proteins to reduce demand for meat and dairy products. Conserving intact forests with effective surveillance can mitigate the risk of disease transmission at the interface, especially in edge or transition areas. In contrast, fragmented forests increase the likelihood of wildlife being exposed to livestock and humans, leading to an elevated risk of disease transmission (Keesing et al., 2010).

Livestock vaccination is crucial for reducing outbreak incidences of endemic diseases, requiring approximately 80% coverage to effectively prevent disease transmission, particularly in high-risk areas and populations, as part of routine practice (Hopker et al., 2021; Porco et al., 2023). However, capturing and delivering parenteral-route vaccinations to free-ranging wild bovids pose significant challenges, especially in tropical forests where animals might be hidden. Consequently, various aspects must be carefully considered in the vaccination plan, including the target population, coverage, safety, and efficiency, to effectively stimulate herd immunity (Treanor et al., 2010). Non-invasive vaccination methods, like tuberculosis oral vaccination, have been tested in domestic cattle and some wildlife and are planned for use in wild cattle (Buddle et al., 2018). Research and development for other endemic diseases like FMD, HS, and brucellosis is still ongoing (Gortazar et al., 2015; Lee et al., 2023; Olsen et al., 2006) . Culling livestock infected with zoonotic diseases (e.g., bTB, brucellosis) is commonly implemented in Thailand (Peck et al., 2018; Singhla et al., 2017). However, infected animals often undergo illegal translocation, potentially spreading the disease to other locations. To manage this issue, the government should rigorously regulate animal movement, regulating the guidelines for isolation of infectious animals during outbreaks, and providing appropriate compensation for culling cases. The effectiveness of these mitigation actions is influenced by the presence and use of effective infection and disease surveillance, as discussed below.

Livestock and, likely, wildlife disease surveillance in Thailand is based on the DLD, DNP (Thailand) and WOAH guidelines (WOAH, 2024), which cover significant transboundary disease outbreaks in the country. The discrepancy of the number of outbreaks reported and the number of cases observed in reality may reflect the effectiveness of DLD reporting and surveillance system. Even though the passive surveillance system is useful for recording the obvious clinical signs and emerging infectious diseases (like FMD and LSD), there is a gap in collecting non-clinical to subclinical signs of disease due to these being challenging to detect. Moreover, passive surveillance can be underreported by farmers for some zoonoses like bovine tuberculosis and brucellosis, for which animals must be condemned due to the slow and partial (not less than 75% of the market price) compensation from the government. Another drawback is the clinical signs reported from passive surveillance may not refer to the place where the animal got infected if those are moved from the original area. Therefore, active surveillance such as risk-based

(Sansamur et al., 2020), disease surveys (Arjkumpa et al., 2020) screening or detecting seroprevalence (Simking et al., 2014; Yatbantoong & Chaiyarat, 2019) are necessary in hotspots or endemic areas to effectively allocate resources for disease mitigation and control strategies. Furthermore, even when reported, further work must be undertaken to understand the disease risk in depth. Reported data might refer to one event being a single case or multiple cases, and infectious diseases are, by default, dynamic in their nature. Without significant further work, passive surveillance data may offer a limited and biased understanding of the true disease risk in a location at a particular time. The impact of the detection of some infections on trade must be addressed, as this might be a barrier to effective surveillance and reporting (Khengwa et al., 2015; Wiratsudakul & Sekiguchi, 2018). The involvement of field authorities is another crucial aspect of data collection, indispensable for obtaining real-time information. Modern technologies or data sharing can help identify risk areas and plan preparedness implementations (Goutard et al., 2015; Innes et al., 2022; Pruvot et al., 2020). Therefore, one should consider investing more in field data collection and incorporating field practitioners or epidemiologists into the team before formulating policies (Iamsirithaworn et al., 2014).

Using a One Health approach, a framework for disease surveillance has been developed, incorporating essential considerations of spillover events into the processes. To sustainably manage data collection and surveillance systems, collaboration among government organisations and stakeholders is a key step in the process, involving considerations of political, ethical, administrative, regulatory, and legal (PEARL) aspects through all approaches (Hayman et al., 2023). An effective surveillance system, characterised by rapid detection and accurate results, not only monitors emerging diseases but also reduces the risk of disease transmission and minimises the impact on lives, economies, and biodiversity during disease outbreaks (Ryser-Degiorgis, 2013). Also, the wildlife non-invasive data collection for disease surveillance and survey, such as faces, urine, saliva and environmental samples (e.g. soil, water) should be considered to avoid direct contact and reduce disturbing wildlife during capturing and data collection (Schilling et al., 2022). Further studies may consider including other risk factors such as multi-species host distribution, the distance of risk factors and contact pattern (Pepin et al., 2022; Sangrat et al., 2020), as well as improving the model by using updated disease surveillance data and wild bovid species occurrences, especially for areas where the uncertainty of model predictions is high.

4.5 Conclusion

Our study predicted the potential risk areas by using the interface areas between wildlife and domestic cattle, where livestock disease is frequently reported. We overlaid suitable habitats of three large wild bovids in Thailand with cattle density to create potential risk maps. High-risk areas were identified in locations with both high cattle density and high habitat suitability, particularly at the edges of forest-protected areas. Notably, small, fragmented forest areas with high cattle density presented the highest proportion of the high-risk areas. Among various land-use types, cropped land exhibited the largest interface areas. Our findings highlight the importance of wildlife habitat and intact forest conservation to mitigate contact and reduce vulnerability to extinction, reduce shared areas and address the potential risk areas for disease transmission between wild bovids and livestock. This methodology not only supports disease surveillance but also facilitates the implementation of effective mitigation and control measures.

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Chapter 5

General discussion and future perspective

5.1 General discussion

Wild bovids play a vital role in ecosystem functioning by supporting vegetation structure, plant species, and animal diversity (Trepel et al., 2024). In Thailand, the five remaining wild bovid species are all either vulnerable [gaur (*Bos gaurus*), Chinese goral (*Naemorhedus griseus*), mainland serow (*Capricornis sumatraensis*)] or endangered [banteng (*Bos javanicu*s) and the wild water buffalo *(Bubalus arnee*)], so at risk of extinction. Conservation plans and habitat management should be considered to ensure the survival of these populations. Here in this thesis, I focus on three main research questions relating to the conservation of Thai wild bovids:

1) What are the suitable habitats for the remaining wild bovid species in Thailand?
2) What are the consequences of introducing infection into their populations?
3) Where are the areas at risk of disease transmission between wild bovids and livestock?

To address these questions, in Chapter 2 I conducted Ecological niche modelling (ENM) to identify suitable habitats for Thai wild bovid species. Chapter 3 on dynamic infectious disease modelling to simulate population dynamics following the introduction of infected animals using a gaur population as a model. Then, in Chapter 4, I used spatial analyses to map potential risk areas of disease transmission at the interface between wild bovids and domestic cattle and discuss possible measures.

My work in Chapter 2 shows that the best supported ecological niche model for gaur and banteng predicted that their suitable areas were primarily in Southeast Asia and India. Specifically, models for gaur predicted the largest suitable areas in Thailand and India, while those for banteng were mainly located in Cambodia and Thailand. For wild water buffalo, their suitable areas were identified in India. However, due to limited data availability for Chinese goral and mainland serow, models provided a low prediction accuracy of suitable habitats. Consequently, these two species were excluded from the analysis (their model results can be found in the Appendix 1). Moreover, my findings indicated that more than 50% of the total predicted suitable areas were found outside the protected areas and were close to agricultural areas or human communities.

I used mathematical models in Chapter 3 to simulate the population dynamics of gaur over 100 years, with 100 stochastic repetitions, both with and without disease, introduced from a reservoir, such as domestic cattle. The results indicated that acute infections with very high or low fatality had the lowest impact on populations, while chronic infections caused the greatest population declines. These findings covered models for six important and/or common bovine infectious diseases, comprising anthrax, bovine tuberculosis, haemorrhagic septicaemia, lumpy skin disease, foot and mouth disease and bovine brucellosis. The starting population of 300 individuals was assumed to represent one large herd of gaur living in a protected area (Duengkae et al., 2022). The disease-free population has an average increase of 228% from the starting population, showing there is a strong intrinsic growth rate. Among the infectious disease models, brucellosis showed the highest average population declines at -97%, with extinction occurring in 16% of simulations. In contrast, with frequency-dependent transmission, foot and mouth disease demonstrated the lowest impact, with an average population increase of 200%. Together, this work underscores the likely traits of infections that might affect threatened wild bovids, emphasising that chronic infections that kill adults will likely have the greatest impact on populations.

I assumed that domestic cattle are the main reservoir of bovine infectious diseases and that high cattle density is a proxy for a higher risk of disease transmission in Chapter 4. My study indicates that the highest risk areas for native species are at the forest edges, where there is an overlap between high habitat suitability for wild bovids and high cattle density. Wild water buffalo showed the largest risk areas, covering 8% of Thailand, while gaur and banteng showed similar risk areas, each covering 4% of Thailand. Among all protected areas, Namtok Sam Lan National Park contained the largest proportion of risk areas overlapping with protected areas for all species. The largest risk areas are identified in the southwestern part of Thailand, around Kuiburi National Park, Huai Thabthan-Had Samran Wildlife Sanctuary, and Kaengkrachan National Park.

For practical purposes, the results and findings in this thesis can benefit stakeholders such as farmers, land managers and policymakers. Knowing the potential risk areas of disease transmission due to wildlife suitable habitat and their potential distribution helps decision-making prioritisation and land use management, enabling managers to minimise potential contact and conflict between livestock and wildlife. Also, this knowledge may help farmers understand the consequences of raising free-grazing animals near or within forest edges, which can impact wild bovids populations. For policymakers, our results can help decisions where to implement and invest the disease control, targeted surveillance, optimising resource allocation and manpower. Moreover, our habitat suitability maps can also identify areas where wild bovid populations are likely to use areas outside protected forests, which may lead to conflict, and action may need to be taken to either prevent contact, movements, or help protect these species. Surveillance protocols can also implement in the livestock close to the forest and high risk areas to monitor the disease prevalence and use this information to help reduce risk of disease transmission.

Together, the results of this study contribute to addressing how habitat suitability maps can be estimated and validated, how infectious diseases might impact wild bovid populations and how integrating these findings together may be valuable for infectious disease prevention and control strategies targeting native fauna. Below, I describe how this work fits into the broader picture of wildlife conservation and wildlife health before identifying key methodological and data gaps and providing future perspectives.

5.2 Wild bovid conservation and infectious diseases

Disease may lead to biodiversity loss, and losing biodiversity may influence the emergence of infectious diseases by driving disease transmission and altering host diversity, density, abundance, distribution and behaviour (Keesing et al., 2010). Maintaining high biodiversity can help retain a diversity of hosts and vector abundance, therefore mitigating the risk of disease transmission (Ostfeld, 2017). However, deforestation and habitat fragmentation not only affect global and local species decline or extinction but also increase contact areas and the risk of pathogen spillover in humans, livestock and wildlife populations (Muylaert et al., 2023; Rulli et al., 2017; Wilkinson et al., 2018).

The extinction risk of large bovids is associated with both environmental factors and intrinsic traits. The environmental factors include extensive suitable habitats and home ranges for foraging on various types of vegetation and vulnerability to hunting pressure, while intrinsic traits correlated to long gestation and weaning periods, leading to slow reproductive cycles (Cardillo et al., 2005; Traill et al., 2012). In addition, previous studies have shown that the spillover of pathogens from domestic livestock to wild bovids can further drive population decline, local extirpation, or possibly potential extinction (Narongwanichgarn et al., 2014). For example, infections like *Mycoplasma ovipneumoniae* in bighorn sheep (Carpenter et al., 2014) and *Brucella abortus* in the Yak population (Shi et al., 2016) have resulted in population declines.

Domestic and wild bovids share a close phylogenetic relationship (Buntjer et al., 2002), therefore, their populations can be susceptible to the same pathogens. For example, there is a case report of lumpy skin disease in banteng during the outbreak in cattle in Cambodia (Porco et al., 2023). Common diseases such as foot and mouth disease, bovine tuberculosis and brucellosis have been found to circulate within African wild buffalo and cattle populations (Gorsich et al., 2018; A. Jolles et al., 2021), however, the effect on their population may vary based on species susceptibility and pathogen characteristics. In Chapter 3, the results showed that chronic infectious diseases have a greater impact on population decline than highly contagious or high mortality diseases. One possible management problem is linked to the reason that these infections likely have the greatest impact on bovid populations, in that chronic diseases often have a long latent period, are asymptomatic and may persist silently within the population. Therefore, only a small proportion of cases may be detected, while the rest remain without clinical signs and are undetectable, making it more challenging to estimate the prevalence and the overall impact on the population (Aranaz et al., 2004; Ncube et al., 2022).

Social behaviour or the interaction between and within herds also affects the long-term persistence of the disease transmission, for example, bovine tuberculosis transmission exists between cattle and African buffalo (Garine-Wichatitsky et al., 2013), or cattle and wild boar. Furthermore, infectious diseases may not directly decrease the population size but can impact specific susceptible age groups or the reproductive system, leading to changes in the demographic structure. For example, brucellosis causes abortion and severe reproductive disorders in both male and female adult animals, reducing the number of newborn calves and population growth rate, while tuberculosis affects the senescent population mortality rate, reduces body condition score and may decrease the pregnancy rate (Michel et al., 2006). Consequently, the infection can have a long-term effect on population demography, which might take time to recover depending on factors, such as the population size, reproductive capacity, and virulence of the pathogen (Russell et al., 2020; Scheele et al., 2017; White et al., 2011). Hence, studying the consequences of persistent diseases in the population could support the planning of conservation tools based on disease traits and specific parameters.

5.3 Interface areas of wildlife and livestock

The human-wildlife and livestock interface areas have been prolonged and ongoing issues in Thailand. Increasing livestock production and population density are potential threats to wildlife habitats by expanding interface areas (Jori et al., 2021) and increasing natural resources and habitat sharing with wildlife, which also lead to a greater risk of disease transmission via direct or indirect contact (He et al., 2021). The interface areas in Asia, including Thailand, are influenced by various underlying factors related to agricultural production systems, natural resource management, and socioeconomic issues. These interface areas are not only prone to the risk of disease transmission but also conflicts between wildlife-livestock and wildlife-human interactions. These conflicts also involve security concerns, livelihood safety, and food production (He et al., 2021). For instance, conflicts often happen between crop owners and wildlife species or humans who encroach into forests to hunt and collect illegal wildlife products, which results in injuries, fatalities or production loss among humans or wildlife in areas with intense conflict.

This thesis highlights the significance of spatial planning in wildlife conservation by identifying the potentially suitable habitat for habitat management and wildlife conservation. For instance, the results indicated that some suitable habitats are located in non-protected areas mostly connected to cropland (e.g. grassland, sugar cane, pineapple; Chapter 2). Additionally, the edge of forests was identified as potential hotspots for infectious disease transmission in this study because these areas have high habitat suitability and livestock density (Chapter 4). Previous studies have addressed the importance of protecting intact forests to maintain biodiversity, ecosystems, and species populations (Terraube & Fernández-Llamazares, 2020; Watson et al., 2018). Fragmented and isolated forests have a higher proportion of total risk areas compared to larger forests, where the risk is primarily concentrated at the forest border (Hayman, 2016; Wilkinson et al., 2018). Therefore protected areas (discussed below, in the Risk mitigation, control and management section), especially but not only of intact forest, may function as a buffer to infection, mitigating contact rates, transmission-prone areas, and hunting pressures (Terraube & Fernández-Llamazares, 2020). For example, a buffer zone and forest restoration can provide natural resources for local communities and serve as a barrier to mitigate human-wildlife conflicts, as demonstrated in several studies (Budhathoki, 2004; Terraube et al., 2017; Water & Matteson, 2018).

Livestock density may affect wild bovid distribution, behaviour and types of available vegetation. Well-adapted and tolerant to environmental changes, species like gaur and banteng are likely to stay close to humans and livestock, causing more opportunities for infectious disease transmission. For example, foot and mouth disease in cattle and infection in gaur and wild herbivores that live in interface areas has been reported (Chandranaik et al., 2015; Weaver et al., 2013). On the other hand, some endangered species that need specific niches and environmental conditions may be challenged and declined by habitat loss, while also being affected by infectious diseases from domestic livestock, such as infection of goat pox in serow and Himalayan goral (Gortázar et al., 2022). Furthermore, livestock density may impact the ability of their infections persisting and being controlled, with higher density populations typically but not always increasing the ability of infections to spread within populations, depending on the infection traits and population structures, including production systems for livestock (Begon et al., 2002; Nunn et al., 2015; Zagmutt et al., 2016).

5.4 Wildlife conservation, infectious disease prevention and control

In this section, the discussion will follow the disease prevention and control framework to help limit the impact of infectious diseases, provided by Miller et al. (2013) [here], with a slight adaptation to highlight how future work could help reduce the risk of infectious disease transmission and the livestock-wildlife interface.

5.4.1 Horizon scanning

Horizon scanning could identify important issues related to infectious diseases and facilitate early disease detection and rapid response to disease outbreaks in livestock and wildlife populations (Roy et al., 2017; Seymour et al., 2020). It also assesses issues in global biological conservation (Sutherland et al., 2020). Scanning could also be conducted proactively for long-term assessment, focusing on the burden of diseases affecting the endangered species or the effect of the potential issue on regional conservation and infectious disease. For example, transboundary diseases spreading from Africa and Europe to Southeast Asia have been identified in endemic wildlife species, such as lumpy skin disease in banteng (Porco et al., 2023) and African swine fever in wild boar (Luskin et al., 2020). Additionally, zoonoses with a broad host range have infected both free-range and captive wildlife, potentially affecting public health, as observed in tuberculosis infection (Angkawanish et al., 2010; Meesawat et al., 2023). One example of scanning and predicting potential bacterial transmission at interface areas is demonstrated in the study by Evans and Drake (2022). This study collected and integrated several databases, including species interactions, host distributions and bacterial traits for modelling. Domestic cattle (*Bos taurus*) have shown to be one of the most associated hosts and are likely to share bacterial infections with a variety of wildlife hosts such as bighorn sheep, moose, seal and deer. Moreover, global trends of infectious diseases at the interface have addressed by an increasing number of publications on cattle and other artiodactyls, particularly in Europe and Asia. Hence, the scanning framework could be helpful in identifying specific issues related to infectious diseases within the interface areas mapped.

5.4.2 Risk analysis

Risk analysis is a valuable tool used to assess the likelihood and consequences of events within a population of interest for decision-making (Thrusfield et al., 2018). Following the IUCN guidelines (OIE & IUCN, 2014), risk analysis provides the structured framework for addressing uncertainty associated with infectious and non-infectious effects on the environment, humans, wildlife and livestock, including five components: hazard identification, risk assessment, risk management and implementation, and risk communication. In risk assessment, quantitative modelling and GIS are useful for identifying and calculating potential impacts and scenarios to support decision-making and plan disease mitigation strategies. In this thesis, I applied the modelling and GIS methods to identify suitable species, the potential risk of disease transmission at the interface areas and the consequences of various infectious disease traits on a model gaur population to better understand risk.

Modelling can support risk assessment by integrating knowledge from various fields (e.g. wildlife ecology, epidemiology) and illustrating different scenarios based on various assumptions and input parameters (OIE & IUCN, 2014). Ecological niche modelling can predict species niches and identify important environmental factors, which are useful for prioritising species habitats and informing conservation efforts to protect endangered species or manage invasive species (Barbet-Massin et al., 2018; Freeman et al., 2019; Herrera-Sánchez et al., 2020). Moreover, ENM could be used with spatial epidemiology to identify which risk factors correlated to disease occurrences, predicting the potential hotspots for the transmission of pathogens and host or vector distribution (Escobar, 2020; Lawrence et al., 2023), but only when certain assumptions are met, such as the system being in some equilibrium (Contina et al., 2020).

Risk analysis has been implemented to help in disease control and prioritising measures at the wildlife-livestock interface. One example is the study of pneumonia outbreaks transmitted from domestic goats to the bighorn sheep population, which conducted spatial risk assessments and infectious disease modelling (an SEIR model using demographic and epidemiologic data), to predict the risk of disease transmission and select appropriate control measures (Almberg et al., 2022; Carpenter et al., 2014). In Thailand, risk analysis has been focused on identifying risk factors in human and livestock infectious diseases. For example, analysing the behaviour risk of zoonotic spillover from animals to humans (Yadana et al., 2022), mapping the hotspots of HPAI H5N1 in poultry farms (Paul et al., 2016), and identifying the risk areas and factors of rabies distribution in dog population (Thanapongtharm et al., 2021). However, applying a risk analysis framework at the wildlife-livestock interface in Thailand is still challenging due to a limited understanding of the infection pathways from livestock to wildlife or from the environment to wildlife and a lack of data on interaction at the interface areas for some systems. The infection pathway is based on several processes that need to occur concurrently for pathogen spillover from one host to another successfully, including pathogen excretion, animal exposure, infective dose that overcomes wildlife immunity and barriers to being infected at an individual level, as well as spread into the population level (Plowright et al., 2017). Therefore, all these aspects need to be considered when performing risk analyses and may be more or less important, depending on the focus and scale and the goals of the risk analysis. For example, at the national level, the infection pathways would be on a more broader scale, so that a dataset such as host density, population sizes and species distributions could be used to perform the analysis (Cross et al., 2019; Miller et al., 2017)

5.4.3 Risk mitigation, control and management

Effective risk mitigation, control, and management strategies require a comprehensive framework and implementation actions across short-, medium- and long-term measures. Short-term measures are beneficial for immediate response during emergencies or outbreak events. Examples include livestock culling, isolating infected animals, enforcing animal movement regulations and administering treatments. Medium-term measures may include vaccination plans for both livestock and wildlife (e.g. oral or bait vaccine) and longer term, more structural ways to limit the contact between wildlife and livestock through minimising the number of free-ranging livestock and improving farm biosecurity (Jori et al., 2021). For long-term measures, suggestions could be having sustainability plans for wildlife conservation integrated with disease surveillance measures and natural resource management. These measures could focus on preserving wildlife populations, habitats, and biodiversity to mitigate the threats and effects of infectious diseases, along with balancing resources for global livestock production and crop plantations to meet human needs (Pozo et al., 2021). Implementations may include reducing shared habitats through reforestation and establishing forest connections to maintain biodiversity and wildlife populations. Moreover, there is research developing alternative protein sources to substitute or reduce livestock production and meat consumption, including plant-based protein, insect protein, single-cell protein, and cultured meat (Hadi & Brightwell, 2021; Post et al., 2020).

My study identified the potential risk areas at the forest edges, so habitat management becomes crucial to mitigate contact and reduce disease transmission. One strategy for managing the habitat to conserve large, intact forests involves managing community forests and spatial planning taking into account buffer areas between the forest and human activities. Some protected areas arrange zoning into core habitat preserve zones and buffer zones. The core habitat zones are delineated as legally well-preserved habitats with less disturbance, while the buffer zones are the bordering areas in-between the core zones or protected forest and human zones, which often allow for certain use of resources to benefit to local people (Hull et al., 2011; McNeely, 1994). Establishing buffer zones may reduce human pressure, reduce encroachment and so wildlife-livestock contact, and preserve the core habitat of wildlife within the protected areas, though they might not entirely prevent livestock from encroaching into protected areas (Hull et al., 2011). The buffer zones could be implemented along with the stakeholder's and community's agreement. In that sense, communicating and engaging in discussions with local people and other stakeholders to plan the use of the buffer zone is the main key to making long-term successful conservation plans (Stræde & Treue, 2006).

Other practical measures to mitigate infectious disease risk might be to consider building physical barriers (e.g. fencing, ditches and canals) or increasing vaccination coverage in livestock populations to enhance the disease surveillance systems in some target areas. One suggestion to reduce hotspots of animal aggregations and interactions is to strategically manage the main resources for foraging and water supplies, especially during a dry season, such as increasing watering holes and managing open grassland, as well as segregating the food, minerals and water supplies between wildlife and livestock (De Garine-Wichatitsky et al., 2021; Gortazar et al., 2015).

5.4.4 Surveillance and monitoring

Disease surveillance is the continuous and systematic collection of data to build a scientific database, inform decision-making, and conduct disease prevention and control. Clearly defining the objectives and case definitions is essential as it provides direction for surveillance, leading to collecting necessary data, early detection and rapid responses during disease outbreaks. Efficient surveillance can also mitigate health-related impacts, economic losses, and the consequences of infection spreading into a new population due to delayed detection.(Thacker & Birkhead, 2008).

Passive surveillance is suitable for routine data collection for monitoring disease incidences and trends at a national level with less budget compared to active surveillance. But passive surveillance still has drawbacks in getting reliable data, standardising collection methods, and detecting some subclinical or rare disease incidences. Active surveillance is designed for studying particular diseases within specific populations, places and times, like risk-based and target-based surveillance and disease prevalence, potentially requiring higher budgets and more resources to be implemented (Cardoso et al., 2022)

Modelling could be valuable for simulating various scenarios and selecting optimal disease control measures. These models are also supported in the study design or disease surveillance programs for disease transmission (Herzog et al., 2017; Restif et al., 2012). For example, spatiotemporal models were used to design sample collection methods for disease surveillance of white-nose syndrome (Oh et al., 2023) or epidemiological models to help plan risk-based surveillance (Willeberg et al., 2011). In this thesis, modelling provided significant findings, including habitat suitability maps of wild bovids, potential risk maps, and the estimated impact of population change on infectious diseases. These findings may provide insights for both pre- and post-surveillance systems, by providing more knowledge to focus surveillance efforts, but also testable hypotheses that can then be updated with future data. For example, the results highlighted the western part of Thailand as a potential risk area for disease transmission, suggesting this area should be targeted in disease surveillance plans. The modelling results also identified which infectious diseases are most important, with bovine tuberculosis and brucellosis likely to have the most negative impacts on wild bovid populations. But, in the surveillance database, these diseases showed only a few outbreak records in cattle, so this result informs the important disease information required for monitoring at the interface areas and helps identify where those areas are to improve disease detection and mitigation.

Standardised methods and guidelines would be ideal to reach the goals of disease surveillance, and setting up working groups and improving diagnostic laboratory centres and database networks for data sharing are required. Integrating ecological with epidemiological parameters could improve the estimation of disease prevalence and sample size, leading to better surveillance design and accuracy in disease risk assessment (Walton et al., 2016). For example, wildlife population data such as herd size, abundance and density was integrated into wildlife disease surveillance guidelines and management programs in Europe (Cardoso et al., 2022).

In Thailand, disease surveillance systems have been developed for domestic livestock at both national and regional levels, focusing on endemic diseases such as foot and mouth disease (Arjkumpa et al., 2020), brucellosis (*B. melitensis*) (Peck et al., 2018), bovine tuberculosis (*M. bovis*) (Singhla & Boonyayatra, 2022). National disease surveillance efforts have allowed for the monitoring and recording of these diseases in living databases, enabling data analysis and informing disease prevention and control measures such as vaccination programs, culling, and active target-based surveillance.

However, wildlife disease surveillance at the interface areas usually prioritises zoonotic diseases and wildlife reservoirs. For example, the study of rodent-borne diseases in deforested areas (Morand et al., 2019) or Nipah surveillance in bats in long-term surveillance (Wacharapluesadee et al., 2021). Some disease prevalence surveys in domestic cattle have detected pathogens like *Leptospira* (Yatbantoong & Chaiyarat, 2019) and *Babesia* (Simking et al., 2014) found in cattle farms near the habitat of wild bovids. Additionally, a recent study conducted in Nan province considered spillover events at interface areas and predicted nearly 60 viruses shared among 43 host species of wildlife and domestic animals (Thinphovong et al., 2024). Therefore, the government could develop long-term wildlife disease surveillance programs focusing on infectious diseases and wildlife conservation. These programs should be integrated into policies in order to get the necessary funding, facilities, and resources for conducting surveillance of priority pathogens and infectious diseases at interface areas.

5.4.5 Inter-agency and cross-sector collaborations and partnership

As wildlife and livestock disease transmission involves complex issues, including environmental, health and socio-economic problems, which threaten wildlife conservation, using integrative methods may lead to problem-solving (Waltner-Toews, 2017). The One Health (human, animal and ecosystem health) approach is a multidisciplinary field that integrates various disciplines, collaborations, and expertise to tackle complex problems. Developing collaborations among different backgrounds, agencies, and sectors could be challenging but beneficial to connecting people, brainstorming, and sharing data to make guidelines or strategies for protecting wildlife health and conservation. For example, the One Health High-Level Expert Panel (OHHLEP) includes members from human, livestock, agricultural and wildlife global health sectors (Panel One Health High-Level Expert et al., 2022). In Southeast Asia, there is the Wildlife Health Network that incorporates people from several stakeholders (e.g. local communities, livestock and human health, patrol rangers, and diagnostic laboratories) and forms a working group focusing on the interface issues. This network has detected infectious diseases in wildlife in Laos, Cambodia, and Vietnam (Pruvot et al., 2020). In Thailand, there is a study assessing the attitude of the One Health approach to wildlife disease surveillance in Thailand revealed that the biggest challenges are data accessibility and barriers working across departments and sectors of the government authorities, mostly difficult to communicate and require legal documents. The study recommends increasing collaborations among the departments, human resources, budget allocations, and communication clarity to improve the system (George et al., 2023).

5.5 Methodological gaps

The methodology in this thesis mainly involved the use of data analysis, modelling, and GIS, which can be further improved and analysed. The ENM used in this study provided constant habitat suitability maps, but, in reality, the species' habitat or distribution might be changing (e.g., expanding or contracting). Changes in factors such as environmental conditions, biological interactions, and disease outbreaks, can lead to either the expansion or contraction of suitable habitats over time. Therefore, including temporal variables (e.g. vegetation condition, seasonality, land use change) (Leitão & Santos, 2019) as input parameters might be helpful in predicting the dynamics of habitat suitability. The spatiotemporal risk map could estimate the potential hotspots of disease transmission between wildlife and livestock interface, helping prioritise disease monitoring areas.

Furthermore, incorporating the contact network, pattern, and rate of transmission in the population dynamic model could understand the pathway of disease spread between and within wildlife and livestock populations. Wildlife and livestock interactions might be collected from several fieldwork methods (e.g. questionnaires, GPS locations, camera traps, proximity loggers) or reviewed literature from relevant populations and pathogens (Craft, 2015; Triguero-Ocaña et al., 2021). Additionally,]including an environmental compartment in disease modelling could fill the gap in the pathogen transmission between environmental contamination and animals, for example, the spores transmitted from environment to animals in anthrax (Furniss & Hahn, 1981; Saad-Roy et al., 2017). For certain infections with a wide host range, incorporating multiple host species into infectious disease modelling might be necessary to capture the pathways of disease transmission (Renwick et al., 2007). Moreover, sensitivity analysis of the parameters in the population dynamic models could answer which disease parameters show the greatest influence on the population changes. This analysis may also guide in selecting the optimal prevention and control measures (Pepin et al., 2022).

Lastly, there are methodological gaps in how to generate truly integrated systems and approaches to problems, such as how to develop integrated surveillance systems and management plans that integrate human, livestock and wildlife, and environmental data (Hayman et al., 2023).

5.6 Data gaps

Addressing data gaps is crucial for enhancing the robustness of modelling. These gaps may include data availability, quality, quantity, accuracy, and collection methods. Key factors affecting data availability include data collection methods and survey techniques, which can be provided through a well-designed guideline and framework with sufficient human resources and funding. Both ecological niche models and infectious disease models rely on parameter inputs such as species occurrences, spatial environmental data, biological and disease parameters, and surveillance data. Limited availability and quality of such data can lead to uncertainty in model predictions and poor model performance. However, collecting those data can be challenging, as it may not always be available from open sources or accessible to the public. Organisations or websites like IUCN, eMammals and GBIF provide important information on wildlife species based on the researcher’s request, but for endangered species like the wild water buffalo in Thailand, the database is restricted to government authorities. Although sharing sensitive data may not be available to the public, governments could consider, at least, making it available for academic purposes under restricted conditions.

Continual data collection and management in wildlife conservation and epidemiological studies are essential processes to enhance both the quantity and quality of data. For example, collection of infection data may not be systematic and only responsive to outbreaks or other priorities, such as trade. The model framework presented by Restif et al. (2012) outlines a cycle of modelling steps, which include data collection and analysis for fitting and validation. Performing a priori modelling can assist in planning fieldwork for data collection, determining the type of data needed, how to collect it, and how to integrate it with other data sources. For example, long-term wildlife disease research for more than four consecutive years in wildlife and livestock helps to observe the disease dynamics and future trends of foot and mouth disease, bovine tuberculosis, and bovine brucellosis (Barroso et al., 2021; Jolles et al., 2021; Jolles et al., 2005; Olsen, 2010). Moreover, estimating population numbers, abundance, and density provides important insights into ecosystem dynamics. Effective conservation and management requires robust data collection and analysis, including updating species occurrence data to create maps showing where species have potentially suitable habitats. Together, better data would enable better understanding of the systems and testing of model predictions and validation.

5.7 Future Perspective

Based on the above mentioned issues, I have identified the potential future works that could be performed to develop the work in this thesis:

- Collect and update species occurrence data to improve habitat suitability and species distribution maps, along with estimating population numbers, occupancy, and density.
- Study contact rates, networks and patterns of humans, wildlife and livestock at interface areas.
- Incorporate temporal variables on species habitat suitability and potential risk maps of disease transmission.
- Enhance disease surveillance systems (e.g. database, facilities, fundings) and continue collecting infectious disease data in livestock and identify risk factors of disease transmission in high-risk areas at high-risk times.
- Integrating disease monitoring and surveillance into wildlife conservation plans.

5.8 Concluding remarks

Understanding infectious diseases and population dynamics in ecosystems is crucial for making effective conservation plans and habitat management in wildlife conservation. Here, I identified suitable habitats for threatened Thai bovids, modelled population dynamics following the introduction of infected animals, and mapped the interface areas between wild bovids and domestic cattle to identify potential risk areas for disease transmission, surveillance, and mitigation. Wildlife habitat management, along with agricultural area management, should aim to reduce interactions among multiple species in shared areas to reduce the disease risk, with an emphasis on the high-risk areas identified in Chapter 4. I suggest that improving the efficiency of field epidemiologists and ecologists through supporting collaboration, coordination and capacity building through training along with greater resources for this work can enhance the reporting and handling of threats (e.g. outbreaks and hunting) to wildlife populations. In Thailand, conservation plans often overlook the impact of infectious diseases on wildlife health. Integrating multidisciplinary approaches, such as One Health, and formulating well-designed studies that consider ecological and epidemiological factors are crucial for sustainable conservation practices to protect the health of wild bovid and other wildlife populations.

Appendices

Appendix 1

Mapping threatened Thai bovids provides opportunities for improved conservation outcomes in Asia

includes

- Table S1.1 to S1.6
- Table S1.7 (link)
- Figure S1.1 to S1.10

Table S1.1 Environmental factors used for modelling.

No.	Variables	Description	Code	Source	Resolution	Spatial extent	Temporal range	CRS	Citation
1	Human population density	Total number of human population in grid cell (1 km)	hpop	WorldPop	~1 km^2	World	2020	WGS84	Stevens et al. (2015) https://www.worldpop.org/geodata/summary?id=24777
2	Slope	the rate of elevation change along the direction of the water flow, and calculated using a 3 × 3 cell moving window.	slope	OpenTopography	250 m^2	World	2018	WGS84	Amatulli et al. (2020) http://spatial-ecology.net/dokuwiki/doku.php?id=topovar90m
3	Elevation (m)	World elevation	elev	Shuttle Radar Topography Mission (SRTM)	~1 km^2	World	2000	WGS84	Fick & Hijmans (2017) https://www.worldclim.org/data/worldclim21.html#
4	Annual Mean Temperature		bio1	Shuttle Radar Topography Mission (SRTM)	~1 km^2	World	2000	WGS84	Fick & Hijmans (2017) https://www.worldclim.org/data/worldclim21.html#
5	Mean Diurnal Range (Mean of monthly (max temp - min temp))		bio2						
6	Isothermality (BIO2/BIO7) (×100)		bio3						
7	Temperature Seasonality (standard deviation ×100)		bio4						
8	Max Temperature of Warmest Month		bio5						
9	Min Temperature of Coldest Month		bio6						
10	Temperature Annual Range (BIO5-BIO6)		bio7						
11	Mean Temperature of Wettest Quarter		bio8						
12	Mean Temperature of Driest Quarter		bio9						
13	Mean Temperature of Warmest Quarter		bio10						
14	Mean Temperature of Coldest Quarter		bio11						
15	Annual Precipitation		bio12						
16	Annual Mean Temperature		bio13						
17	Precipitation of Driest Month		bio14						

No.	Variables	Description	Code	Source	Resolution	Spatial extent	Temporal range	CRS	Citation
18	Precipitation Seasonality (Coefficient of Variation)		bio15						Fick & Hijmans (2017) https://www.worldclim.org/data/worldclim21.html#
19	Precipitation of Wettest Quarter		bio16						
20	Precipitation of Driest Quarter		bio17						
21	Precipitation of Warmest Quarter		bio18						
22	Precipitation of Coldest Quarter		bio19						
23	Normalized Difference Vegetation Index (NDVI)	NDVI (MODIS/Terra Vegetation Indices 16-Day L3 Global 1km-MODIS13A2), time series record for historical and climate applications	ndvi	MODIS, NASA	~1 km^2	Asia	31-Dec-2019, time-series (16 days data)	sinusoidal	Didan, K. (2015) https://search.earthdata.nasa.gov/search?q=C194001238-LPDAAC_ECS
24	Crop	Crop cover fraction (%)	crop	Copernicus Global Land Service (CGLS): Land Cover 100 m: epoch 2015: Globe, version 2.0.2	100 m^2	World	2015	WGS84	Buchhorn et al. (2019) https://zenodo.org/record/3243509#.YSve0C0RpQI
25	Grass	Grass cover fraction (%)	grass			World	2015		
26	Tree	Tree cover fraction (%)	tree			World	2015		
27	Urban	Urban cover fraction (%)	urban			World	2015		
28	Water	Water cover fraction (%)	water			World	2015		

Table S1.2 Terrestrial ecoregion names and the accessible areas used for modelling. The numbers mean that those accessible areas were included for modelling.

	Accessible areas					
		species-specific accessible area				
Ecoregions	**Large accessible areas**	**banteng**	**buffalo**	**gaur**	**goral**	**serow**
Afghan Mountains semi-desert	1					
Alashan Plateau semi-desert	1					
Altai alpine meadow and tundra	1					
Altai montane forest and forest steppe	1					
Altai steppe and semi-desert	1					
Amur meadow steppe	1					
Baluchistan xeric woodlands	1		1			
Bohai Sea saline meadow	1					
Borneo lowland rain forests	1	1				
Borneo montane rain forests	1	1				
Borneo peat swamp forests	1	1				
Brahmaputra Valley semi-evergreen forests	1		1	1	1	1
Cardamom Mountains rain forests	1		1	1		1
Central Afghan Mountains xeric woodlands			1			
Central China loess plateau mixed forests	1				1	
Central Deccan Plateau dry deciduous forests	1		1	1		
Central Indochina dry forests	1	1	1	1	1	1
Central Tibetan Plateau alpine steppe	1					
Changbai Mountains mixed forests	1					
Changjiang Plain evergreen forests	1				1	1
Chao Phraya freshwater swamp forests	1	1	1	1		1
Chao Phraya lowland moist deciduous forests	1	1	1	1		1
Chhota-Nagpur dry deciduous forests	1		1	1		
Chin Hills-Arakan Yoma montane forests	1		1	1	1	1
Da Hinggan-Dzhagdy Mountains conifer forests	1					
Daba Mountains evergreen forests	1				1	1
Deccan thorn scrub forests	1		1	1		
East Afghan montane conifer forests	1		1			
East Deccan dry-evergreen forests	1		1	1		
Eastern Gobi desert steppe	1					
Eastern highlands moist deciduous forests	1		1	1		
Eastern Himalayan alpine shrub and meadows	1		1	1	1	1
Eastern Himalayan broadleaf forests	1		1	1	1	1
Eastern Himalayan subalpine conifer forests	1		1	1	1	1
Eastern Java-Bali montane rain forests	1	1				
Eastern Java-Bali rain forests	1					
Emin Valley steppe	1					
Ghorat-Hazarajat alpine meadow	1					
Goadavari-Krishna mangroves	1		1	1		

	Accessible areas					
		species-specific accessible area				
Ecoregions	**Large accessible areas**	**banteng**	**buffalo**	**gaur**	**goral**	**serow**
Guizhou Plateau broadleaf and mixed forests	1				1	1
Hainan Island monsoon rain forests	1				1	1
Helanshan montane conifer forests	1					
Hengduan Mountains subalpine conifer forests	1				1	1
Himalayan subtropical broadleaf forests	1		1	1	1	1
Himalayan subtropical pine forests	1		1	1		1
Hindu Kush alpine meadow	1					
Huang He Plain mixed forests	1				1	
Indochina mangroves	1	1	1	1		1
Indus River Delta-Arabian Sea mangroves	1		1	1		
Indus Valley desert	1		1			
Irrawaddy dry forests	1	1	1	1	1	1
Irrawaddy freshwater swamp forests	1	1	1	1	1	1
Irrawaddy moist deciduous forests	1	1	1	1	1	1
Jian Nan subtropical evergreen forests	1				1	1
Junggar Basin semi-desert	1					
Karakoram-West Tibetan Plateau alpine steppe	1		1			1
Kayah-Karen montane rain forests	1		1	1	1	1
Khathiar-Gir dry deciduous forests	1		1	1		
Kinabalu montane alpine meadows	1	1				
Lower Gangetic Plains moist deciduous forests	1		1	1	1	1
Luang Prabang montane rain forests	1		1	1	1	1
Malabar Coast moist forests	1		1	1		
Manchurian mixed forests	1					
Meghalaya subtropical forests	1		1	1	1	1
Mizoram-Manipur-Kachin rain forests	1		1	1	1	1
Mongolian-Manchurian grassland	1					
Myanmar Coast mangroves	1	1	1	1	1	1
Myanmar coastal rain forests	1		1	1	1	1
Narmada Valley dry deciduous forests	1		1	1		
Nenjiang River grassland	1					
North Tibetan Plateau-Kunlun Mountains alpine desert	1					
North Western Ghats moist deciduous forests	1		1	1		
North Western Ghats montane rain forests	1		1	1		
Northeast China Plain deciduous forests	1				1	
Northeast India-Myanmar pine forests	1		1	1	1	1
Northeastern Himalayan subalpine conifer forests	1		1	1	1	1
Northern Annamites rain forests	1		1	1		1
Northern dry deciduous forests	1		1	1		
Northern Indochina subtropical forests	1		1	1	1	1

	Accessible areas					
		species-specific accessible area				
Ecoregions	Large accessible areas	banteng	buffalo	gaur	goral	serow
Northern Khorat Plateau moist deciduous forests	1		1	1		1
Northern Thailand-Laos moist deciduous forests	1		1	1	1	1
Northern Triangle subtropical forests	1		1	1	1	1
Northern Triangle temperate forests	1		1	1	1	1
Northern Vietnam lowland rain forests	1		1	1		1
Northwestern Himalayan alpine shrub and meadows	1		1			1
Northwestern thorn scrub forests	1		1			
Nujiang Langcang Gorge alpine conifer and mixed forests	1		1	1	1	1
Ordos Plateau steppe	1				1	
Orissa semi-evergreen forests	1		1	1		
Pamir alpine desert and tundra	1					
Peninsular Malaysian montane rain forests	1	1	1	1		1
Peninsular Malaysian peat swamp forests	1	1	1	1		1
Peninsular Malaysian rain forests	1		1	1		1
Qaidam Basin semi-desert	1					
Qilian Mountains conifer forests	1				1	1
Qilian Mountains subalpine meadows	1					
Qin Ling Mountains deciduous forests	1				1	1
Qionglai-Minshan conifer forests	1				1	1
Rann of Kutch seasonal salt marsh	1		1			
Red River freshwater swamp forests	1		1			1
Registan-North Pakistan sandy desert			1			
Rock and Ice	1		1	1	1	1
Sichuan Basin evergreen broadleaf forests	1				1	1
South China-Vietnam subtropical evergreen forests	1				1	1
South Deccan Plateau dry deciduous forests	1		1	1		
South Iran Nubo-Sindian desert and semi-desert	1		1			
South Western Ghats moist deciduous forests	1		1	1		
South Western Ghats montane rain forests	1		1	1		
Southeast Tibet shrublands and meadows	1				1	1
Southeastern Indochina dry evergreen forests	1		1	1		1
Southern Annamites montane rain forests	1	1	1	1		1
Southern Vietnam lowland dry forests	1	1	1	1		1
Southwest Borneo freshwater swamp forests	1	1				
Sri Lanka dry-zone dry evergreen forests	1		1			
Sri Lanka lowland rain forests	1		1			
Sri Lanka montane rain forests	1		1			

	Accessible areas					
		species-specific accessible area				
Ecoregions	**Large accessible areas**	**banteng**	**buffalo**	**gaur**	**goral**	**serow**
Suiphun-Khanka meadows and forest meadows	1					
Sulaiman Range alpine meadows	1		1			
Sumatran freshwater swamp forests	1					1
Sumatran lowland rain forests	1					1
Sumatran montane rain forests	1					1
Sumatran peat swamp forests	1					1
Sumatran tropical pine forests	1					1
Sunda Shelf mangroves	1	1				1
Sundaland heath forests	1	1				
Sundarbans freshwater swamp forests	1		1	1		
Sundarbans mangroves	1		1	1		
Taklimakan desert	1					
Tarim Basin deciduous forests and steppe	1					
Tenasserim-South Thailand semi-evergreen rain forests	1	1	1	1		1
Terai-Duar savanna and grasslands	1		1	1	1	1
Thar desert	1		1			
Tian Shan montane conifer forests	1					
Tian Shan montane steppe and meadows	1					
Tibetan Plateau alpine shrublands and meadows	1					1
Tonle Sap freshwater swamp forests	1	1	1	1		1
Tonle Sap-Mekong peat swamp forests	1	1	1	1		1
Upper Gangetic Plains moist deciduous forests	1		1	1		1
Western Himalayan alpine shrub and Meadows	1		1			1
Western Himalayan broadleaf forests	1		1			1
Western Himalayan subalpine conifer forests	1		1			1
Western Java montane rain forests	1	1				
Western Java rain forests	1					
Yarlung Tsangpo arid steppe	1		1			1
Yellow Sea saline meadow	1					
Yunnan Plateau subtropical evergreen forests	1			1	1	1
Grand Total	**144**	**24**	**83**	**64**	**43**	**71**

Table S1.3 Algorithms used in the modelling process

Algorithm	Abbreviations	Data used to create models	strength	limitations	Reference
Bioclim (Envelope Score)	BIO	Presences-only	consider only climatic variables, not complicated using percentile distribution for prediction, easy to understand	has limitation on interpretation a non-climatic variables which can cause model inaccuracies	Pearson and Dawson (2003)
Generalized Linear Models	GLM	Presences and pseudo-absences	strong statistical foundation, flexible for modelling ecological relationship other than Gaussian distributions	use only for linear regression, not effective when occurrence data is small	Guisan et al. (2002)
Generalized Additive Models	GAM	Presences and pseudo-absences	fit highly non-linear and non-monotonic and complicated functions	not effective when occurrence data is small	Guisan et al. (2002); Ishihama et al. (2019)
Support Vector Machine	SVM	Presences and pseudo-absences	machine learning algorithm, reduce overprediction, alleviate multicollinearity	need absence (or pseudo-absence data)	Drake et al. (2006); Farrell et al. (2019)
Random Forest	RDF	Presences and pseudo-absences	machine learning algorithm, reduce overprediction, alleviate multicollinearity	non-parametric	Evans et al. (2011);Farrell et al. (2019)
Maximum Likelihood	MLK	Presences and background points	can use presence-only data, can estimate probability of occurrence using conventional likelihood methods	simulation can be slow, may have bias in small sample size	Royle et al. (2012)
Bayesian Gaussian Process	GAU	Presences and pseudo-absences	create joint models, conditional modelling, flexible, dealing with complex models	non-parametric, using presence/absence data, need experienced	Golding and Purse (2016)
Maximum Entropy default (all features)	MXD	Presences and background points	can use presence-only data, high performance which can differentiate between unsuitable and suitable area, can work with small sample size	cannot model a species fundamental niche, less localize, overfitting, prediction is not directly related to the actual parameter of interest, cannot estimate the probability of occurrence	Phillips et al. (2006)

Table S1.4 Loading factors of the first two principal components (PC), PC1 and PC2, of the predictive environmental variables used in ecological niche modelling.

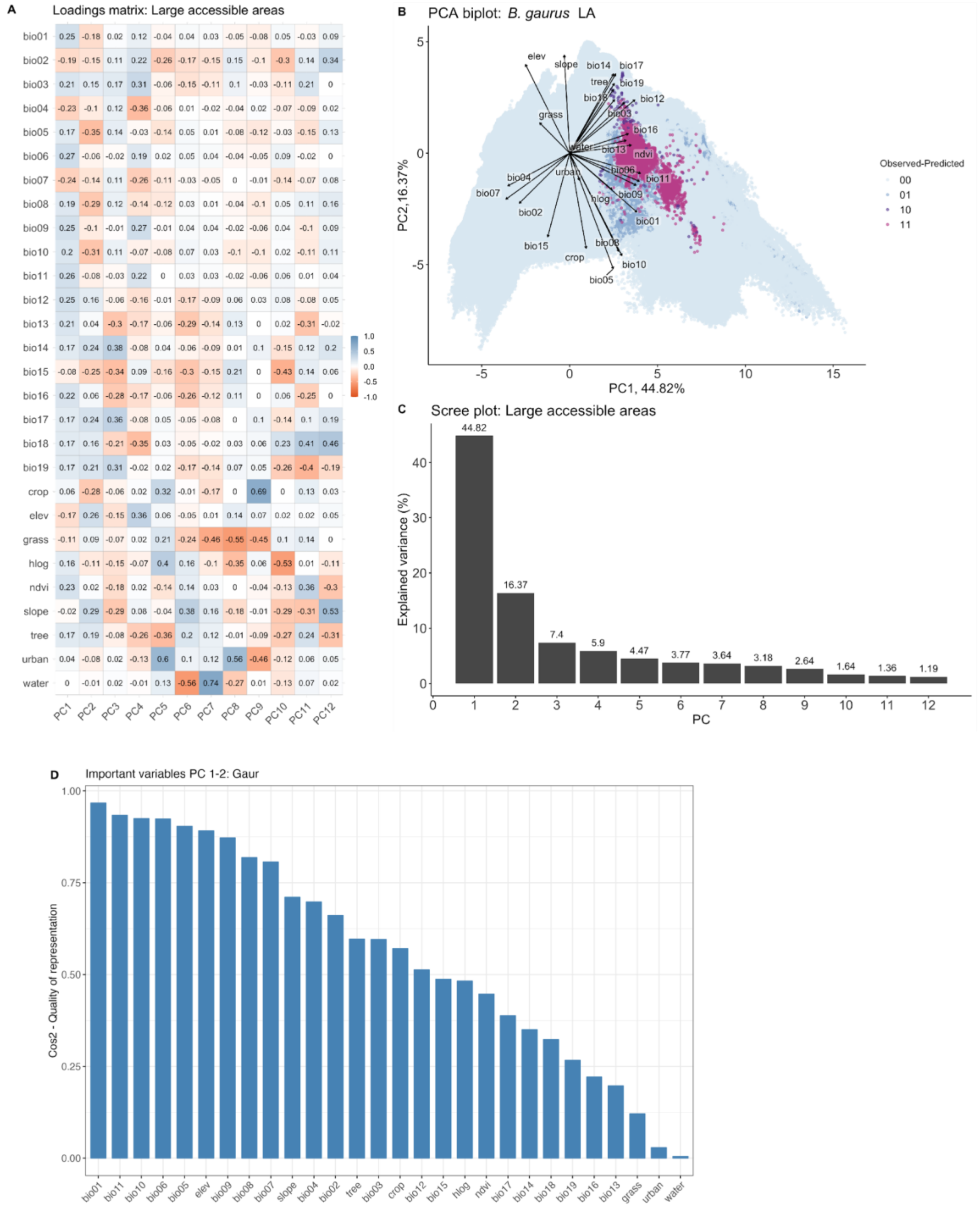
The high values were highlighted in boldface.

		LA		SSA									
		All species		*B. gaurus*		*B. javanicus*		*B. arnee*		*C. sumatraensis*		*N. griseus*	
		PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Cumulative proportion		45%	16%	32%	24%	34%	27%	29%	28%	46%	14%	42%	19%
Environmental variables		PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Annual Mean Temperature	bio01	**0.25**	0.18	**0.29**	0.17	0.24	0.23	**0.34**	0.02	**0.27**	0.12	**0.28**	0.03
Mean Diurnal Range	bio02	-0.19	0.15	0.15	**-0.26**	-0.17	0.10	0.02	**-0.31**	-0.17	0.05	**0.24**	0.20
Isothermality	bio03	0.21	-0.15	-0.02	**0.29**	**0.28**	-0.12	0.08	0.24	0.14	-0.26	**0.27**	-0.08
Temperature Seasonality	bio04	-0.23	0.10	0.01	**-0.32**	**-0.29**	0.04	-0.10	**-0.29**	-0.19	0.15	0.24	-0.15
Max Temperature of Warmest Month	bio05	0.17	**0.35**	**0.32**	-0.02	0.06	**0.32**	0.30	-0.15	0.23	0.24	0.20	-0.17
Min Temperature of Coldest Month	bio06	**0.27**	0.06	0.19	**0.29**	**0.31**	0.07	0.29	0.18	**0.27**	0.03	0.14	0.17
Temperature Annual Range	bio07	-0.24	0.14	0.11	**-0.32**	-0.28	0.12	-0.03	**-0.32**	-0.22	0.20	-0.11	-0.12
Mean Temperature of Wettest Quarter	bio08	0.19	**0.29**	**0.29**	0.10	0.15	**0.27**	0.30	-0.02	0.25	0.20	0.20	-0.19
Mean Temperature of Driest Quarter	bio09	**0.25**	0.10	0.28	0.16	**0.29**	0.15	**0.32**	0.02	**0.26**	0.08	0.15	0.15
Mean Temperature of Warmest Quarter	bio10	0.20	**0.31**	**0.32**	0.05	0.13	**0.30**	**0.32**	-0.10	0.24	0.21	0.17	-0.16
Mean Temperature of Coldest Quarter	bio11	**0.26**	0.08	0.24	0.25	**0.29**	0.14	**0.31**	0.13	**0.27**	0.05	0.16	0.14
Annual Precipitation	bio12	**0.25**	-0.16	-0.09	0.25	0.20	-0.18	0.03	**0.31**	0.23	-0.15	-0.20	-0.10
Precipitation of Wettest Month	bio13	0.21	-0.04	-0.03	0.17	0.03	-0.07	0.05	0.23	0.19	0.00	0.05	**-0.34**
Precipitation of Driest Month	bio14	0.17	-0.24	-0.09	0.20	0.24	-0.19	-0.03	0.19	0.13	**-0.31**	-0.16	**0.31**
Precipitation Seasonality	bio15	0.08	0.25	0.17	-0.18	-0.25	0.15	0.13	-0.17	-0.08	**0.26**	0.22	0.20
Precipitation of Wettest Quarter	bio16	0.22	-0.06	-0.04	0.17	0.03	-0.08	0.05	0.24	0.19	-0.02	**0.28**	-0.04
Precipitation of Driest Quarter	bio17	0.18	-0.24	-0.09	0.21	0.25	-0.19	-0.04	0.21	0.14	**-0.31**	-0.21	0.24
Precipitation of Warmest Quarter	bio18	0.17	-0.16	-0.17	0.09	-0.01	-0.23	-0.07	0.21	0.12	-0.08	0.23	0.17
Precipitation of Coldest Quarter	bio19	0.17	-0.21	-0.03	0.19	0.26	-0.14	0.00	0.16	0.14	**-0.31**	**0.27**	-0.07
Crop cover fraction	crop	0.06	**0.28**	0.23	-0.12	-0.03	**0.26**	0.18	-0.15	0.06	**0.35**	0.01	**0.27**
Elevation	elev	-0.17	-0.26	-0.27	-0.18	-0.22	-0.22	**-0.33**	-0.04	**-0.25**	-0.16	-0.21	-0.25
Grass cover fraction	grass	-0.11	-0.09	-0.04	-0.12	-0.05	0.12	-0.10	-0.05	-0.20	-0.07	-0.21	-0.10
Human population density	hlog	0.16	0.11	0.23	-0.07	-0.03	0.21	0.21	-0.08	0.15	0.22	0.12	**0.26**
Normalized Difference Vegetation Index	ndvi	0.23	-0.02	-0.15	0.19	0.01	-0.26	0.05	0.27	0.21	-0.10	0.22	-0.17
Slope	slope	-0.02	**-0.29**	**-0.28**	-0.03	-0.14	-0.23	-0.26	0.11	-0.12	-0.20	-0.06	**-0.27**
Tree cover fraction	tree	0.17	-0.19	-0.21	0.18	0.04	**-0.29**	-0.06	**0.27**	0.15	-0.23	0.16	-0.21
Urban cover fraction	urban	0.04	0.08	0.05	0.02	0.02	0.10	0.05	0.00	0.03	0.12	0.02	0.20
Water cover fraction	water	0.00	0.01	0.01	0.02	0.02	0.04	0.01	0.01	0.01	0.03	0.02	0.05

Figure S1.1 Principal Component Analysis (PCA) for five bovid species: gaur (*Bos gaurus*), banteng (*Bos javanicus*), wild water buffalo (*Bubalus arnee*), mainland serow (*Capricornis sumatraensis*) and Chinese goral (*Naemorhedus griseus*).

> (A) The negative (red) and positive (blue) relationships between the loading of important principal components (PC) that are used in model building and environmental variables.
>
> (B) The first two PCA axes (PC 1 and PC2) of the most explained variance plotted with variable loadings (arrows) and species' locations. The loadings arrows represent relationships and importance of environmental variables and species presence-absence (the longer line = more important with the negative-positive influence). The points represent species' locations for 4 categories: 00 (light blue) = absence observation, absence prediction; 01 (blue) = absence observation; 10 (purple) = presence observation, absence prediction, 11 (pink) = presence observation, presence prediction.
>
> (C) Scree plot of explained variance for important PC (%).
>
> (D) The important variables used in PC one and two.

1. Gaur (*Bos gaurus*)



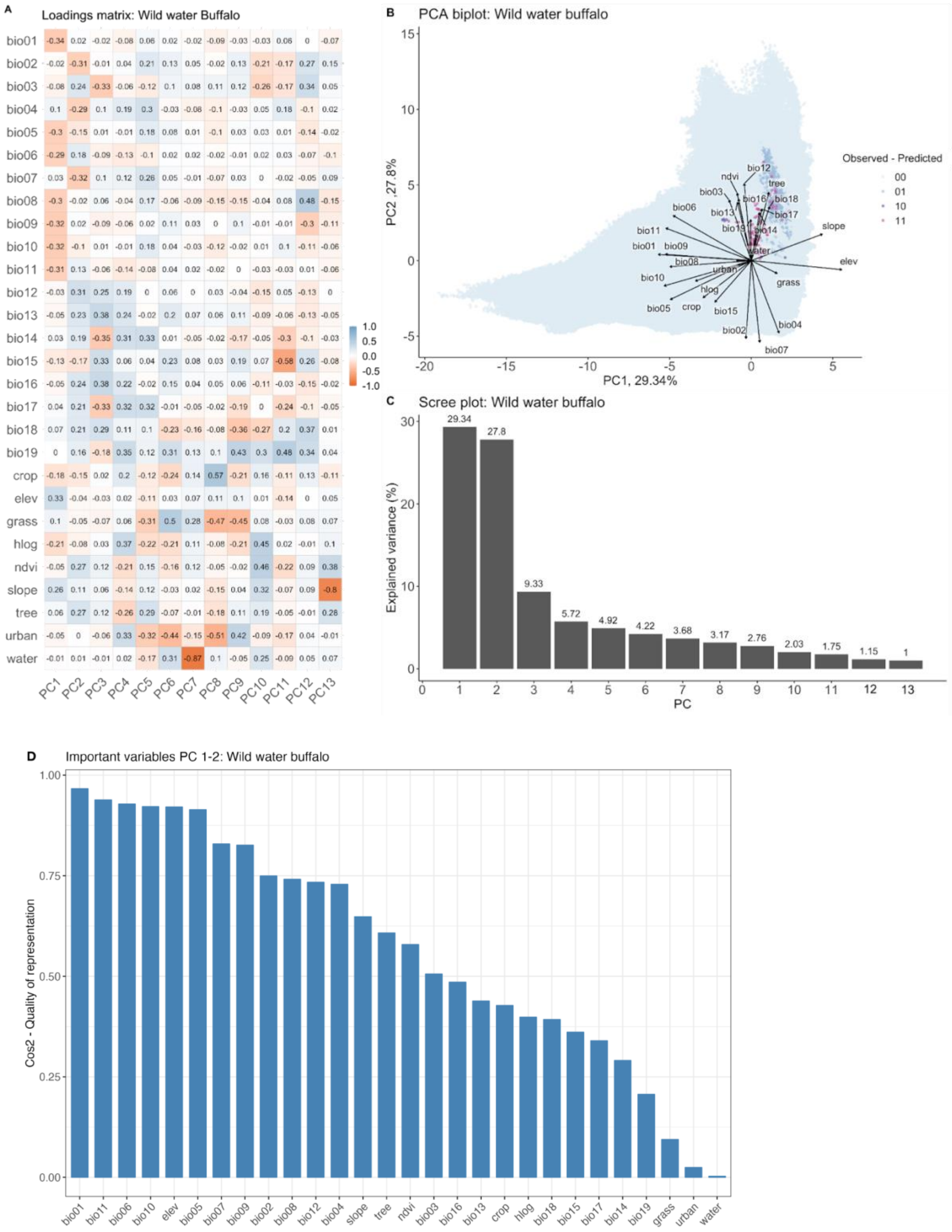
A Loadings matrix: Large accessible areas

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12
bio01	0.25	-0.18	0.02	0.12	-0.04	0.04	0.03	-0.05	-0.08	0.05	-0.03	0.09
bio02	-0.19	-0.15	0.11	0.22	-0.26	-0.17	-0.15	0.15	-0.1	-0.3	0.14	0.34
bio03	0.21	0.15	0.17	0.31	-0.06	-0.15	-0.11	0.1	-0.03	-0.11	0.21	0
bio04	-0.23	-0.1	0.12	-0.36	-0.06	0.01	-0.02	-0.04	0.02	-0.07	-0.09	0.02
bio05	0.17	-0.35	0.14	-0.03	-0.14	0.05	0.01	-0.08	-0.12	-0.03	-0.15	0.13
bio06	0.27	-0.06	-0.02	0.19	0.02	0.05	0.04	-0.04	-0.05	0.09	-0.02	0
bio07	-0.24	-0.14	0.11	-0.26	-0.11	-0.03	-0.05	0	-0.01	-0.14	-0.07	0.08
bio08	0.19	-0.29	0.12	-0.14	-0.12	0.03	0.01	-0.04	-0.1	0.05	0.11	0.16
bio09	0.25	-0.1	-0.01	0.27	-0.01	0.04	0.04	-0.02	-0.06	0.04	-0.1	0.09
bio10	0.2	-0.31	0.11	-0.07	-0.08	0.07	0.03	-0.1	-0.1	0.02	-0.11	0.11
bio11	0.26	-0.08	-0.03	0.22	0	0.03	0.03	-0.02	-0.06	0.06	0.01	0.04
bio12	0.25	0.16	-0.06	-0.16	-0.01	-0.17	-0.09	0.06	0.03	0.08	-0.08	0.05
bio13	0.21	0.04	-0.3	-0.17	-0.06	-0.29	-0.14	0.13	0	0.02	-0.31	-0.02
bio14	0.17	0.24	0.38	-0.08	0.04	-0.06	-0.09	0.01	0.1	-0.15	0.12	0.2
bio15	-0.08	-0.25	-0.34	0.09	-0.16	-0.3	-0.15	0.21	0	-0.43	0.14	0.06
bio16	0.22	0.06	-0.28	-0.17	-0.06	-0.26	-0.12	0.11	0	0.06	-0.25	0
bio17	0.17	0.24	0.36	-0.08	0.05	-0.05	-0.08	0	0.1	-0.14	0.1	0.19
bio18	0.17	0.16	-0.21	-0.35	0.03	-0.05	-0.02	0.03	0.06	0.23	0.41	0.46
bio19	0.17	0.21	0.31	-0.02	0.02	-0.17	-0.14	0.07	0.05	-0.26	-0.4	-0.19
crop	0.06	-0.28	-0.06	0.02	0.32	-0.01	-0.17	0	0.69	0	0.13	0.03
elev	-0.17	0.26	-0.15	0.36	0.06	-0.05	0.01	0.14	0.07	0.02	0.02	0.05
grass	-0.11	0.09	-0.07	0.02	0.21	-0.24	-0.46	-0.55	-0.45	0.1	0.14	0
hlog	0.16	-0.11	-0.15	-0.07	0.4	0.16	-0.1	-0.35	0.06	-0.53	0.01	-0.11
ndvi	0.23	0.02	-0.18	0.02	-0.14	0.14	0.03	0	-0.04	-0.13	0.36	-0.3
slope	-0.02	0.29	-0.29	0.08	-0.04	0.38	0.16	-0.18	-0.01	-0.29	-0.31	0.53
tree	0.17	0.19	-0.08	-0.26	-0.36	0.2	0.12	-0.01	-0.09	-0.27	0.24	-0.31
urban	0.04	-0.08	0.02	-0.13	0.6	0.1	0.12	0.56	-0.46	-0.12	0.06	0.05
water	0	-0.01	0.02	-0.01	0.13	-0.56	0.74	-0.27	0.01	-0.13	0.07	0.02

2. Banteng (*Bos javanicus*)

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
bio01	0.24	0.23	-0.06	-0.15	0.02	0	0	0.03	-0.02	-0.07
bio02	-0.17	0.1	0.1	-0.18	-0.48	-0.19	-0.1	0.11	-0.52	0.08
bio03	0.28	-0.12	0.14	0.08	-0.07	-0.04	0.02	-0.04	-0.12	0.05
bio04	-0.29	0.04	-0.08	-0.05	-0.08	-0.01	-0.05	0.26	0.24	-0.04
bio05	0.06	0.32	-0.06	-0.25	-0.12	-0.04	-0.03	0.09	-0.17	-0.1
bio06	0.31	0.07	0	0	0.15	0.05	0.05	-0.1	0.03	-0.05
bio07	-0.28	0.12	-0.04	-0.15	-0.23	-0.07	-0.07	0.15	-0.13	-0.01
bio08	0.15	0.27	-0.12	-0.18	-0.05	0	-0.05	0.29	0.25	-0.09
bio09	0.29	0.15	0	-0.08	0.04	0.01	0.03	-0.09	-0.14	-0.04
bio10	0.13	0.3	-0.11	-0.19	-0.01	0	-0.03	0.15	0.1	-0.12
bio11	0.29	0.14	0	-0.07	0.06	0.01	0.02	-0.1	-0.12	-0.03
bio12	0.2	-0.18	-0.3	0.11	-0.18	-0.08	-0.02	-0.02	-0.1	-0.03
bio13	0.03	-0.07	-0.57	0.1	-0.02	-0.05	0.03	-0.13	-0.15	-0.01
bio14	0.24	-0.19	0.1	0.06	-0.27	-0.07	-0.07	0.12	0.03	-0.08
bio15	-0.25	0.15	-0.26	-0.05	0.14	0.02	0.02	-0.11	-0.06	0
bio16	0.03	-0.08	-0.57	0.09	-0.04	-0.05	0.03	-0.12	-0.17	0
bio17	0.25	-0.19	0.1	0.06	-0.25	-0.06	-0.07	0.12	0.04	-0.08
bio18	-0.01	-0.23	-0.25	0.12	-0.23	-0.07	-0.1	0.36	0.42	0.01
bio19	0.26	-0.14	0.06	0.09	-0.17	-0.05	0.01	0.09	-0.07	-0.02
crop	-0.03	0.26	0.04	0.17	-0.25	-0.25	-0.14	-0.45	0.31	-0.05
elev	-0.22	-0.22	0.14	0.11	-0.06	-0.03	-0.02	-0.17	-0.16	0.06
grass	-0.05	0.12	0.02	0.26	-0.2	0.36	0.72	0.23	-0.12	-0.14
hlog	-0.03	0.21	0.01	0.41	0.19	-0.12	0.1	0.16	-0.02	0.09
ndvi	0.01	-0.26	-0.05	-0.33	0.23	0.01	0.15	0.17	-0.02	0.2
slope	-0.14	-0.23	0.03	-0.08	0.11	0.02	-0.04	-0.07	-0.07	-0.91
tree	0.04	-0.29	-0.04	-0.37	0.19	-0.01	-0.02	0.12	-0.08	0.12
urban	0.02	0.1	0.04	0.39	0.38	-0.31	-0.31	0.42	-0.31	-0.09
water	0.02	0.04	-0.05	0.14	-0.07	0.79	-0.53	0.03	-0.11	0.05

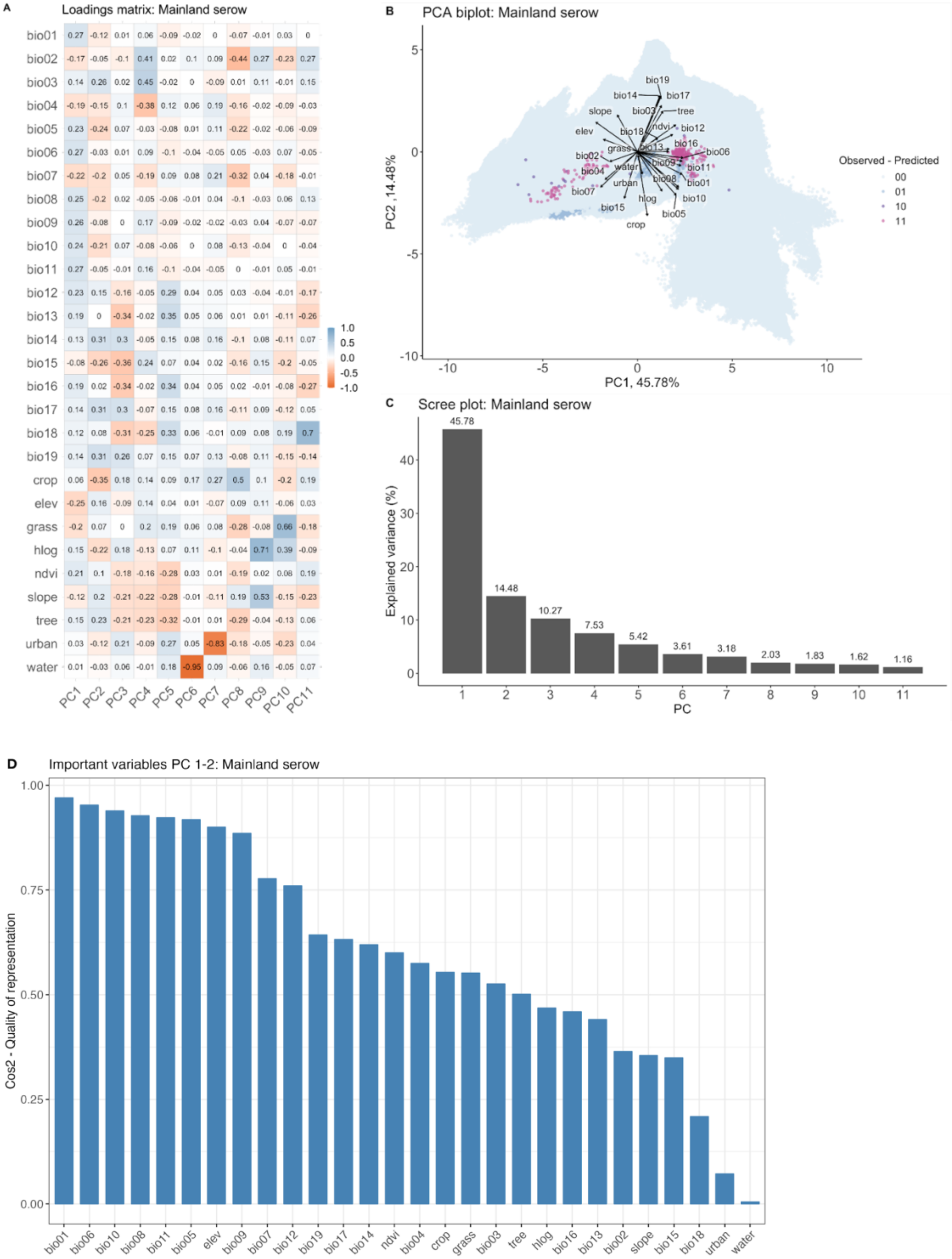
3. Wild water buffalo (*Bubalus arnee*)



A Loadings matrix: Wild water Buffalo

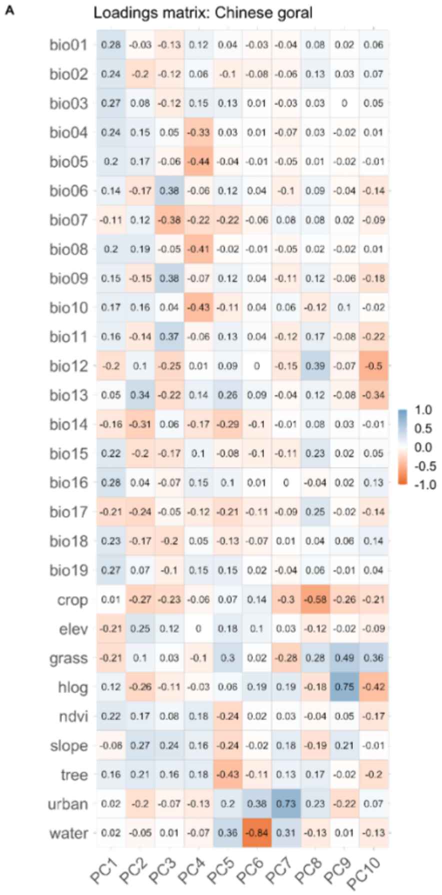
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13
bio01	-0.34	0.02	-0.02	-0.08	0.06	0.02	-0.02	-0.09	-0.03	-0.03	0.06	0	-0.07
bio02	-0.02	-0.31	-0.01	0.04	0.21	0.13	0.05	-0.02	0.13	-0.21	-0.17	0.27	0.15
bio03	-0.08	0.24	-0.33	-0.06	-0.12	0.1	0.08	0.11	0.12	-0.26	-0.17	0.34	0.05
bio04	0.1	-0.29	0.1	0.19	0.3	-0.03	-0.08	-0.1	-0.03	0.05	0.18	-0.1	0.02
bio05	-0.3	-0.15	0.01	-0.01	0.18	0.08	0.01	-0.1	0.03	0.03	0.01	-0.14	-0.02
bio06	-0.29	0.18	-0.09	-0.13	-0.1	0.02	0.02	-0.02	-0.01	0.02	0.03	-0.07	-0.1
bio07	0.03	-0.32	0.1	0.12	0.26	0.05	-0.01	-0.07	0.03	0	-0.02	-0.05	0.09
bio08	-0.3	-0.02	0.06	-0.04	0.17	-0.06	-0.09	-0.15	-0.15	-0.04	0.08	0.48	-0.15
bio09	-0.32	0.02	-0.09	-0.06	0.02	0.11	0.03	0	0.1	-0.01	-0.01	-0.3	-0.11
bio10	-0.32	-0.1	0.01	-0.01	0.18	0.04	-0.03	-0.12	-0.02	0.01	0.1	-0.11	-0.06
bio11	-0.31	0.13	-0.06	-0.14	-0.08	0.04	0.02	-0.02	0	-0.03	-0.03	0.01	-0.06
bio12	-0.03	0.31	0.25	0.19	0	0.06	0	0.03	-0.04	-0.15	0.05	-0.13	0
bio13	-0.05	0.23	0.38	0.24	-0.02	0.2	0.07	0.06	0.11	-0.09	-0.06	-0.13	-0.05
bio14	0.03	0.19	-0.35	0.31	0.33	0.01	-0.05	-0.02	-0.17	-0.05	-0.3	-0.1	-0.03
bio15	-0.13	-0.17	0.33	0.06	0.04	0.23	0.08	0.03	0.19	0.07	-0.58	0.26	-0.08
bio16	-0.05	0.24	0.38	0.22	-0.02	0.15	0.04	0.05	0.06	-0.11	-0.03	-0.15	-0.02
bio17	0.04	0.21	-0.33	0.32	0.32	-0.01	-0.05	-0.02	-0.19	0	-0.24	-0.1	-0.05
bio18	0.07	0.21	0.29	0.11	0.1	-0.23	-0.16	-0.08	-0.36	-0.27	0.2	0.37	0.01
bio19	0	0.16	-0.18	0.35	0.12	0.31	0.13	0.1	0.43	0.3	0.48	0.34	0.04
crop	-0.18	-0.15	0.02	0.2	-0.12	-0.24	0.14	0.57	-0.21	0.16	-0.11	0.13	-0.11
elev	0.33	-0.04	-0.03	0.02	-0.11	0.03	0.07	0.11	0.1	0.01	-0.14	0	0.05
grass	0.1	-0.05	-0.07	0.06	-0.31	0.5	0.28	-0.47	-0.45	0.08	-0.03	0.08	0.07
hlog	-0.21	-0.08	0.03	0.37	-0.22	-0.21	0.11	-0.08	-0.21	0.45	0.02	-0.01	0.1
ndvi	-0.05	0.27	0.12	-0.21	0.15	-0.16	0.12	-0.05	-0.02	0.46	-0.22	0.09	0.38
slope	0.26	0.11	0.06	-0.14	0.12	-0.03	0.02	-0.15	0.04	0.32	-0.07	0.09	-0.8
tree	0.06	0.27	0.12	-0.26	0.29	-0.07	-0.01	-0.18	0.11	0.19	-0.05	-0.01	0.28
urban	-0.05	0	-0.06	0.33	-0.32	-0.44	-0.15	-0.51	0.42	-0.09	-0.17	0.04	-0.01
water	-0.01	0.01	-0.01	0.02	-0.17	0.31	-0.87	0.1	-0.05	0.25	-0.09	0.05	0.07

4. Mainland serow (*Capricornis sumatraensis*)



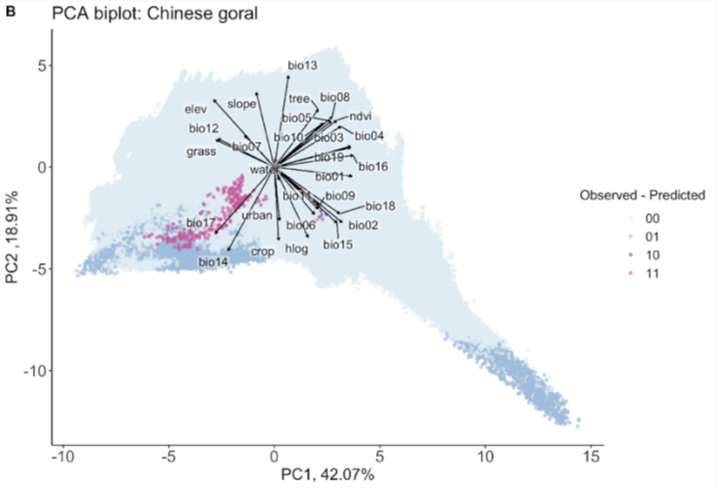
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
bio01	0.27	-0.12	0.01	0.06	-0.09	-0.02	0	-0.07	-0.01	0.03	0
bio02	-0.17	-0.05	-0.1	0.41	0.02	0.1	0.09	-0.44	0.27	-0.23	0.27
bio03	0.14	0.26	0.02	0.45	-0.02	0	-0.09	0.01	0.11	-0.01	0.15
bio04	-0.19	-0.15	0.1	-0.38	0.12	0.06	0.19	-0.16	-0.02	-0.09	-0.03
bio05	0.23	-0.24	0.07	-0.03	-0.08	0.01	0.11	-0.22	-0.02	-0.06	-0.09
bio06	0.27	-0.03	0.01	0.09	-0.1	-0.04	-0.05	0.05	-0.03	0.07	-0.05
bio07	-0.22	-0.2	0.05	-0.19	0.09	0.08	0.21	-0.32	0.04	-0.18	-0.01
bio08	0.25	-0.2	0.02	-0.05	-0.06	-0.01	0.04	-0.1	-0.03	0.06	0.13
bio09	0.26	-0.08	0	0.17	-0.09	-0.02	-0.02	-0.03	0.04	-0.07	-0.07
bio10	0.24	-0.21	0.07	-0.08	-0.06	0	0.08	-0.13	-0.04	0	-0.04
bio11	0.27	-0.05	-0.01	0.16	-0.1	-0.04	-0.05	0	-0.01	0.05	-0.01
bio12	0.23	0.15	-0.16	-0.05	0.29	0.04	0.05	0.03	-0.04	-0.01	-0.17
bio13	0.19	0	-0.34	-0.02	0.35	0.05	0.06	0.01	0.01	-0.11	-0.26
bio14	0.13	0.31	0.3	-0.05	0.15	0.08	0.16	-0.1	0.08	-0.11	0.07
bio15	-0.08	-0.26	-0.36	0.24	0.07	0.04	0.02	-0.16	0.15	-0.2	-0.05
bio16	0.19	0.02	-0.34	-0.02	0.34	0.04	0.05	0.02	-0.01	-0.08	-0.27
bio17	0.14	0.31	0.3	-0.07	0.15	0.08	0.16	-0.11	0.09	-0.12	0.05
bio18	0.12	0.08	-0.31	-0.25	0.33	0.06	-0.01	0.09	0.08	0.19	0.7
bio19	0.14	0.31	0.26	0.07	0.15	0.07	0.13	-0.08	0.11	-0.15	-0.14
crop	0.06	-0.35	0.18	0.14	0.09	0.17	0.27	0.5	0.1	-0.2	0.19
elev	-0.25	0.16	-0.09	0.14	0.04	0.01	-0.07	0.09	0.11	-0.06	0.03
grass	-0.2	0.07	0	0.2	0.19	0.06	0.08	-0.28	-0.08	0.66	-0.18
hlog	0.15	-0.22	0.18	-0.13	0.07	0.11	-0.1	-0.04	0.71	0.39	-0.09
ndvi	0.21	0.1	-0.18	-0.16	-0.28	0.03	0.01	-0.19	0.02	0.08	0.19
slope	-0.12	0.2	-0.21	-0.22	-0.28	-0.01	-0.11	0.19	0.53	-0.15	-0.23
tree	0.15	0.23	-0.21	-0.23	-0.32	-0.01	0.01	-0.29	-0.04	-0.13	0.06
urban	0.03	-0.12	0.21	-0.09	0.27	0.05	-0.83	-0.18	-0.05	-0.23	0.04
water	0.01	-0.03	0.06	-0.01	0.18	-0.95	0.09	-0.06	0.16	-0.05	0.07

5. Chinese goral (*Naemorhedus griseus*)

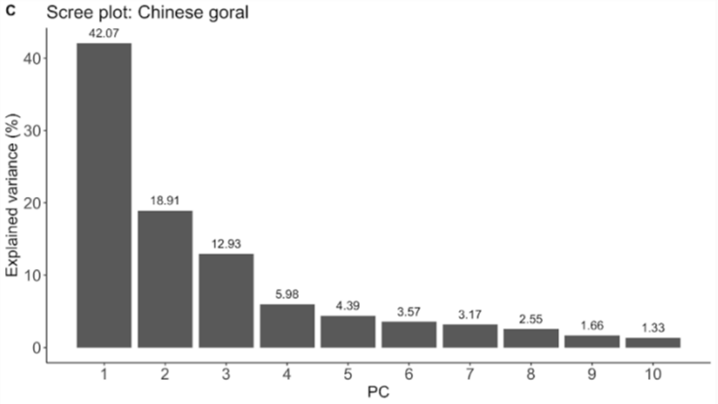


Loadings matrix: Chinese goral

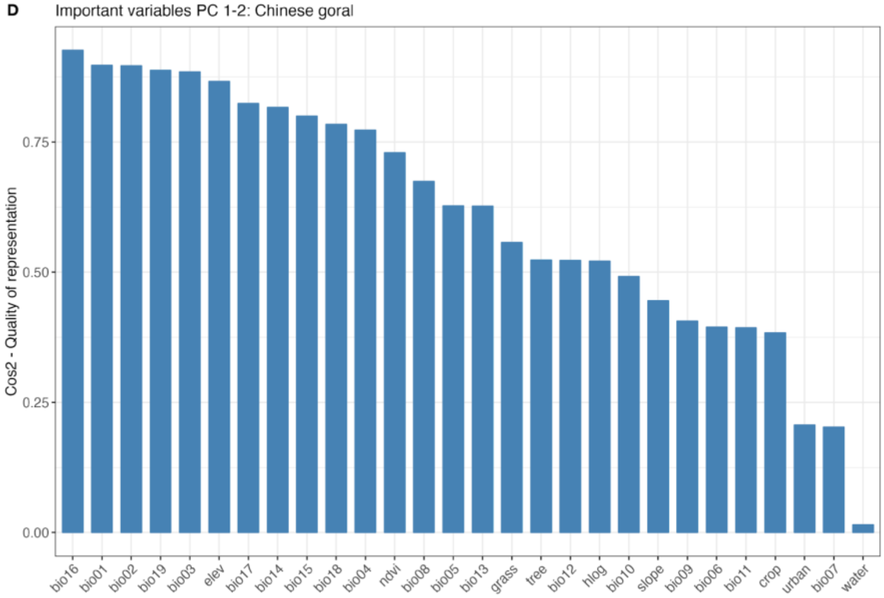
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
bio01	0.28	-0.03	-0.13	0.12	0.04	-0.03	-0.04	0.08	0.02	0.06
bio02	0.24	-0.2	-0.12	0.06	-0.1	-0.08	-0.06	0.13	0.03	0.07
bio03	0.27	0.08	-0.12	0.15	0.13	0.01	-0.03	0.03	0	0.05
bio04	0.24	0.15	0.05	-0.33	0.03	0.01	-0.07	0.03	-0.02	0.01
bio05	0.2	0.17	-0.06	-0.44	-0.04	-0.01	-0.05	0.01	-0.02	-0.01
bio06	0.14	-0.17	0.38	-0.06	0.12	0.04	-0.1	0.09	-0.04	-0.14
bio07	-0.11	0.12	-0.38	-0.22	-0.22	-0.06	0.08	0.08	0.02	-0.09
bio08	0.2	0.19	-0.05	-0.41	-0.02	-0.01	-0.05	0.02	-0.02	0.01
bio09	0.15	-0.15	0.38	-0.07	0.12	0.04	-0.11	0.12	-0.06	-0.18
bio10	0.17	0.16	0.04	-0.43	-0.11	0.04	0.06	-0.12	0.1	-0.02
bio11	0.16	-0.14	0.37	-0.06	0.13	0.04	-0.12	0.17	-0.08	-0.22
bio12	-0.2	0.1	-0.25	0.01	0.09	0	-0.15	0.39	-0.07	-0.5
bio13	0.05	0.34	-0.22	0.14	0.26	0.09	-0.04	0.12	-0.08	-0.34
bio14	-0.16	-0.31	0.06	-0.17	-0.29	-0.1	-0.01	0.08	0.03	-0.01
bio15	0.22	-0.2	-0.17	0.1	-0.08	-0.1	-0.11	0.23	0.02	0.05
bio16	0.28	0.04	-0.07	0.15	0.1	0.01	0	-0.04	0.02	0.13
bio17	-0.21	-0.24	-0.05	-0.12	-0.21	-0.11	-0.09	0.25	-0.02	-0.14
bio18	0.23	-0.17	-0.2	0.05	-0.13	-0.07	0.01	0.04	0.06	0.14
bio19	0.27	0.07	-0.1	0.15	0.15	0.02	-0.04	0.06	-0.01	0.04
crop	0.01	-0.27	-0.23	-0.06	0.07	0.14	-0.3	-0.58	-0.26	-0.21
elev	-0.21	0.25	0.12	0	0.18	0.1	0.03	-0.12	-0.02	-0.09
grass	-0.21	0.1	0.03	-0.1	0.3	0.02	-0.28	0.28	0.49	0.36
hlog	0.12	-0.26	-0.11	-0.03	0.06	0.19	0.19	-0.18	0.75	-0.42
ndvi	0.22	0.17	0.08	0.18	-0.24	0.02	0.03	-0.04	0.05	-0.17
slope	-0.06	0.27	0.24	0.16	-0.24	-0.02	0.18	-0.19	0.21	-0.01
tree	0.16	0.21	0.16	0.18	-0.43	-0.11	0.13	0.17	-0.02	-0.2
urban	0.02	-0.2	-0.07	-0.13	0.2	0.38	0.73	0.23	-0.22	0.07
water	0.02	-0.05	0.01	-0.07	0.36	-0.84	0.31	-0.13	0.01	-0.13



PCA biplot: Chinese goral



Scree plot: Chinese goral



Important variables PC 1-2: Chinese goral

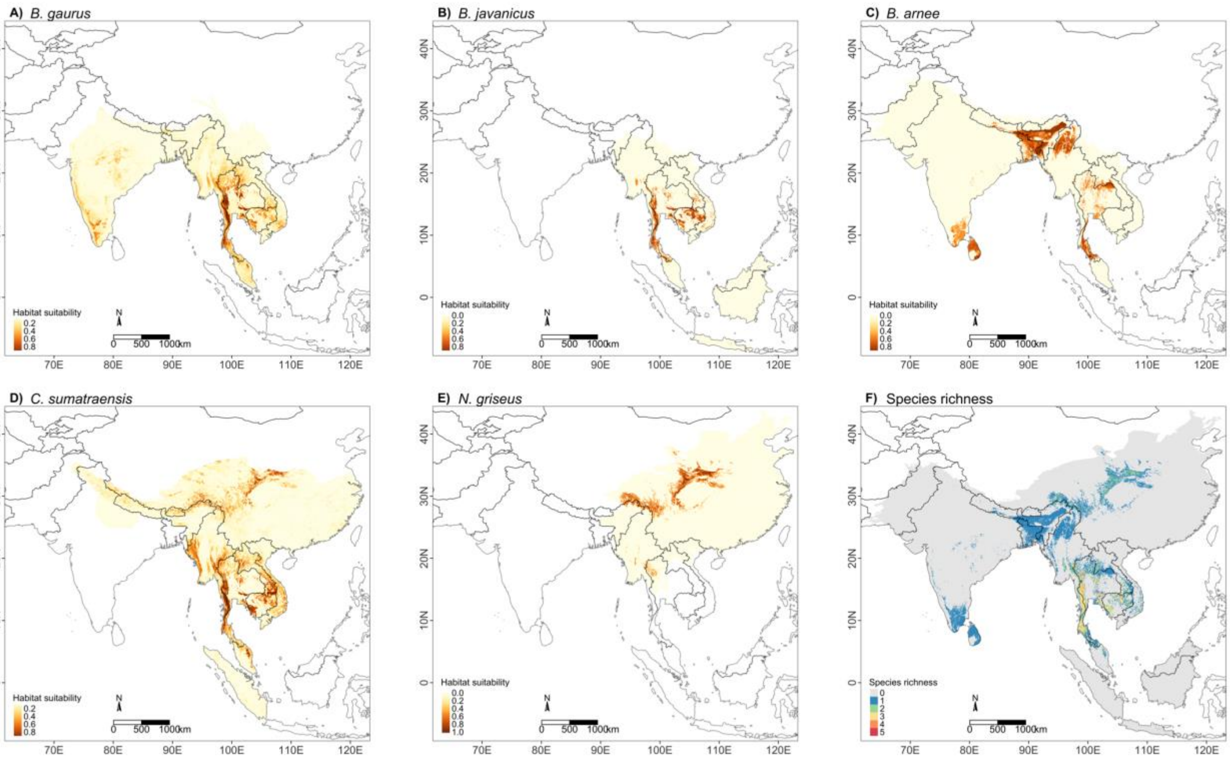


Figure S1.2 Habitat suitability prediction maps of the best-performing models for five species using species-specific accessible areas and weighted average ensemble models (A-E). The value ranges from 0 – 1: yellow represents low suitability and dark brown represents high suitability. (F) presents the species richness map for five species using the binary suitability results, ranging from 0 (not suitable area for the five species) to 5 (suitable area for all five species).

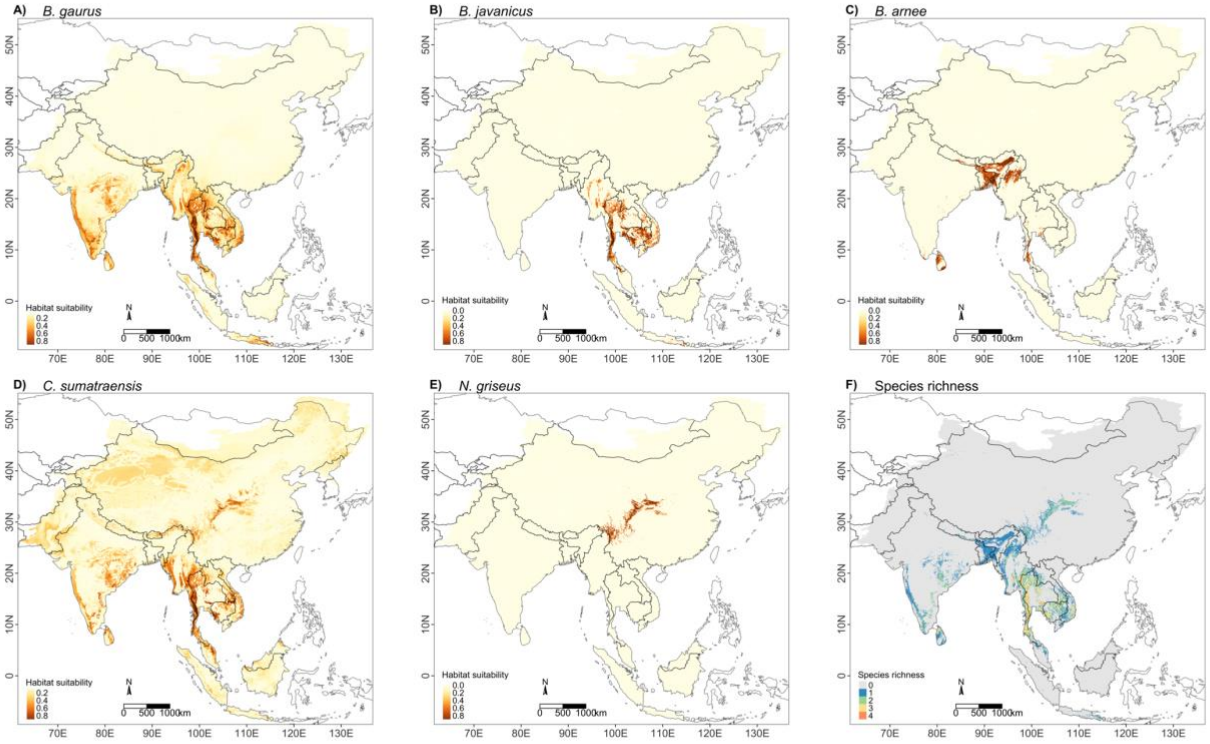


Figure S1.3 Habitat suitability prediction maps for five species using the large accessible area (A-E). The value ranges from 0 – 1: yellow represents low suitability and dark brown represents high suitability. (F) Species richness map for five species which range from 0 (no suitable area for the five species) to 4 (suitable area for four species), which is the highest value range for the large accessible area model predictions.

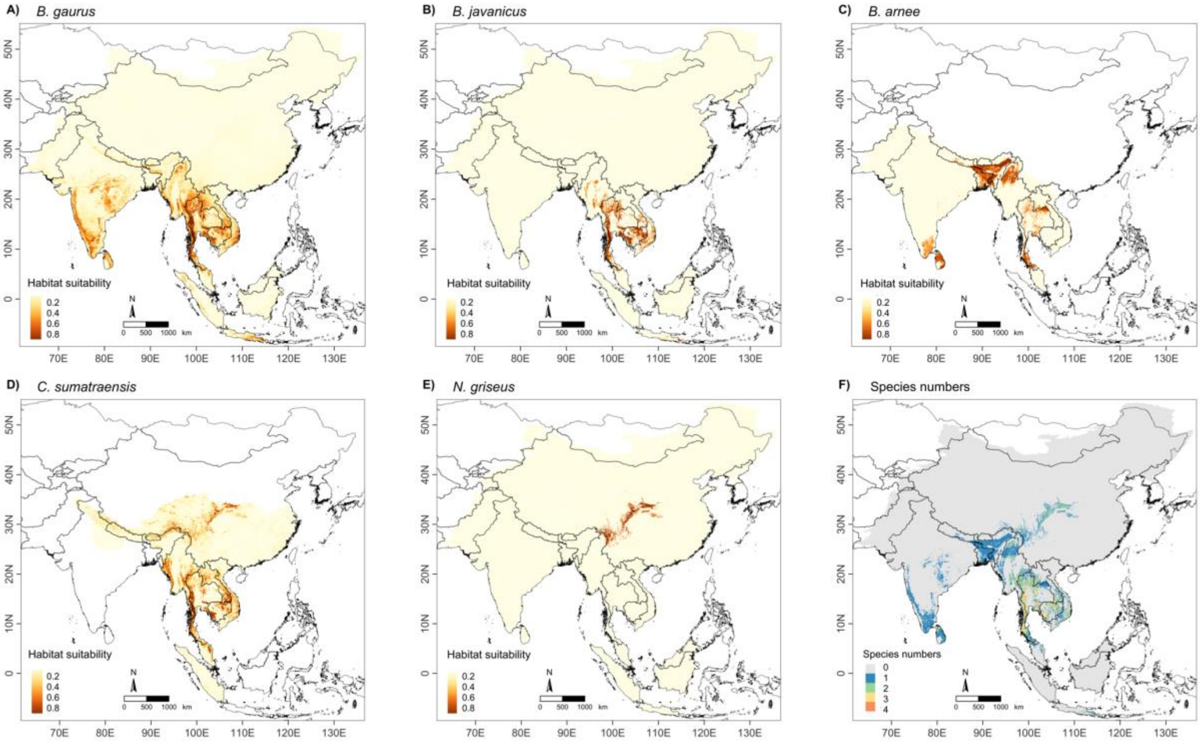


Figure S1.4 Habitat suitability prediction maps for five species using the best model from either accessible areas and the weighted average ensemble (A-E). The value ranges from 0 – 1: yellow represents low suitability and dark brown represents high suitability. (F) presents the map of species numbers for five species using the binary suitability results, ranging from 0 (not suitable area for the five species) to 4 (suitable area for four species), which is the highest value range for the best model predictions. Interactive maps are provided in the supplementary material (link).

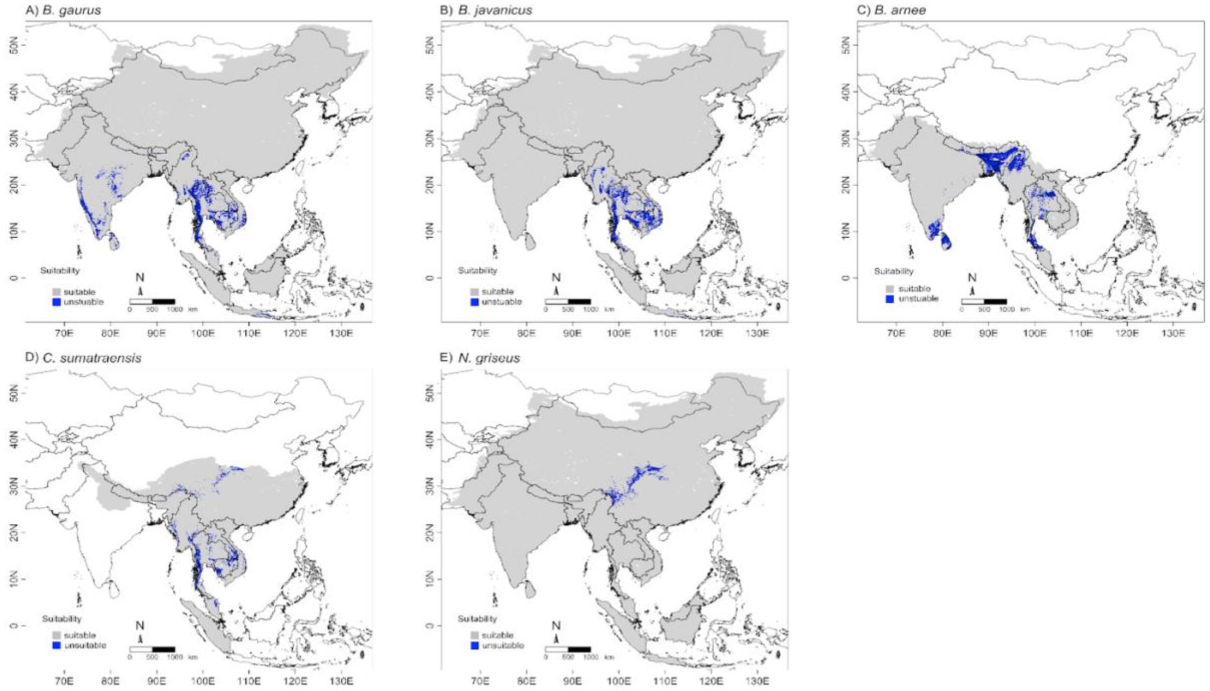


Figure S1.5 The best TSS models of binary maps of suitable areas for five bovid species (A-E). The grey colour is unsuitable and blue is suitable areas.

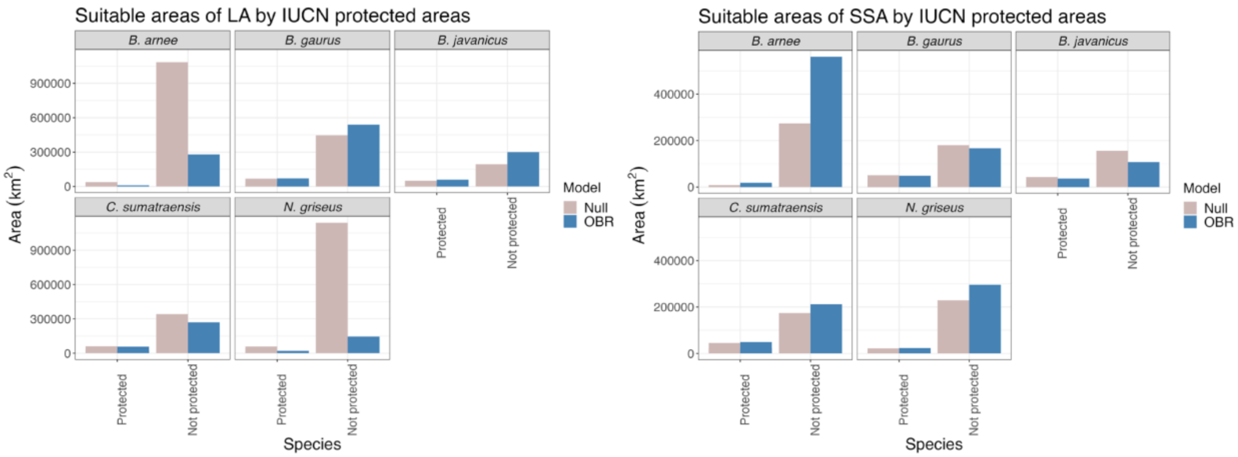


Figure S1.6 The suitable area for five species classified by spatially restrictions: Null (No MSDM; pink) and OBR (occurrences-based threshold; blue) in both IUCN protected areas (PA) and non PA between two types of accessible areas (A) LA and (B) SSA and All models have the suitable areas outside IUCN PA, and the largest one outside PAs is *B.arneee*. OBR has similar results with Null in *B. gaurs, B. javanicus and C. sumatraensis* but show a huge difference for *B. arnee* (both LA and SSA) and *N. griseus* (LA). Thus, we recommend using the SSA for confined species to increase the model precision.

Table S1.5 Suitable areas calculated from the best model and classified by country.

			Species-specific accessible areas		Large accessible areas	
		Country area	Suitable area per country		Suitable area per country	
species	Country	(sq.km)	(sq.km)	(%)	(sq.km)	(%)
Gaur	Bangladesh	147,570	0	0	180	0
(*Bos gaurus*)	Bhutan	38,394	0	0	117	0
	Cambodia	181,035	38,465	13	59,140	10
	China	9,706,961	0	0	1	0
	India	3,287,590	44,856	15	176,830	29
	Indonesia	1,904,569	0	0	14,090	2
	Laos	236,800	21,838	7	41,553	7
	Malaysia	329,847	5,285	2	3,389	1
	Myanmar	676,578	45,829	15	97,763	16
	Nepal	147,181	1	0	2,097	0
	Sri Lanka	65,610	0	0	12,475	2
	Thailand	513,120	138,892	46	177,216	29
	Vietnam	331,210	7,853	3	26,343	4
	Total		**303,019**	**100**	**611,192**	**100**
Banteng	Bangladesh	147,570	35	0	0	0
(*Bos javanicus*)	Brunei Darussalam	5,765	0	0	0	0
	Cambodia	181,035	68,463	24	87,388	20
	China	9,706,961	20	0	5	0
	India	3,287,590	4	0	0	0
	Indonesia	1,904,569	5,209	2	10,801	2
	Laos	236,800	14,337	5	31,742	7
	Malaysia	329,847	5,985	2	4,652	1
	Myanmar	676,578	39,596	14	78,203	18
	Thailand	513,120	125,307	44	180,275	40
	Vietnam	331,210	23,761	8	52,150	12
	Total		**282,717**	**100**	**445,216**	**100**
Wild water buffalo	Bangladesh	147,570	90,097	15	75,175	25
(*Bubalus arnee*)	Bhutan	38,394	846	0	324	0
	Cambodia	181,035	283	0	14	0
	China	9,706,961	546	0	106	0
	India	3,287,590	213,247	35	106,149	35
	Laos	236,800	16,353	3	244	0
	Malaysia	329,847	3,744	1	0	0
	Myanmar	676,578	99,844	16	63,246	21
	Nepal	147,181	11,729	2	5,642	2
	Sri Lanka	65,610	43,010	7	27,254	9
	Thailand	513,120	135,552	22	28,450	9
	Total		**615,250**	**100**	**306,603**	**100**
Mainland serow	Bangladesh	147,570	9	0	6	0
(*Capricornis sumatraensis*)	Bhutan	5,765	1,167	0	1,178	0
	Cambodia	181,035	40,718	14	31,572	7
	China	9,706,961	55,528	19	60,890	13
	India	3,287,590	5,709	2	84,742	18
	Indonesia	1,904,569	3	0	1,259	0
	Laos	236,800	37,884	13	27,309	6
	Malaysia	329,847	7,318	2	11,170	2
	Myanmar	676,578	66,892	23	122,728	26
	Nepal	147,181	275	0	305	0
	Sri Lanka	65,610	0	0	9,895	2
	Thailand	513,120	68,534	23	109,782	23
	Vietnam	331,210	9,708	3	19,784	4
	Total		**293,746**	**100**	**480,620**	**100**
Chinese goral	China	9,706,961	285,073	86	162,929	96
(*Naemorhedus griseus*)	India	3,287,590	15,413	5	1,067	1
	Myanmar	676,578	16,369	5	5,884	3
	Thailand	513,120	14,847	4	0	0
	Total		**331,701**	**100**	**169,881**	**100**

Table S1.6 Suitable areas classified by IUCN protected area categories 1 to 7, not applicable and non protected areas.

		Species-specific accessible areas			**Large accessible areas**		
			Suitable areas overlap with IUCN category			**Suitable areas overlap with IUCN category**	
species	IUCN protected areas category	Model	(sq.km)	%	Model	(sq.km)	%
Gaur	IUCN PA Ia, Ib	No MSDM	28,904	10	No MSDM	39,219	6
(Bos gaurus)	IUCN PA II		50,497	17		67,587	11
	IUCN PA III		3,919	1		291	0
	IUCN PA IV		17,714	6		31,345	5
	IUCN PA V		492	0		607	0
	IUCN PA VI		14,689	5		19,986	3
	Not applicable		6,570	2		7,057	1
	Not protected area		180,380	60		446,456	73
	Total		303,165	100		612,548	100
Banteng	IUCN PA Ia, Ib	No MSDM	21,987	8	OBR	30,500	7
(Bos javanicus)	IUCN PA II		42,459	15		57,894	13
	IUCN PA III		4,141	1		253	0
	IUCN PA IV		30,649	11		32,650	7
	IUCN PA V		2,646	1		520	0
	IUCN PA VI		19,852	7		21,879	5
	Not applicable		6,272	2		2,094	0
	Not protected area		156,505	55		300,285	67
	Total		284,510	100		446,075	100
Wild water buffalo	IUCN PA Ia, Ib	OBR	16,623	3	OBR	8,815	3
(Bubalus arnee)	IUCN PA II		17,677	3		8,551	3
	IUCN PA III		0	0		0	0
	IUCN PA IV		12,521	2		4,137	1
	IUCN PA V		19	0		8	0
	IUCN PA VI		2,528	0		505	0
	Not applicable		6,010	1		5,746	2
	Not protected area		560,521	91		279,180	91
	Total		615,899	100		306,942	100
Mainland serow *(Capricornis sumatraensis*)	IUCN PA Ia, Ib	No MSDM	23,034	8	No MSDM	35,965	7
	IUCN PA II		44,754	15		59,875	12
	IUCN PA III		1,344	0		349	0
	IUCN PA IV		18,760	6		16,894	4
	IUCN PA V		2,683	1		265	0
	IUCN PA VI		19,960	7		14,170	3
	Not applicable		9,195	3		11,995	2
	Not protected area		174,153	59		341,728	71
	Total		293,883	100		481,241	100
Chinese goral *(Naemorhedus griseus*)	IUCN PA Ia, Ib	OBR	3,368	1	OBR	0	0
	IUCN PA II		6,635	2		2,886	2
	IUCN PA III		0	0		0	0
	IUCN PA IV		611	0		33	0
	IUCN PA V		0	0		0	0
	IUCN PA VI		1,250	0		985	1
	Not applicable		23,749	7		20,332	12
	Not protected area		296,091	89		145,646	86
	Total		331,704	100		169,882	100

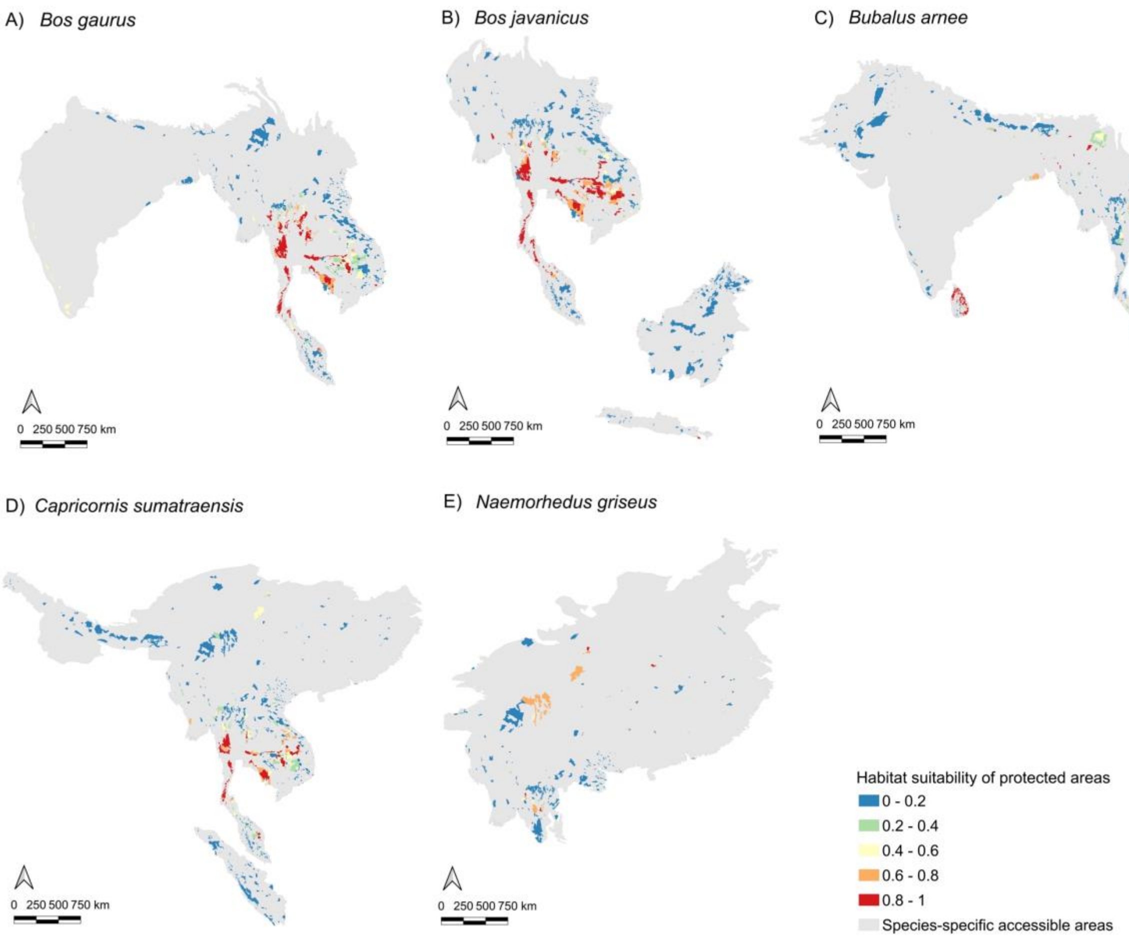


Figure S1.7 The proportion of suitable areas for five species and their best performing models. The values ranges from 0 (unsuitable) to 1 (high proportion of suitable) with species accessible area model. (A) Guar (*Bos gaurus*), (B) Banteng (*Bos javanicus*), (C) wild water buffalo (*Bubalus arnee*), (D) mainland serow (*Capricornis sumatraensis*), and (E) Chinese goral (*Naemorhedus griseus*).

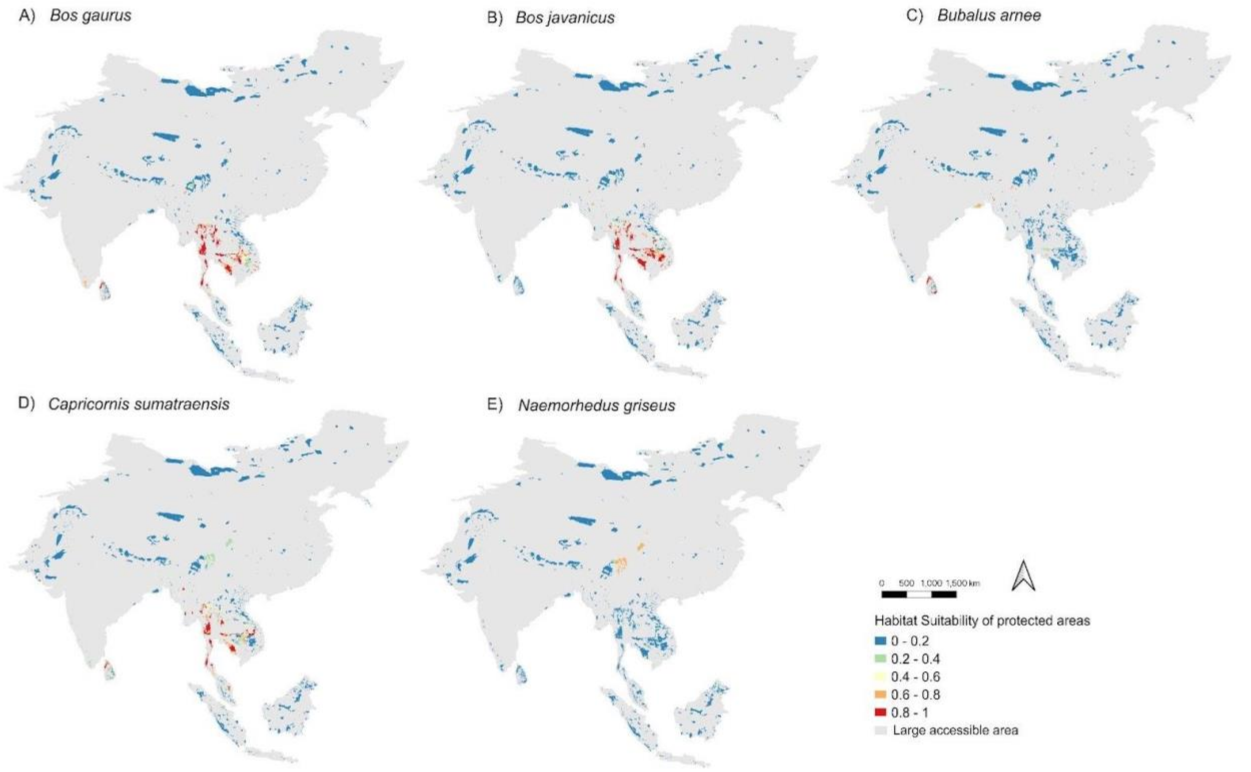


Figure S1.8 The proportion of suitable areas for five species and their best performing models range from 0 (unsuitable) to 1 (high proportion of suitable) with large accessible area models: (A) Guar (*Bos gaurus*), (B) Banteng (*Bos javanicus*), (C) wild water buffalo (*Bubalus arnee*), (D) mainland serow (*Capricornis sumatraensis*), and (E) Chinese goral (*Naemorhedus griseus*).

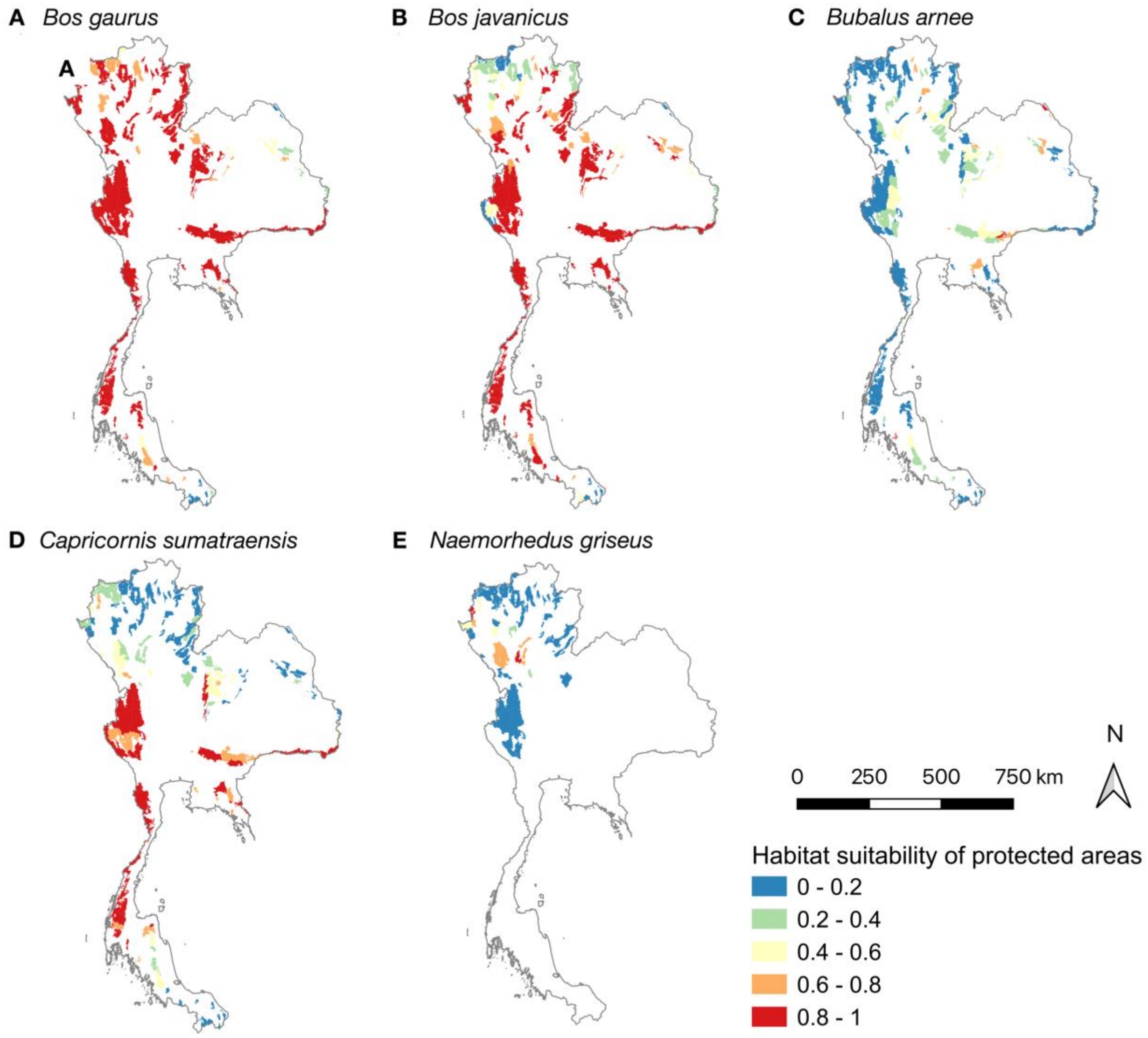
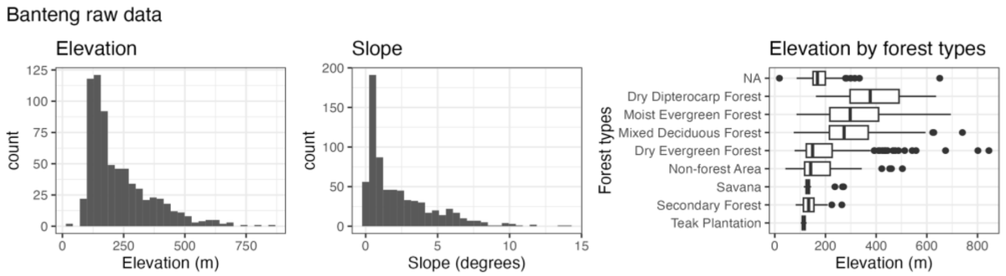


Figure S1.9 The proportion of suitable areas focusing on Thailand range from 0 (unsuitable) to 1 (high proportion of suitable) PAs for five species and their best performing models: (A) Guar (*Bos gaurus*), (B) Banteng (*Bos javanicus*), (C) wild water buffalo (*Bubalus arnee*), (D) mainland serow (*Capricornis sumatraensis*), and (E) Chinese goral (*Naemorhedus griseus*).

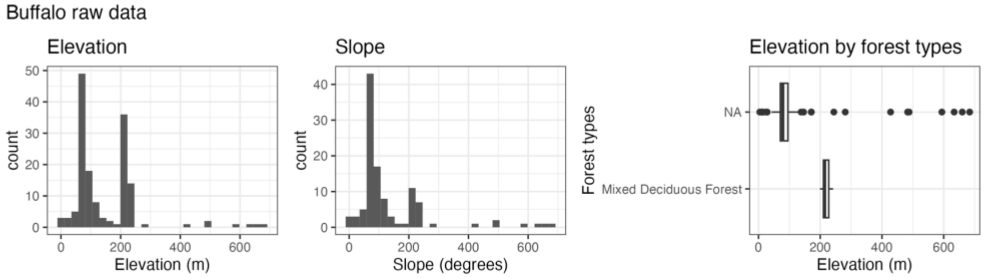
A)



Banteng

Forest type	Number of observation
NA	68
Dry Dipterocarp Forest	16
Moist Evergreen Forest	72
Mixed Deciduous Forest	174
Dry Evergreen Forest	241
Non-forest Area	44
Savana	20
Secondary Forest	63
Teak Plantation	2
Total	700

B)



Buffalo

Forest type	Number of observation
Mixed Deciduous Forest	50
NA	100
Total	150

Figure S 1.10 Histograms and boxplots of the raw observation data for banteng (A) and wild water buffalo (B). Based on the modelling, our suitable habitat for banteng and wild water buffalo have predicted highly suitable areas at high elevation in some forests, and less likely, suitable habitat from what we consider for banteng and wild water buffalo, such as in montane forest. To better understand the model prediction, we used Thai forest types and plotted the raw data of elevation and slope and the number of observations of each forest type. The raw data show here: (A) For banteng, the elevation ranged from 18 – 801 meters, and slope ranged from 0.03 – 14 degrees, with the highest number of observations found in dry dipterocarp forest and moist evergreen and mixed deciduous forest. (B) For wild water buffalo, the elevation ranged from 4 – 684 meters, and slope ranged from 0.02 – 9 degrees with observations mainly found in mixed deciduous forest. NA in the boxplot means the locations outside Thailand. These forest types, elevation and slope are within the typical species distribution. So, based on the important variables in the PCA (Table S2 – the loading factor and Figure S2 (D) – variable contribution to model building), we assume that the model used bioclimatic variables as the main predictors rather than topographic variables like elevation and slope.

Appendix 2

Impact of Infectious Diseases on Wild Bovidae Populations in Thailand: Insights from Population Modelling and Disease Dynamics

Includes:

- Population dynamics model results (Figure S2.1)
- Infectious disease model structures and results (Figure S2.2 – S2.16)
- The average of the total population changes for all models (Table S2.1)
- PCA biplot (Figure S2.17-S2.18)

Abbreviation

Symbol	Description
N_0	Starting total population
S	Susceptible
E	Exposed
I	Infected
R	Recovered
M	Calves with maternally derived immunity
a	Adult
sa	Subadult
C	Calf
μ_b	Birth rate
μ_a	Adult death rate
μ_{sa}	Subadult death rate
μ_c	Calf death rate
δ	Ageing rate
β	Disease transmission rate
σ	1/Incubation period
γ	Infectious period
ρ	Disease-induced fatality
α	Infected female will produce infected calf
μ_{bI}	Birth rate for infectious individuals
ω	Loss of immunity for calves
ω_m	Waning of maternal immunity
ϵ	External force of infection rate
$*$	Rescaling of the transmission mode

Model structures and results

All models used three age structures (adult, subadult and calf). For more details of the disease parameters and values, see the main text.

1. Population dynamics

The population dynamics model included demography (birth, death and ageing rate), and no infection importation.

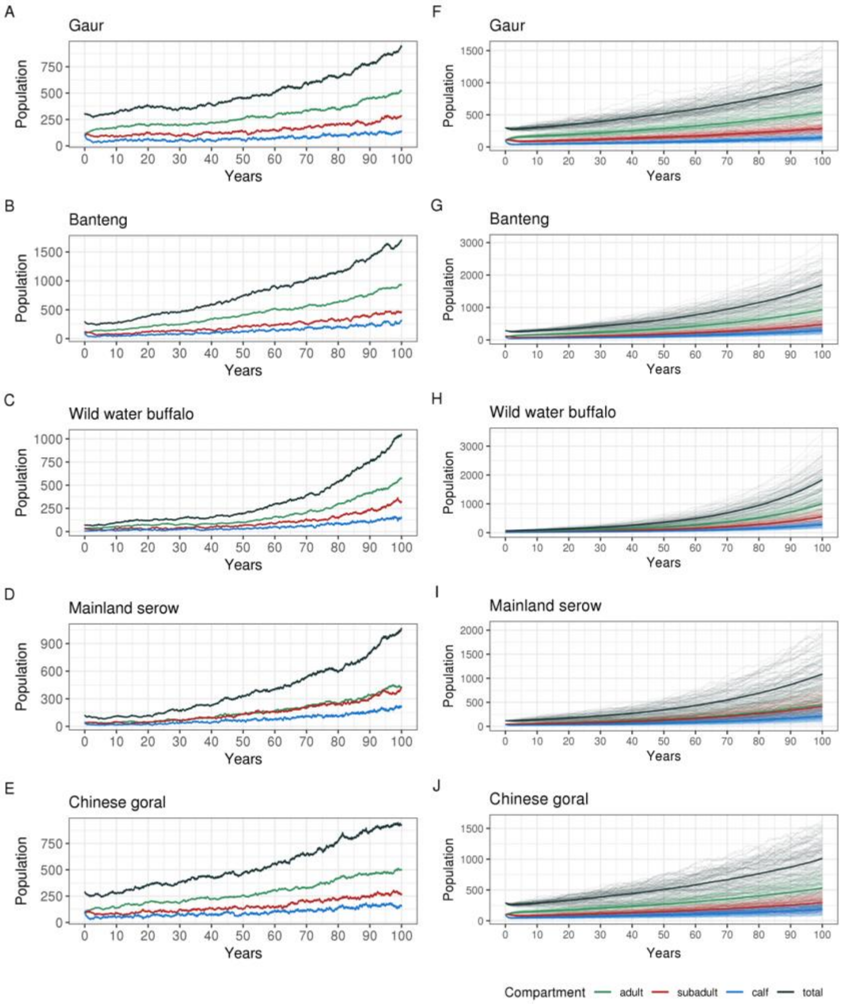


Figure S2.1 Single and 100 stochastic simulations of population dynamics for five wild bovids. A-E are single simulations; F-J are 100 simulations.

2. Infectious disease models

The population dynamics model with demography and infection importation (using infectious (I) = 1 for all models). The rescaled (*) β rates were used to examine the consistency of the results between frequency-dependent (FD) and density-dependent (DD).

Anthrax (*Bacillus anthracis*)

The SI model for anthrax with a 100% fatality rate (all infected will die).

$$
\begin{aligned}
N &= S_c + I_c + S_{sa} + I_{sa} + S_a + I_a \\
\frac{dS_c}{dt} &= \mu_b S_a - \beta_c S_c (I_c + I_{sa} + I_a) - \delta_c S_c - \mu_c S_c - \epsilon S_c \\
\frac{dS_{sa}}{dt} &= -\beta_{sa} S_{sa} (I_c + I_{sa} + I_a) + \delta_c S_c - \delta_{sa} S_{sa} - \mu_{sa} S_{sa} - \epsilon S_{sa} \\
\frac{dS_a}{dt} &= -\beta_a S_a (I_c + I_{sa} + I_a) + \delta_{sa} S_{sa} - \mu_a S_a - \epsilon S_a \\
\frac{dI_c}{dt} &= \beta_c S_c (I_c + I_{sa} + I_a) - \rho_c I_c + \epsilon S_c \\
\frac{dI_{sa}}{dt} &= \beta_{sa} S_{sa} (I_c + I_{sa} + I_a) - \rho_{sa} I_{sa} + \epsilon S_{sa} \\
\frac{dI_a}{dt} &= \beta_a S_a (I_c + I_{sa} + I_a) - \rho_a I_a + \epsilon S_a
\end{aligned}
\tag{1}
$$

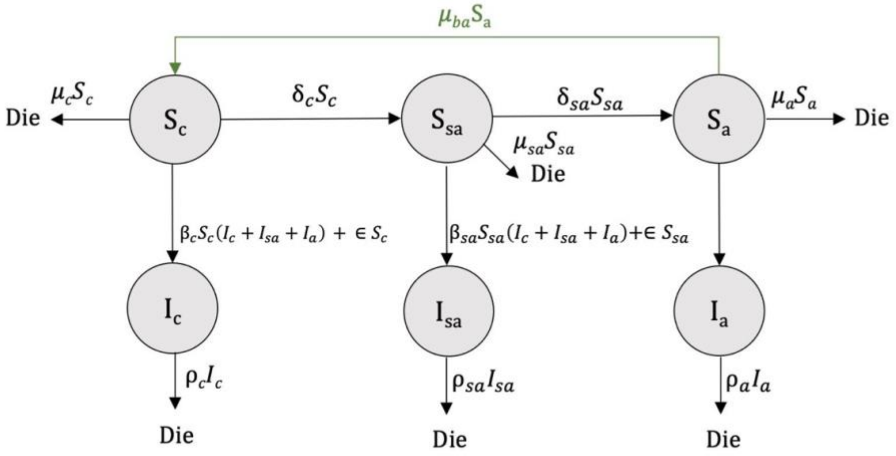
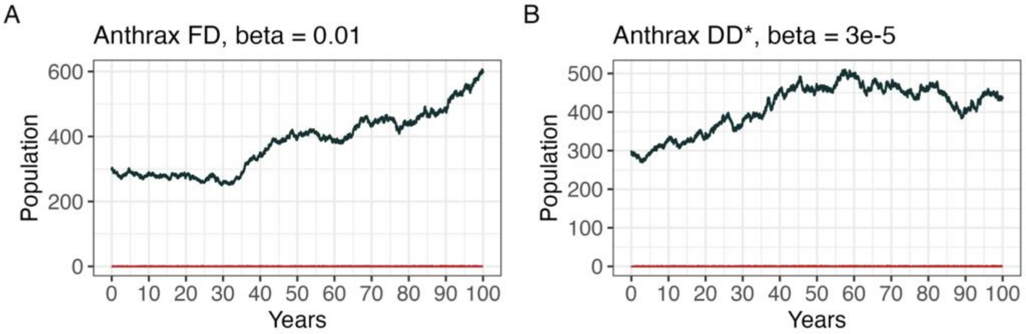


Figure S2.2 SI model diagram of anthrax.

1 simulation



100 simulations

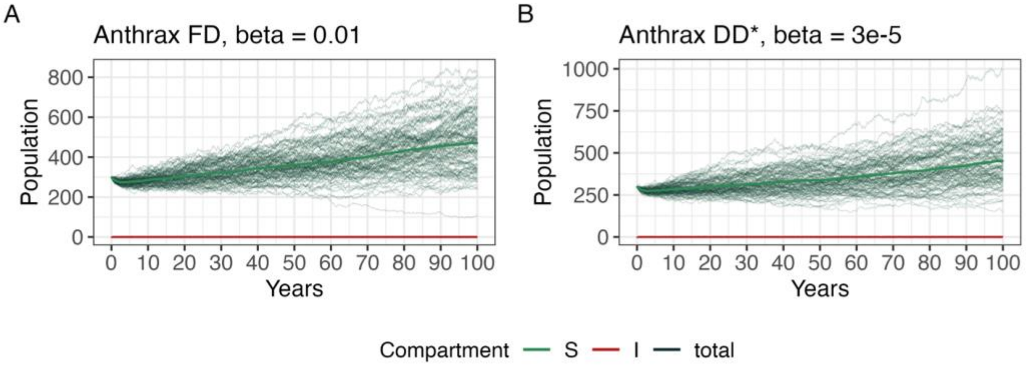


Figure S2.3 Single and 100 stochastic simulations of anthrax show that the population has increased with a few outbreak events, indicating rare animal-to-animal transmission. Changing the β rate (from 0.01 to 3e-5) slightly affects the total population.

Bovine tuberculosis (bTB - *Mycobacterium bovis*)

The *SEI* model for bTB included a lifelong infection with no recovery state. Therefore, an infected individual will remain in the infectious state until die either from disease-induced or natural death.

$$
\begin{aligned}
N &= S_c + E_c + I_c + S_{sa} + E_{sa} + I_{sa} + S_a + E_a + I_a \\
\frac{dS_c}{dt} &= \mu_b(S_a + E_a) + \mu_{bI} I_a - \beta_c S_c(I_c + I_{sa} + I_a) - \delta_c S_c - \mu_c S_c - \epsilon S_c \\
\frac{dS_{sa}}{dt} &= -\beta_{sa} S_{sa}(I_c + I_{sa} + I_a) + \delta_c S_c - \delta_{sa} S_{sa} - \mu_{sa} S_{sa} - \epsilon S_{sa} \\
\frac{dS_a}{dt} &= -\beta_a S_a(I_c + I_{sa} + I_a) + \delta_{sa} S_{sa} - \mu_a S_a - \epsilon S_a \\
\frac{dE_c}{dt} &= \beta_c S_c(I_c + I_{sa} + I_a) - \sigma_c E_c - \delta_c E_c - \mu_c E_c + \epsilon S_c \\
\frac{dE_{sa}}{dt} &= \beta_{sa} S_{sa}(I_c + I_{sa} + I_a) - \sigma_{sa} E_{sa} + \delta_c E_c - \delta_{sa} E_{sa} - \mu_{sa} E_{sa} + \epsilon S_{sa} \\
\frac{dE_a}{dt} &= \beta_a S_a(I_c + I_{sa} + I_a) - \sigma_a E_a + \delta_{sa} E_{sa} - \mu_a E_a + \epsilon S_a \\
\frac{dI_c}{dt} &= \sigma_c E_c - (\rho_c + \mu_I) I_c - \delta_c Ic \\
\frac{dI_{sa}}{dt} &= \sigma_{sa} E_{sa} - (\rho_{sa} + \mu_{sa}) I_{sa} + \delta_c Ic - \delta_{sa} Isa \\
\frac{dI_a}{dt} &= \sigma_a E_a - (\rho_{sa} + \mu_a) I_a + \delta_{sa} Isa
\end{aligned}
\tag{2}
$$

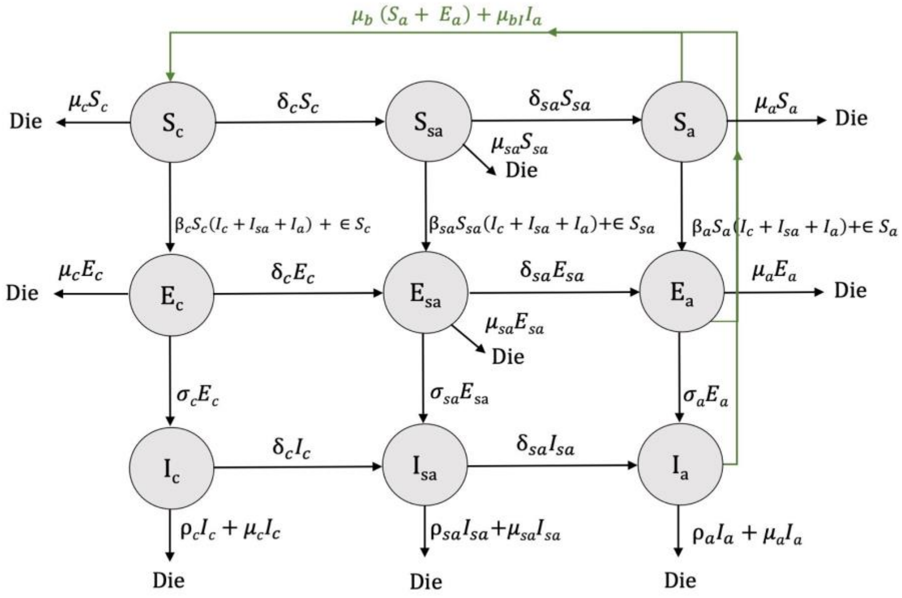


Figure S2.4 *SEI* model diagram of bTB.

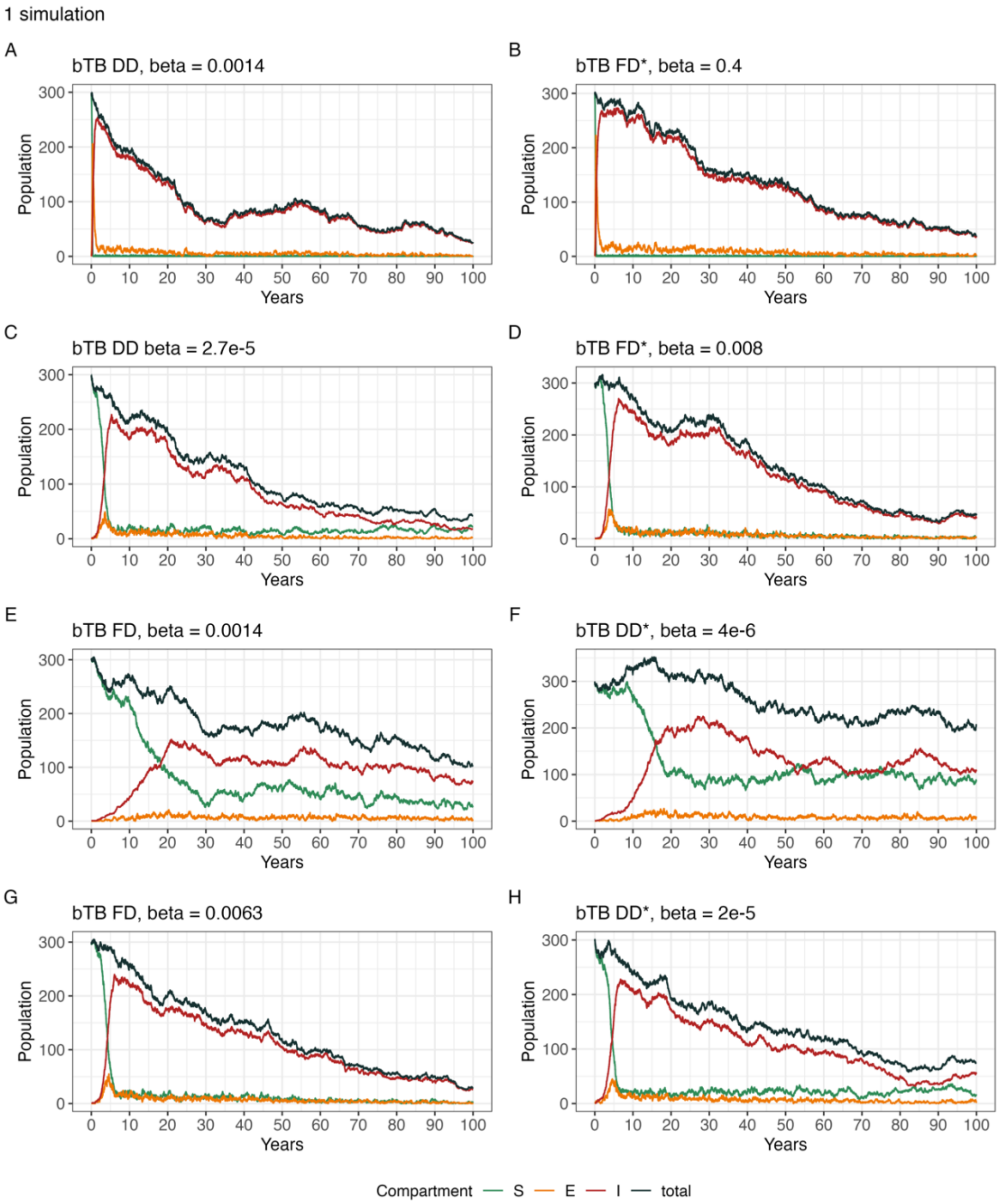


Figure S2.5 Single stochastic simulations of bTB.

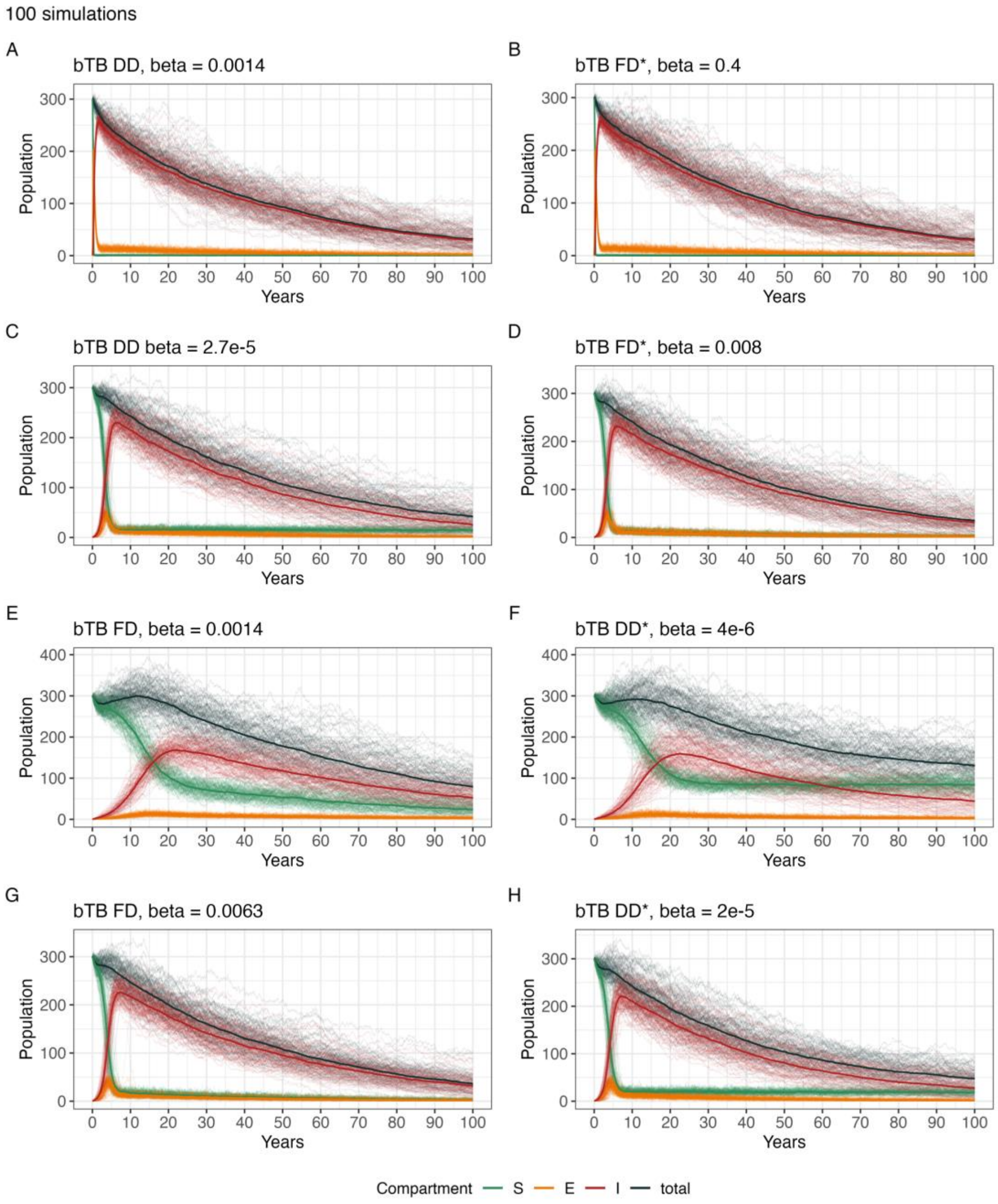


Figure S2.6 Hundred stochastic simulations of bTB.

Haemorrhagic septicaemia (HS -*Pasteurella multocida*)

The *SIRS* model for HS used two fatality rates, 0.5% and 5%.

$$
\begin{aligned}
N &= S_c + I_c + R_c + S_{sa} + I_{sa} + R_{sa} + S_a + I_a + R_a \\
\frac{dS_c}{dt} &= \mu_b N_a - \beta_c S_c (I_c + I_{sa} + I_a) - \delta_c S_c - \mu_c S_c + \omega_c R_c - \epsilon S_c \\
\frac{dS_{sa}}{dt} &= -\beta_{sa} S_{sa} (I_c + I_{sa} + I_a) + \delta_c S_c - \delta_{sa} S_{sa} - \mu_{sa} S_{sa} + \omega_{sa} R_{sa} - \epsilon S_{sa} \\
\frac{dS_a}{dt} &= -\beta_a S_a (I_c + I_{sa} + I_a) + \delta_{sa} S_{sa} - \mu_a S_a + \omega_a R_a - \epsilon S_a \\
\frac{dI_c}{dt} &= \beta_c S_c (I_c + I_{sa} + I_a) - (1 - \rho_c)\gamma_c I_c - \rho_c \gamma_c I_c - \delta_c I_c - \mu_c I_c + \epsilon S_c \\
\frac{dI_{sa}}{dt} &= \beta_{sa} S_{sa} (I_c + I_{sa} + I_a) - (1 - \rho_{sa})\gamma_{sa} I_{sa} - \rho_{sa} \gamma_{sa} I_{sa} + \delta_c I_c - \delta_{sa} S_{sa} - \mu_{sa} I_{sa} + \epsilon S_{sa} \\
\frac{dI_a}{dt} &= \beta_a S_a (I_c + I_{sa} + I_a) - (1 - \rho_a)\gamma_a I_a - \rho_a \gamma_a I_a + \delta_{sa} S_{sa} - \mu_a I_a + \epsilon S_a \\
\frac{dR_c}{dt} &= (1 - \rho_c)\gamma_c I_c - \omega_c R_c - \delta_c R_c - \mu_c R_c \\
\frac{dR_{sa}}{dt} &= (1 - \rho_{sa})\gamma_{sa} I_{sa} - \omega_{sa} R_{sa} + \delta_c R_c - \delta_{sa} R_{sa} - \mu_{sa} R_{sa} \\
\frac{dR_a}{dt} &= (1 - \rho_a)\gamma_a I_a - \omega_a R_a + \delta_{sa} R_{sa} - \mu_a R_a
\end{aligned} \tag{3}
$$

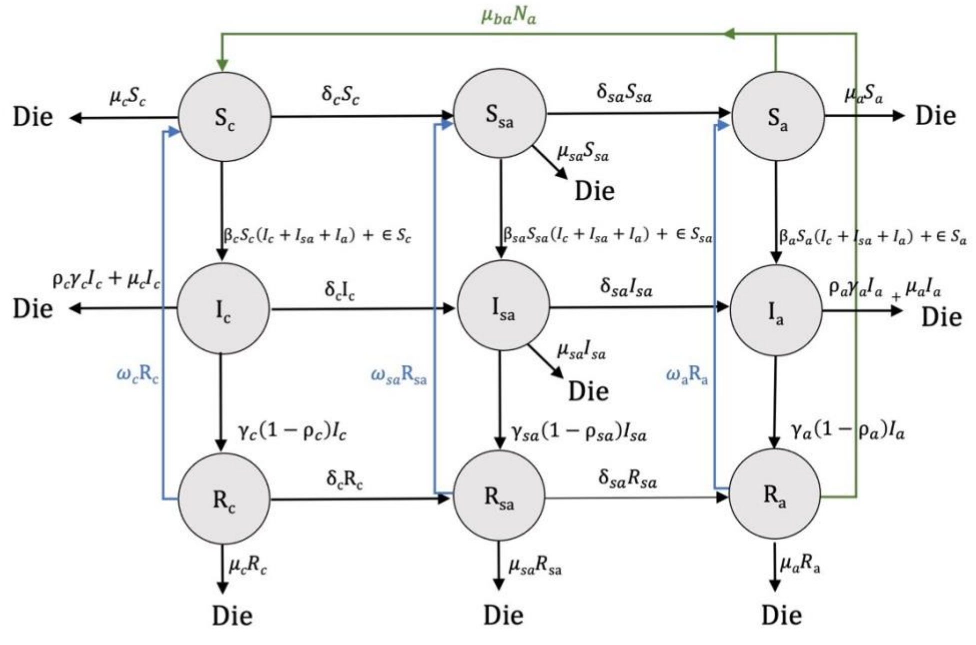


Figure S2.7 *SIRS* model diagram of HS.

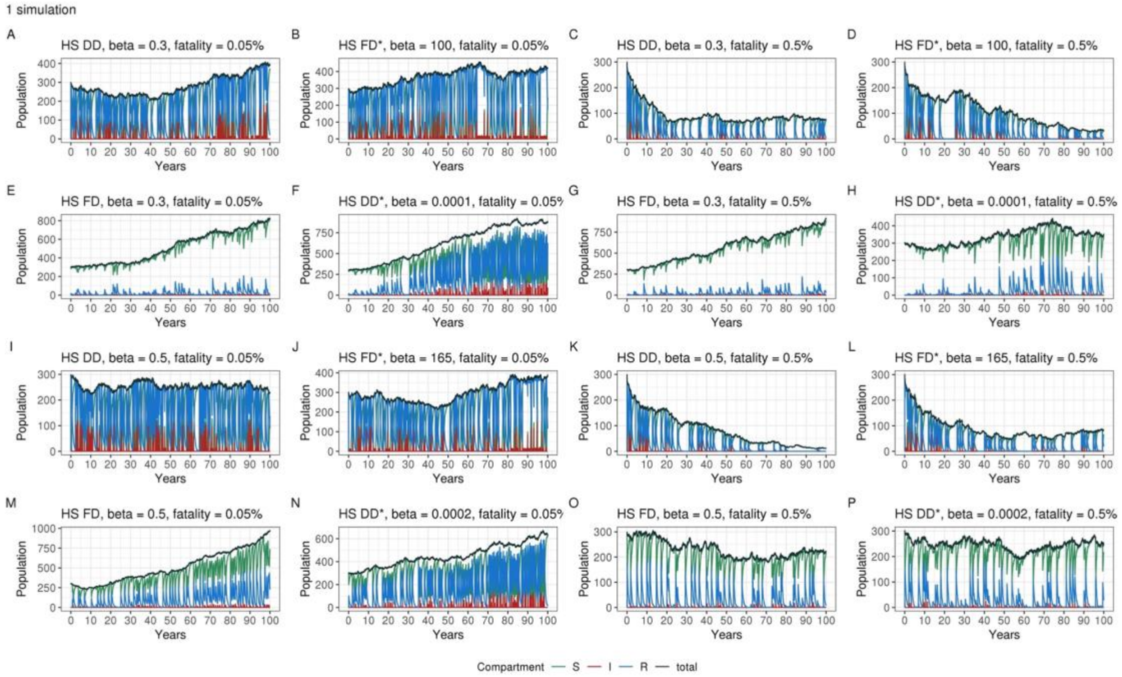


Figure S2.8 Single stochastic simulations of HS show that increasing the β rate (0.3 → 0.5) affects the population number for DD models (A, I) but not for FD models (E, M). However, increasing the fatality rate (0.05% → 0.5%) shows a significant impact on DD models for both β rates (A, C & I, K) and the FD model for a 0.5 transmission rate (K).

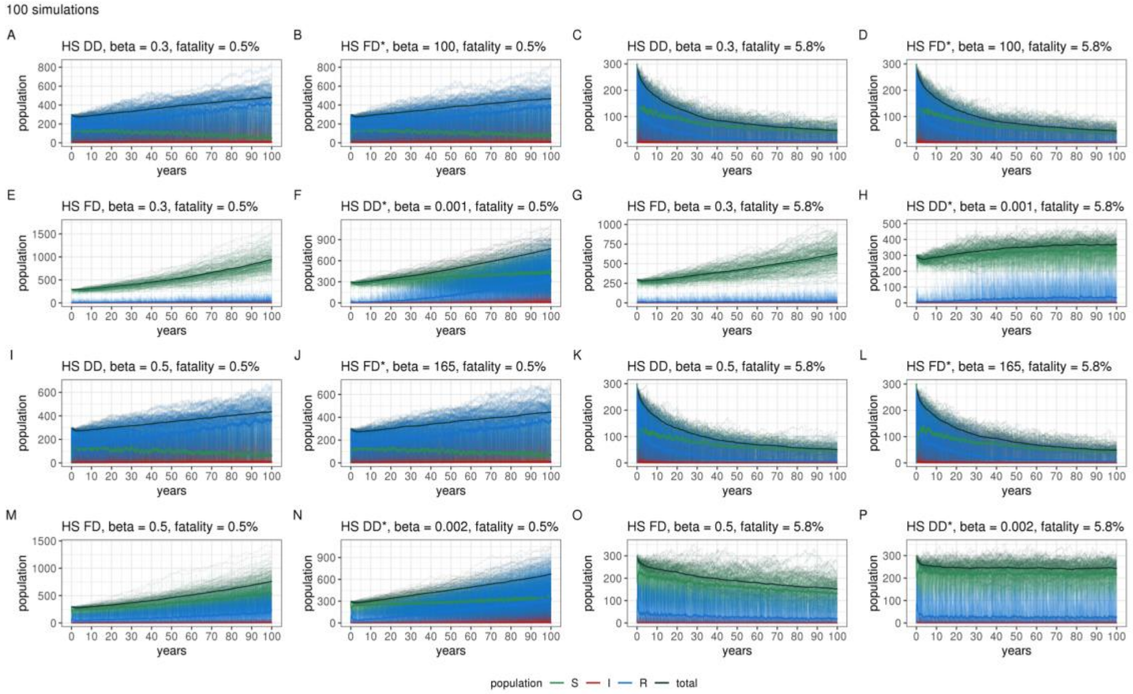


Figure S2.9 Hundred stochastic simulations of HS.

Lumpy skin disease (LSD - Capripoxvirus)

The $SEIRS$ model for LSD included the exposed and recovery state with the birth rate for infected mothers.

$$\begin{aligned}
N &= S_c + E_c + I_c + R_c + S_{sa} + +E_{sa} + I_{sa} + R_{sa} + S_a + E_a + I_a + R_a \\
\frac{dS_c}{dt} &= \mu_b(S_a + E_a + R_a) + \mu_b I_a - \beta_c S_c(I_c + I_{sa} + I_a) - \delta_c S_c - \mu_c S_c + \omega_c R_c - \epsilon S_c \\
\frac{dS_{sa}}{dt} &= -\beta_{sa} S_{sa}(I_c + I_{sa} + I_a) + \delta_c S_c - \delta_{sa} S_{sa} - \mu_{sa} S_{sa} + \omega_{sa} R_{sa} - \epsilon S_{sa} \\
\frac{dS_a}{dt} &= -\beta_a S_a(I_c + I_{sa} + I_a) + \delta_{sa} S_{sa} - \mu_a S_a + \omega_a R_a - \epsilon S_a \\
\frac{dE_c}{dt} &= \beta_c S_c(I_c + I_{sa} + I_a) - \sigma_c E_c - \delta_c E_c - \mu_c E_c + \epsilon S_c \\
\frac{dE_{sa}}{dt} &= \beta_{sa} S_{sa}(I_c + I_{sa} + I_a) - \sigma_{sa} E_{sa} + \delta_c E_c - \delta_{sa} E_{sa} - \mu_{sa} E_{sa} + \epsilon S_{sa} \\
\frac{dE_a}{dt} &= \beta_a S_a(I_c + I_{sa} + I_a) - \sigma_a E_a + \delta_{sa} E_{sa} - \mu_a E_a + \epsilon S_a \\
\frac{dI_c}{dt} &= \sigma_c E_c - (1 - \rho_c)\gamma_c I_c - \rho_c \gamma_c I_c - \delta_c I_c - \mu_c I_c \\
\frac{dI_{sa}}{dt} &= \sigma_{sa} E_{sa} - (1 - \rho_{sa})\gamma_{sa} I_{sa} - \rho_{sa} \gamma_{sa} I_{sa} + \delta_c I_c - \delta_{sa} I_{sa} - \mu_{sa} I_{sa} \\
\frac{dI_a}{dt} &= \sigma_a E_a - (1 - \rho_a)\gamma_a I_a - \rho_a \gamma_a I_a + \delta_{sa} S_{sa} - \mu_a I_a \\
\frac{dR_c}{dt} &= (1 - \rho_c)\gamma_c I_c - \omega_c R_c - \delta_c R_c - \mu_c R_c \\
\frac{dR_{sa}}{dt} &= (1 - \rho_{sa})\gamma_{sa} I_{sa} - \omega_{sa} R_{sa} + \delta_c R_c - \delta_{sa} R_{sa} - \mu_{sa} R_{sa} \\
\frac{dR_a}{dt} &= (1 - \rho_a)\gamma_a I_a - \omega_a R_a + \delta_{sa} R_{sa} - \mu_a R_a
\end{aligned} \tag{4}$$

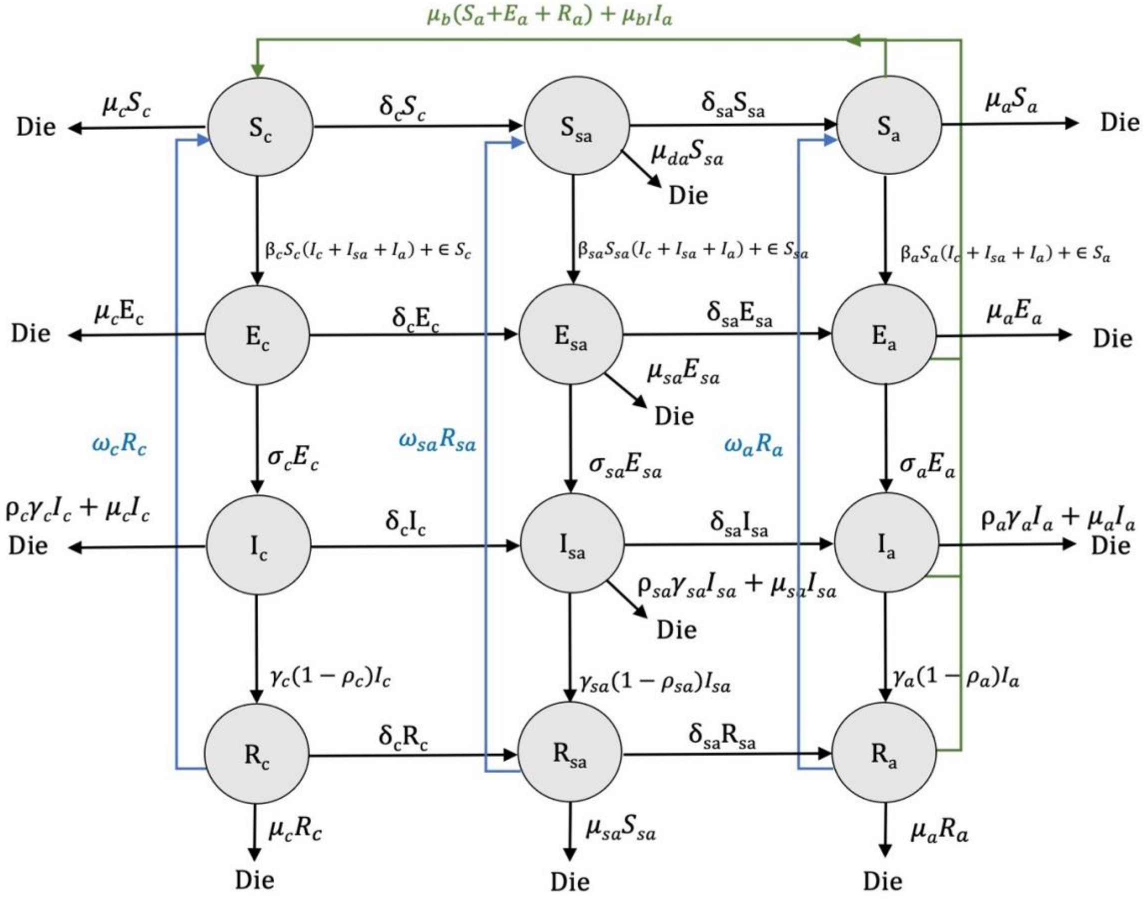
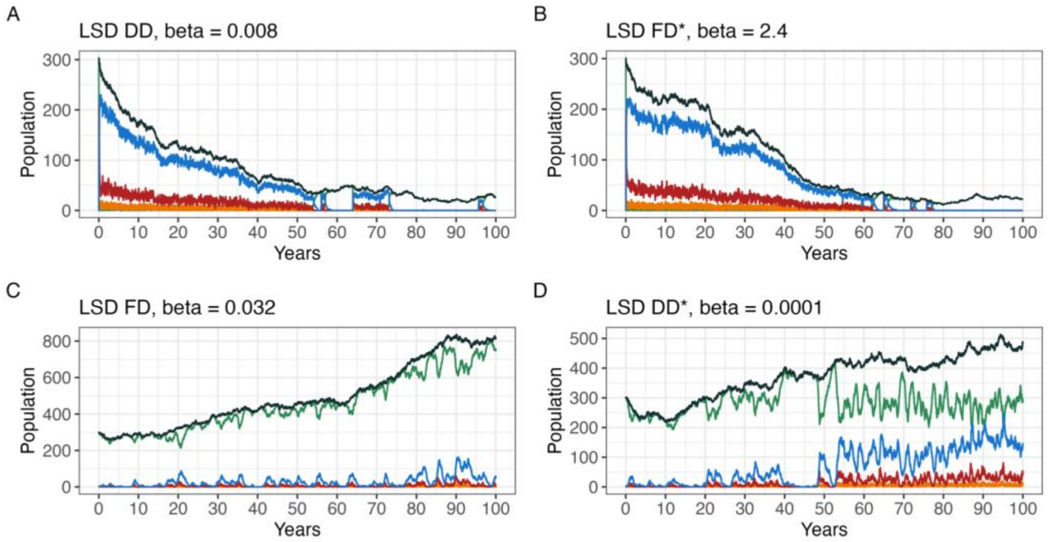


Figure S2.10 $SEIRS$ model diagram of LSD.

1 simulation



100 simulstions

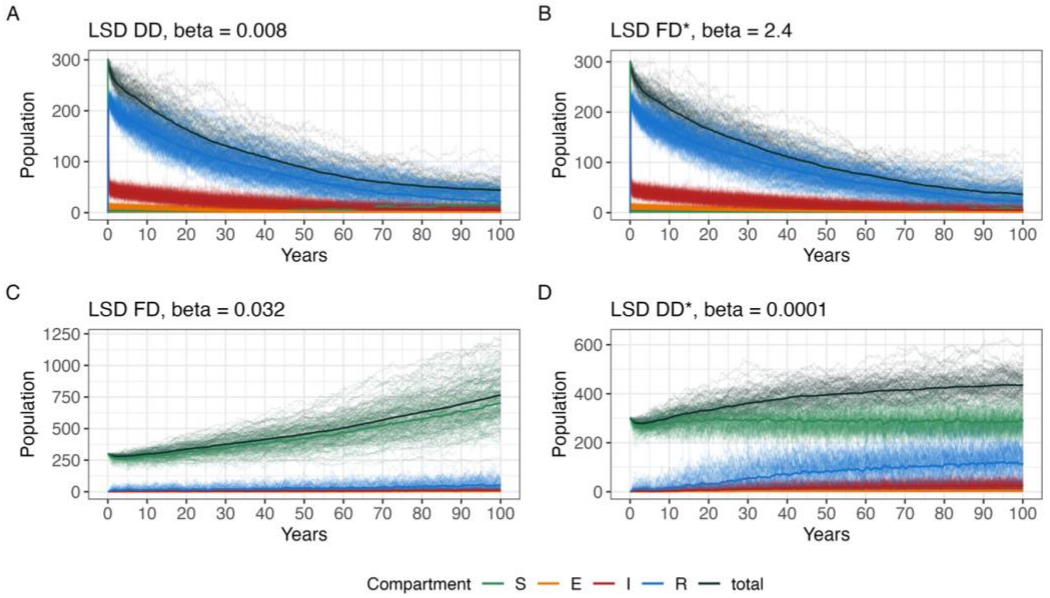


Figure S2.11 Single and 100 stochastic simulations of LSD. FD LSD transmission had less impact on the populations than DD transmission, which resulted in a total population decrease over time.

Foot and mouth disease (FMD - Aphthovirus) & Bovine Brucellosis (*Brucella abortus*)

The *SEIRM/E* model for FMD and Brucellosis included calves with derived maternal immunity, susceptible calves after waning maternal immunity, and the effect on the birth rate of an infectious mother.

$$\begin{aligned}
N &= S_c + E_c + I_c + R_c + S_{sa} + E_{sa} + I_{sa} + R_{sa} + S_a + E_a + I_a + R_a + M + S_m \\
\frac{dS_c}{dt} &= \mu_b(S_a + E_a) + (1-\alpha)\mu_b I_a - \beta_c S_c(I_c + I_{sa} + I_a) - \delta_c S_c - \mu_c S_c + \omega_c R_c - \epsilon S_c \\
\frac{dS_{sa}}{dt} &= -\beta_{sa} S_{sa}(I_c + I_{sa} + I_a) + \delta_c S_c - \delta_{sa} S_{sa} - \mu_{sa} S_{sa} + \omega_{sa} R_{sa} + \delta_m S_m - \epsilon S_{sa} \\
\frac{dS_a}{dt} &= -\beta_a S_a(I_c + I_{sa} + I_a) + \delta_{sa} S_{sa} - \mu_a S_a + \omega_a R_a - \epsilon S_a \\
\frac{dE_c}{dt} &= \beta_c S_c(I_c + I_{sa} + I_a) + \beta_c S_m(I_c + I_{sa} + I_a) - \sigma_c E_c - \delta_c E_c - \mu_c E_c + \epsilon S_c \\
\frac{dE_{sa}}{dt} &= \beta_{sa} S_{sa}(I_c + I_{sa} + I_a) - \sigma_{sa} E_{sa} + \delta_c E_c - \delta_{sa} E_{sa} - \mu_{sa} E_{sa} + \epsilon S_{sa} \\
\frac{dE_a}{dt} &= \beta_a S_a(I_c + I_{sa} + I_a) - \sigma_a E_a + \delta_{sa} E_{sa} - \mu_a E_a + \epsilon S_a \\
\frac{dI_c}{dt} &= \sigma_c E_c - (1-\rho_c)\gamma_c I_c - \rho_c \gamma_c I_c - \delta_c I_c - \mu_c I_c + \alpha \mu_{bI} I_a \\
\frac{dI_{sa}}{dt} &= \sigma_{sa} E_{sa} - (1-\rho_{sa})\gamma_{sa} I_{sa} - \rho_{sa}\gamma_{sa} I_{sa} + \delta_c I_c - \delta_{sa} I_{sa} - \mu_{sa} I_{sa} \\
\frac{dI_a}{dt} &= \sigma_a E_a - (1-\rho_a)\gamma_a I_a - \rho_a \gamma_a I_a + \delta_{sa} S_{sa} - \mu_a I_a \\
\frac{dR_c}{dt} &= (1-\rho_c)\gamma_c I_c - \omega_c R_c - \delta_c R_c - \mu_c R_c \\
\frac{dR_{sa}}{dt} &= (1-\rho_{sa})\gamma_{sa} I_{sa} - \omega_{sa} R_{sa} + \delta_c R_c - \delta_{sa} R_{sa} - \mu_{sa} R_{sa} \\
\frac{dR_a}{dt} &= (1-\rho_a)\gamma_a I_a - \omega_a R_a + \delta_{sa} R_{sa} - \mu_a R_a \\
\frac{dM}{dt} &= \mu_b R_a - \omega_M M - \mu_c M \\
\frac{dS_m}{dt} &= \omega_M M - \delta_m S_m - \beta_m S_m(I_c + I_{sa} + I_a) - \mu_c S_m
\end{aligned} \tag{5}$$

Note: $1/\delta_c = 1/(\delta_m + \omega_M)$ i.e., a calf that received maternal immunity will enter the susceptible calf class at the (δ_m) calf ageing rate plus calf loss of immunity rate (ω_M).

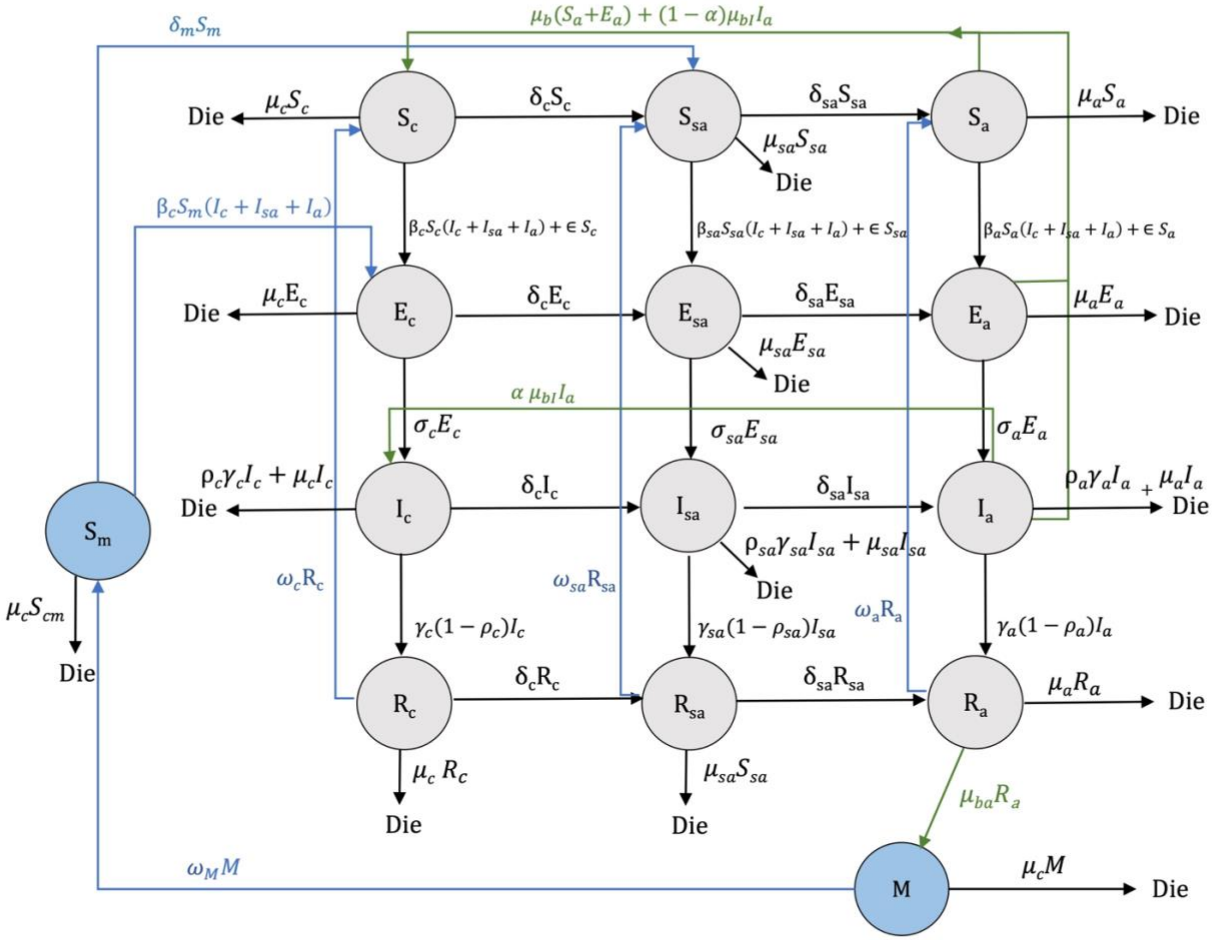


Figure S2.12 *SEIRMS/E* model of FMD and brucellosis.

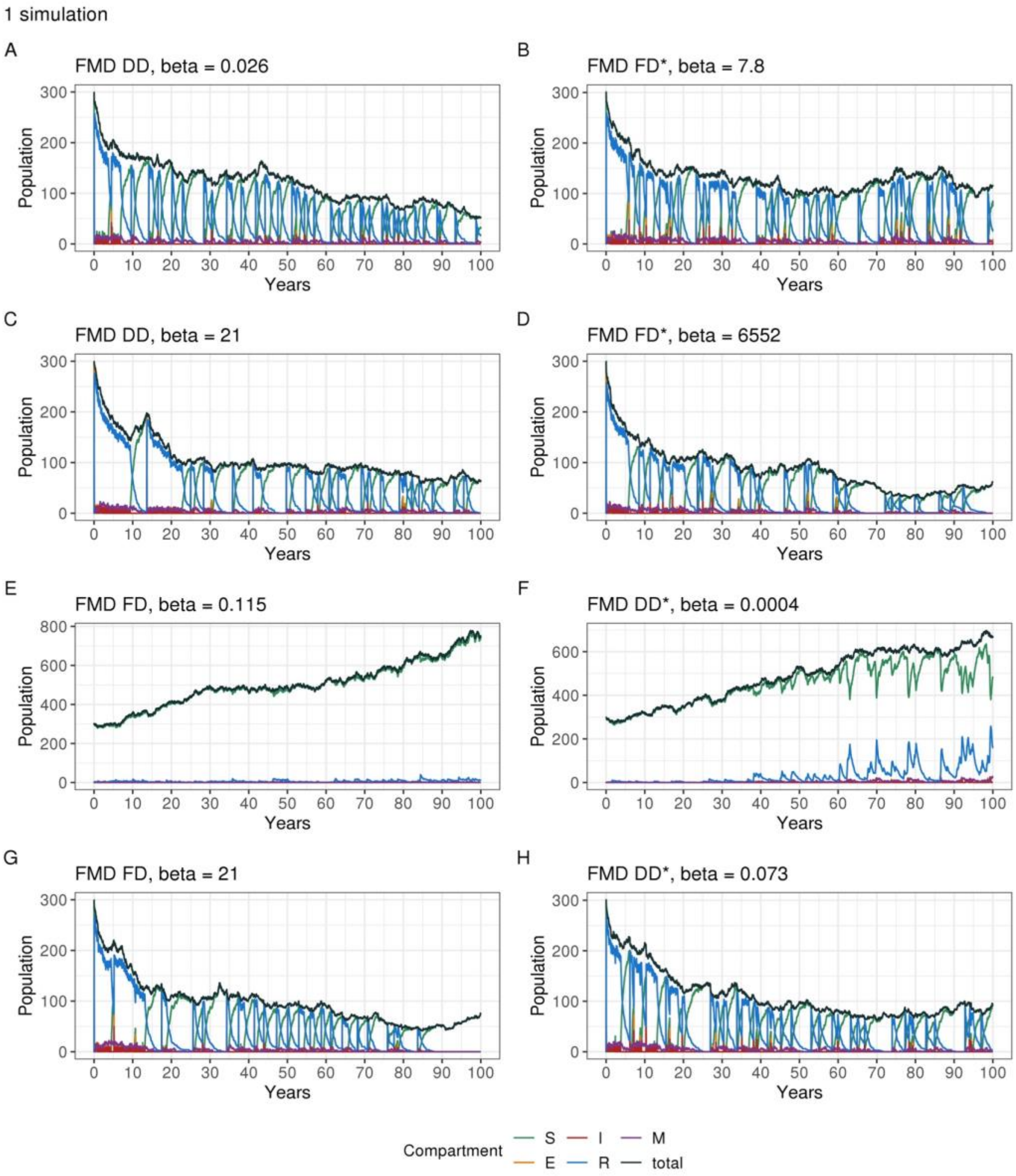


Figure S2.13 Single stochastic simulations of FMD. FMD FD with β = 0.115 (E) had the least population impact, while the other models decreased the total population. All models with different in β rates (0.026, 21) showed a cyclic pattern of outbreaks around every 5 years, except E & F.

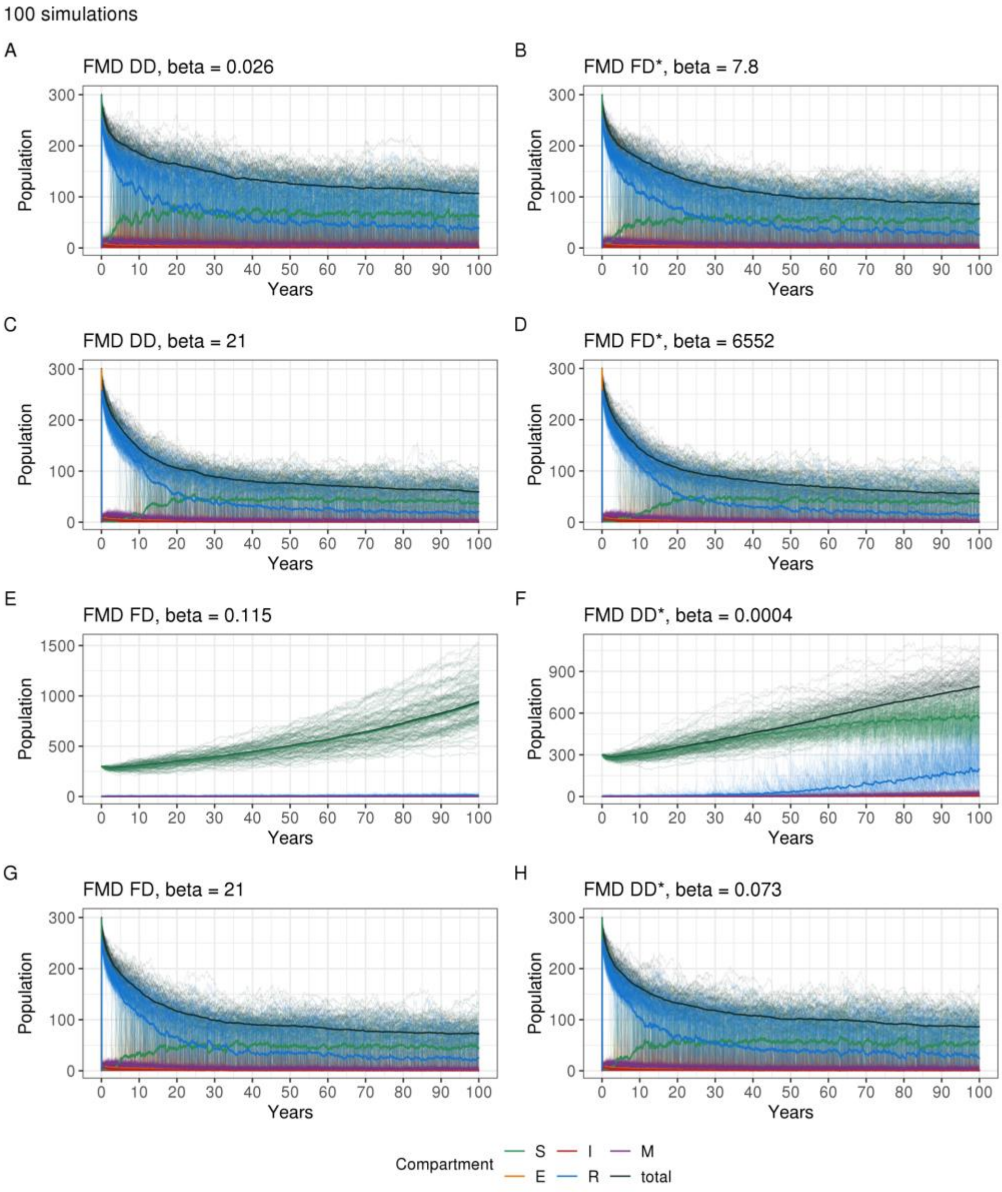


Figure S2.14 Hundred stochastic simulations of FMD.

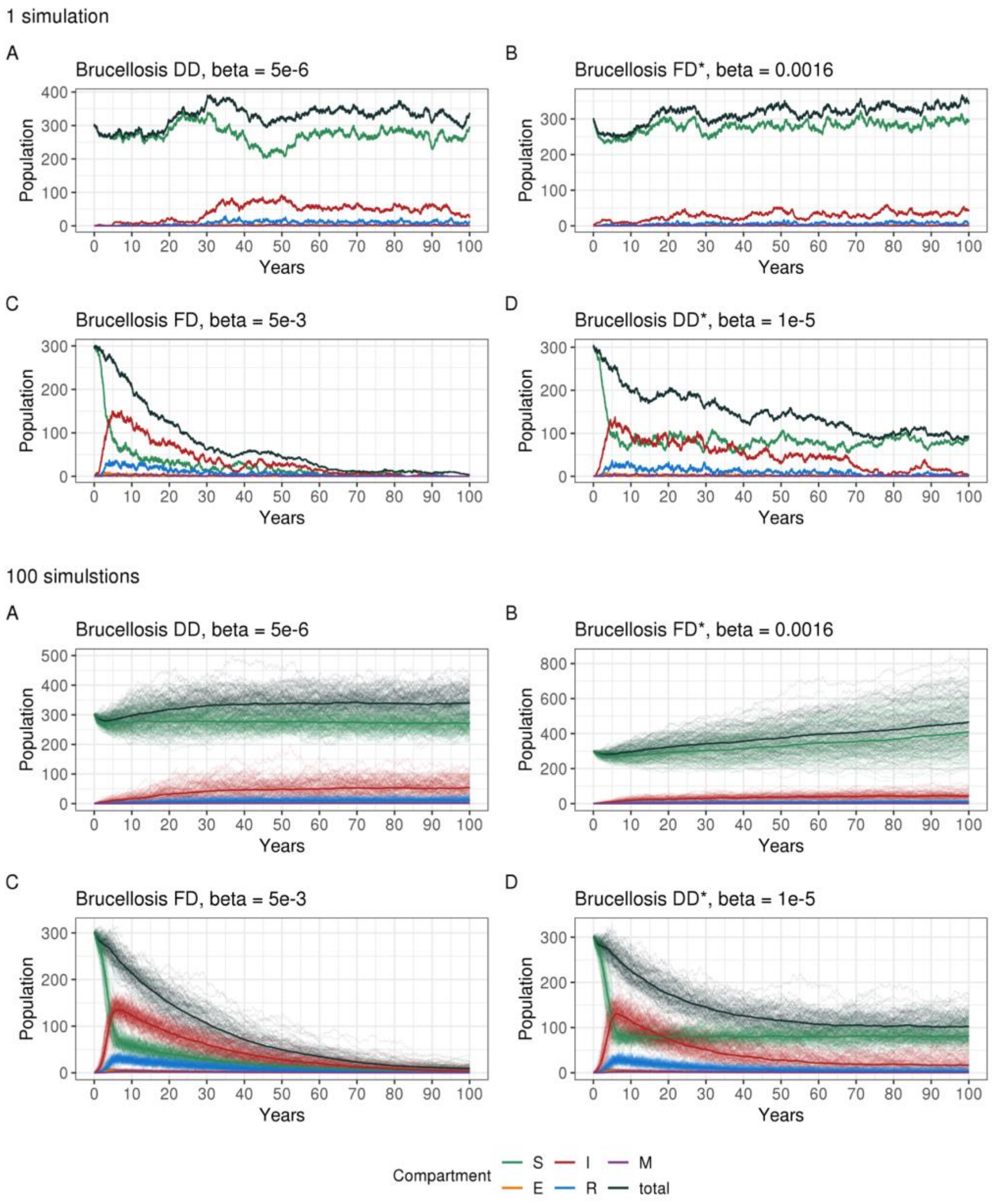


Figure S2.15 Single and 100 stochastic simulations of brucellosis. Brucellosis with FD transmission (C, D) had the most impact on populations, with a chance of population decline to zero. DD transmission showed a constant (A) and increase (B) in the populations.

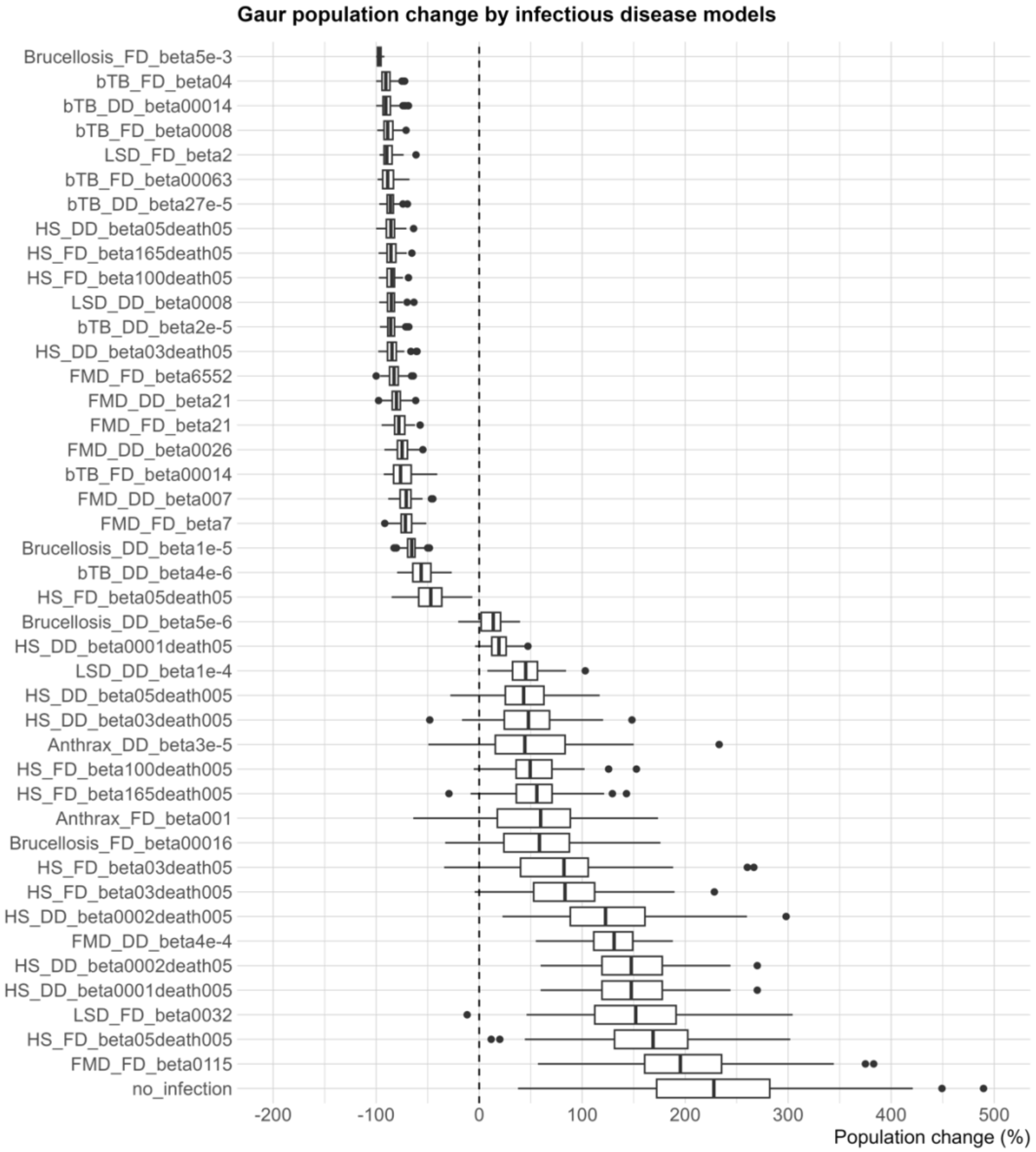


Figure S2.16 The average of the total population changes for all models. The boxplot presents the average percentage of the total population change compared to the no infection model (M1) to all the infectious disease models from the lowest to the highest (M2 to M38) of the population change in model simulations (N=100).

Table S2.1 The average of the total population changes for all models.

No.	Model name	Model code	Average of the total population changes (%)
1	no_infection	M1	228
2	FMD_FD_beta0115	M2	200
3	HS_FD_beta05death005	M3	167
4	LSD_FD_beta0032	M4	155
5	HS_DD_beta0001death005	M5	149
6	HS_DD_beta0002death05	M6	149
7	FMD_DD_beta3e-4	M7	130
8	HS_DD_beta0002death005	M8	127
9	HS_FD_beta03death005	M9	85
10	HS_FD_beta03death05	M10	79
11	Brucellosis_FD_beta00016	M11	60
12	Anthrax_FD_beta001	M12	57
13	HS_FD_beta165death005	M13	55
14	HS_FD_beta100death005	M14	53
15	Anthrax_DD_beta3e-5	M15	51
16	HS_DD_beta03death005	M16	47
17	HS_DD_beta05death005	M17	46
18	LSD_DD_beta1e-4	M18	45
19	HS_DD_beta0001death05	M19	20
20	Brucellosis_DD_beta5e-6	M20	11
21	HS_FD_beta05death05	M21	-48
22	bTB_DD_beta4e-6	M22	-55
23	Brucellosis_DD_beta1e-5	M23	-66
24	FMD_FD_beta7	M24	-71
25	FMD_DD_beta007	M25	-71
26	bTB_FD_beta00014	M26	-74
27	FMD_DD_beta0026	M27	-74
28	FMD_FD_beta21	M28	-78
29	FMD_DD_beta21	M29	-80
30	FMD_FD_beta6552	M30	-83
31	HS_DD_beta03death05	M31	-84
32	bTB_DD_beta2e-5	M32	-85
33	LSD_DD_beta0008	M33	-85
34	HS_FD_beta100death05	M34	-85
35	HS_FD_beta165death05	M35	-85
36	HS_DD_beta05death05	M36	-86
37	bTB_DD_beta27e-5	M37	-86
38	bTB_FD_beta00063	M38	-88
39	LSD_FD_beta2	M39	-88
40	bTB_FD_beta0008	M40	-88
41	bTB_DD_beta00014	M41	-89
42	bTB_FD_beta04	M42	-90
43	Brucellosis_FD_beta5e-3	M43	-97

PCA biplot

We conducted PCA using four disease parameters: beta transmission rate, incubation period, infectious period, and fatality rate. PCA can identify the contribution of these parameters to the population change. The beta transmission rate and incubation period demonstrated the highest contribution to the FMD FD model (rescaling DD - β = 6552). Nevertheless, the fatality rate had the most significant impact on Anthrax FD and its DD (rescaling FD) with a 100% fatality rate but less effect on the population change. The other diseases showed less influence by a single parameter but had more impact on the population change (population decrease, indicated in red in Figure S2.17 - Figure S2.18), including bTB and Brucellosis.

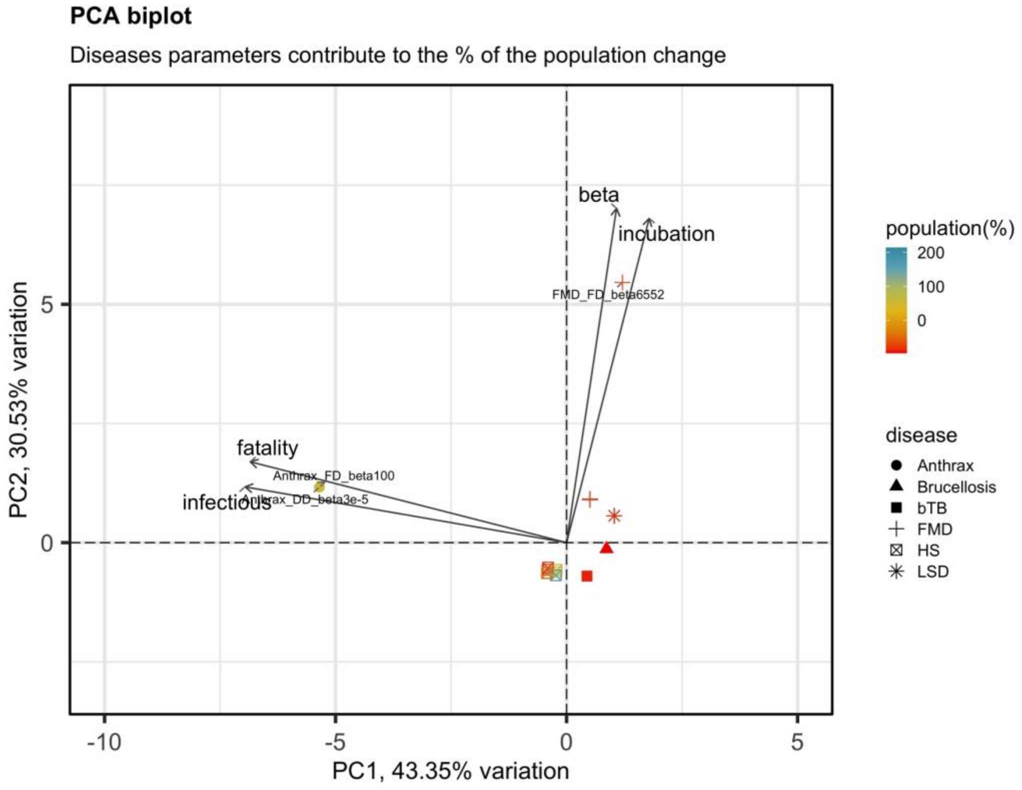


Figure S2.17 PCA biplot of 4 disease parameters , including beta transmission rate, incubation period, infectious period and fatality rate, contributing to the percentage of the total population change.

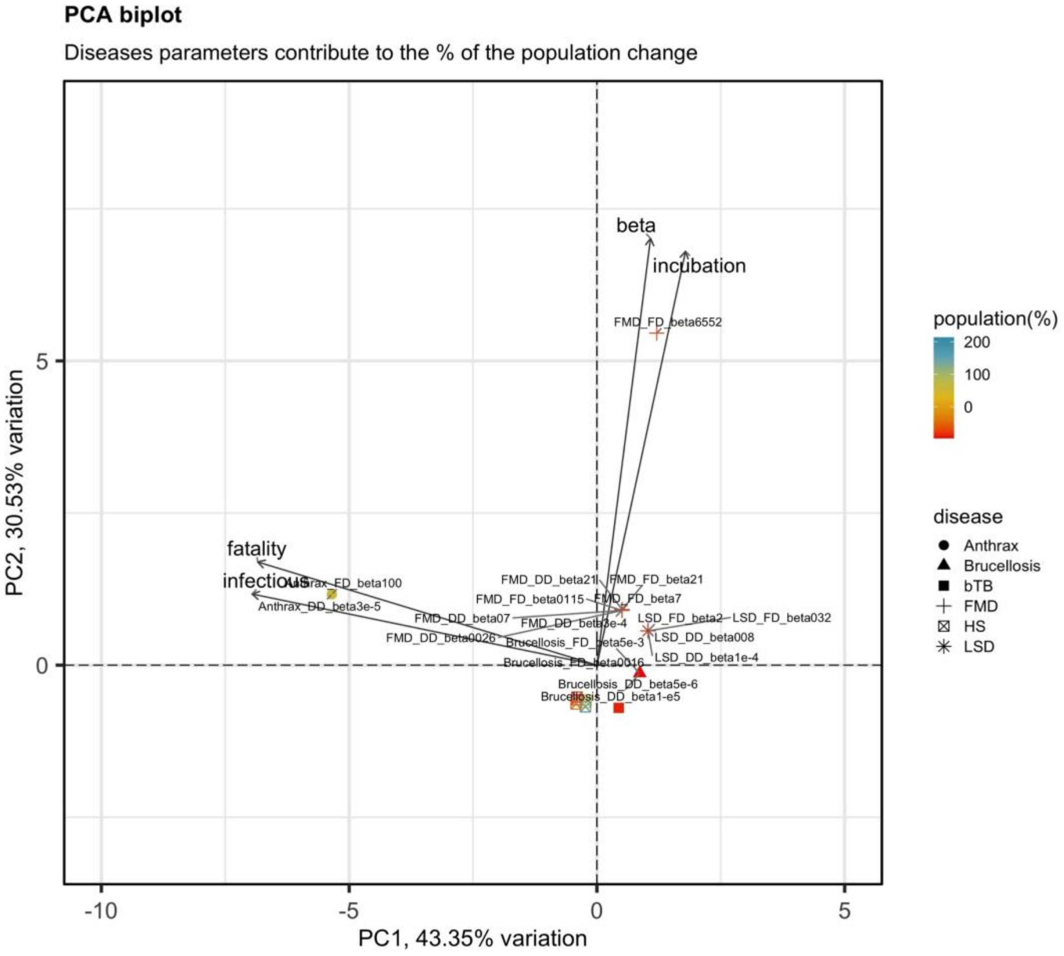


Figure S2.18 PCA biplot of 4 disease parameters with model’s name , including beta transmission rate, incubation period, infectious period and fatality rate, contributing to the percentage of the total population change.

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