Dilution effect and identity effect by wildlife in the persistence and recurrence of bovine tuberculosis

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SUMMARY

Current theories on disease-diversity relationships predict a strong influence of host richness on disease transmission. In addition, identity effect, caused by the occurrence of particular species, can also modify disease risk. We tested the richness effect and the identity effects of mammal species on bovine tuberculosis (bTB), based on the regional bTB outbreak data in cattle from 2005–2010 in Africa. Besides, we also tested which other factors were associated with the regional bTB persistence and recurrence in cattle. Our results suggested a dilution effect, where higher mammal species richness (MSR) was associated with reduced probabilities of bTB persistence and recurrence in interaction with cattle density. African buffalo had a positive effect on bTB recurrence and a positive interaction effect with cattle density on bTB persistence, indicating an additive positive identity effect of buffalo. The presence of greater kudu had no effect on bTB recurrence or bTB persistence. Climatic variables only act as risk factors for bTB persistence. In summary, our study identified both a dilution effect and identity effect of wildlife and showed that bTB persistence and recurrence were correlated with different sets of risk factors. These results are relevant for more effective control strategies and better targeted surveillance measures in bTB.

Key words: Mycobacterium bovis, mammal species richness, African buffalo, greater kudu, cattle density, climate.

INTRODUCTION

Bovine tuberculosis (bTB) caused by *Mycobacterium bovis* is widespread in many countries, especially in Africa, and has caused significant economic losses (Humblet *et al.* 2009). Previous studies have identified various risk factors for bTB transmission at different levels, such as herd size, previous infection status and cattle movements at herd level (Humblet *et al.* 2009; Skuce *et al.* 2012). Increasing evidence suggests that wildlife species play an important role in bTB dynamics as well (Corner, 2006; Renwick *et al.* 2007; Humblet *et al.* 2009; O'Brien *et al.* 2011; De Garine-Wichatitsky *et al.* 2013). This finding invokes further research efforts especially on multi-species transmission in livestock-wildlife interactions, as studies on the role of wildlife species often only involved single-species transmission (Humblet *et al.* 2009; Huang *et al.* 2013*b*).

It has been hypothesized that greater species diversity is able to reduce pathogen transmission, i.e. the dilution effect (Keesing *et al.* 2006, 2010; Ostfeld and Keesing, 2012; Johnson *et al.* 2013; Joseph *et al.* 2013). This dilution effect can operate through different mechanisms, such as decreasing encounter rates among competent hosts or regulating host abundance (Keesing *et al.* 2006). Although the dilution effect has been found in many different disease systems, it is still highly disputed whether the dilution effect generally occurs (Ostfeld and Keesing, 2012; Randolph and Dobson, 2012; Huang *et al.* 2013*a*; Ostfeld, 2013). In Africa, many mammal species can be infected by *M. bovis*, and these species have been classified as maintenance hosts (such as African buffalo, *Syncerus caffer*), spillover hosts or dead-end hosts (Corner, 2006; Renwick *et al.* 2007). Since the competence to transmit *M. bovis* varies among different species, we expect that mammal species diversity can affect bTB transmission. We hypothesized that higher mammal species richness (MSR) may trigger a dilution effect and reduce bTB risk by increasing the abundance of incompetent hosts which are able to interfere with the bTB transmission pathways. On the other hand, there might also be an identity effect, implying that the occurrence of particular species in the community changes the disease risk, either positively or

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negatively (Hantsch *et al.* 2013). In this study, therefore, we tested the identity effect of buffalo, considering that the occurrence of maintenance host species might increase bTB risk because of their high competence in transmitting *M. bovis*. In addition, since studies have not reached an agreement on the role of greater kudu (*Tragelaphus strepsiceros*) in bTB transmission (Renwick *et al.* 2007; Humblet *et al.* 2009), we also tested for an identity effect of this species.

A previous study tested the dilution effect and found that MSR was negatively associated with the probability of bTB presence (Huang *et al.* 2013*b*). However, spatial pathogen dynamics has several distinct epidemiological phases including new establishment in an area, persistence, fade-out and recurrence, and the patterns of different phases might be driven by different determinants (Allepuz *et al.* 2011; Skuce *et al.* 2012). Therefore, we tested the dilution effect as well as the identity effect in the persistence and recurrence of bTB and compared the differences in these two distinct phases. In addition to wildlife species, other factors are also responsible for facilitating bTB transmission, such as cattle density, the status of 'neighbourhoods' and climate (Humblet *et al.* 2009). However, since studies usually investigated the effects of these factors at herd level and relatively fewer studies focus on regional scale (Humblet *et al.* 2009), we also tested whether these variables act as risk factors for bTB risk at regional scale. The present study aimed at testing the dilution effect as well as the identity effects of two wildlife species (African buffalo and greater kudu) in the persistence and recurrence of bTB in cattle. We also examined which other factors were associated with bTB persistence and recurrence and tested whether they are associated with different sets of predictors.

MATERIALS AND METHODS

BTB data

Data of bTB in cattle in Africa from 2005 to 2010 were provided by the World Animal Health Information Database (Ben Jebara *et al.* 2012) from the World Organisation for Animal Health (OIE), which reported the status of bTB at the administrative level every 6 months during this period. The lowest administrative level of reporting was used as the level of analysis in this study. Only countries with bTB outbreak histories were included in the analyses, since we focused on bTB recurrence and persistence. The compiled dataset has 879 rows covering 11 countries and 190 administration areas (Table S1).

We classified a disease fade-out if bTB was not reported in two consecutive reporting periods (therefore one year) following a presence. This criterion has been used in previous studies to identify bTB persistence and fade-out (Brooks-Pollock and

Keeling, 2009; Karolemeas *et al.* 2011). Therefore, a bTB presence in a specific period was considered as bTB recurrence if bTB was not reported in the administrative areas in the previous two reporting periods. BTB persistence was classified if a bTB presence was reported within a year (i.e. within maximally two 6-months reporting periods).

Wildlife data

MSR were calculated from the African Mammal Databank (AMD), an atlas of medium to large mammals (Biotani, 1998). For each mammal species, the AMD includes two polygon coverage files respectively describing the distribution of suitable habitat and the distribution of species occurrence at a 1×1 km resolution (Biotani, 1998). The intersection of these two distribution maps was calculated as the 'actual distribution' for each species (Boitani *et al.* 2008). Since small mammals are less often involved in bTB transmission in Africa, only species with an average body mass ≥ 2 kg from the AMD were used in the analysis. The presence or absence of each mammal species was recorded in each administrative area and were compiled to calculate the species richness of each administrative area. Using species distribution maps from the AMD, the percentage of the area occupied by African buffalo (Buffalo) and greater kudu (Kudu) were calculated for each of the administrative areas to test the identity effects of these two species.

Other predictors

Many studies have identified that cattle density is an important predictor for bTB outbreaks (Gilbert *et al.* 2005; Mathews *et al.* 2006; Humblet *et al.* 2010; Vial and Donnelly, 2012; Huang *et al.* 2013*b*). The bTB status of 'neighbourhoods' might also play an important role in explaining and predicting bTB risk (White *et al.* 2013). In addition, previous studies also indicated that climate can substantially influence bTB dynamics through the influence on the survival of *M. bovis* (Wint *et al.* 2002; Rhodes *et al.* 2007; Humblet *et al.* 2009, 2010). Therefore, we also included these variables to test their effect on bTB persistence and recurrence at a regional scale.

From the Food and Agriculture Organization (FAO), we collected the data of cattle density in 2005, which had a resolution of 0·05 degree. We calculated the mean cattle density for each administrative area. To investigate the effect of 'neighbourhood', the percentage of the border that was shared with neighbouring infected areas in the preceding year (BorPre) was calculated based on the bTB presence/absence data from OIE. Twelve climatic variables (Table 1) representing temperature and precipitation conditions were calculated based on the Climate

Table 1. *Descriptions, abbreviations, units and summaries (mean ± s.d.) of the predictors used in the analysis*

Description of datasets	Abbreviation	Unit	Mean ± s.d.
Cattle density	CattleD	km^{-2}	13·6 ± 18·7
Mammal species richness	MSR	1	49·7 ± 29·2
Percentage of area occupied by buffalo	Buffalo	No unit	36·3 ± 40·9
Percentage of area occupied by kudu	Kudu	No unit	6·6 ± 20·1
Percentage of the border shared with previous infected areas	BorPre	No unit	70·9 ± 35·0
Climatic predictors			
Annual mean temperature	TemMean	°C	24·9 ± 4·1
Mean temperature of the warmest month	TemMax	°C	35·2 ± 3·4
Mean temperature of the coldest month	TemMin	°C	14·9 ± 7·1
Temperature annual range	ATemRng	°C	20·4 ± 6·8
Temperature bi-annual range	BTemRng	°C	21·4 ± 7·0
Annual mean precipitation	RainMean	mm	84·0 ± 47·4
Mean precipitation in driest month in current year	RainMin	mm	3·1 ± 5·5
Annual coefficient of variation for precipitation	RainCV	No unit	0·94 ± 0·26
Mean temperature in preceding year	PreTemMean	°C	24·8 ± 4·1
Mean precipitation in preceding year	PreRainMean	mm	82·6 ± 45·8
Mean temperature of the warmest month in preceding year	PreTemMax	°C	35·2 ± 3·4
Mean precipitation in driest month in preceding year	PreRainMin	mm	2·8 ± 5·1
Interaction terms			
Cattle density × mammal species richness	CattleMSR	km^{-2}	
Cattle density × buffalo	CattleBuff	km^{-2}	
Cattle density × Kudu	CattleKudu	km^{-2}	

Research Unit (CRU) datasets (Harris *et al*. 2013). CRU time-series datasets yield month-by-month variations in climate from 1900 to 2010. These are calculated per (0·5 × 0·5 degree) grid cell, compiled from an archive of monthly mean temperatures provided by more than 4000 weather stations distributed around the world. In addition, to investigate the effect of wildlife-livestock interactions, we included the interaction terms between cattle density and three wildlife variables, i.e. MSR, areas occupied by buffalo and kudu, as potential predictors. The data for all predictor variables were acquired from existing databases (Table S2). All data pre-processing analyses were conducted in ArcGIS 10.0.

Statistical analyses

Generalized linear mixed models (GLMM) with a binary response were used to examine the effects of predictors on bTB persistence and recurrence. In addition, country was included in the models as the random factor to control for possible differences between countries, because of the lack or incompleteness of the data of veterinary service and used control measures. Before performing the GLMMs, we log-transformed, log(x + 0·5), Buffalo, Kudu and BorPre.

Using GLMMs, two approaches were applied to investigate the associations between predictors and bTB persistence or recurrence. First, we used a stepwise selection approach to construct a final multiple regression model. The area of the unit was retained in the model to correct for the effect of area size. We initially included cattle density in the model, since

this predictor was shown to have significant impacts on both bTB persistence and recurrence. Then, other variables were added into the model by a standard-entry stepwise procedure, using a Likelihood Ratio Test (LRT) to test for the difference in the fit of the nested models. For highly correlated independent variables, only the one causing the largest change in the Log-Likelihood (LL) was added to the model to avoid multi-collinearity. We included interaction terms after including all main factors. Main terms were maintained in the model if they were included in a significant interaction term. Second, a 'removal approach' based on multiple regression frameworks (Gilbert *et al*. 2008; Martin *et al*. 2011) was used to test for the consistency of results obtained via the stepwise selection approach. In this approach, all variables, except for those causing multi-collinearity, were forced in the model. Then, the coefficient and the change in −2LL were estimated on the removal of each independent variable. We tested for the spatial autocorrelation of the residuals (final models in stepwise selection approach and full models in removal approach) using Moran's I index and found little evidence of spatial autocorrelation for the models (Table S3). The whole statistical process was conducted in R 2.15.1 with appropriate packages.

RESULTS

Descriptive epidemiology

The regional prevalence of bTB was 36% during the study period (Table 2). The percentage of areas experiencing recurrence of bTB was 14%, and the

Table 2. *Infection prevalence, percentages of persistence and recurrence of bovine tuberculosis (bTB) in the African administrative areas during 2006–2010*

Year	No. of pathogen free area in preceding year	No. of areas with recurrence	Recurrence rate (%)	No. of infected area in the preceding year	No. of areas with fade-out	Fade-out rate (%)	Infection prevalence (%)
2006	112	18	16	53	14	26	32
2007	114	18	16	60	11	18	34
2008	115	18	16	65	13	20	36
2009	110	14	13	70	21	30	39
2010	108	13	12	72	10	14	40
Total	559	81	14	320	69	22	36

Table 3. *Summary statistics (regression coefficient* b ± s.e.*; Adjusted Odds Ratio, AOR and 95% CI, calculated from the first and third quartiles, and P-value) for the predictors correlated with bTB persistence using a stepwise selection procedure and a removal approach (some non-significant variables in the removal approach were not listed)*

	Stepwise selection approach			Removal approach		
Variables	b ± s.e.	AOR (95% CI)	*P*-value	b ± s.e.	$\Delta - 2LL$	*P*-value
Cattle density	0·11 ± 0·03	7·54 (2·07–27·42)	0·002**	0·14 ± 0·06	5·93	0·014*
PreTemMax	− 0·25 ± 0·08	0·64 (0·45–0·87)	0·004**	− 0·23 ± 0·12	3·38	0·066
PreRainMin	− 0·12 ± 0·05	0·64 (0·44–0·92)	0·019*	− 0·16 ± 0·06	7·11	0·008**
MSR	0·03 ± 0·02	3·29 (0·45–24·03)	0·241	0·02 ± 0·03	0·26	0·613
Buffalo	− 0·65 ± 0·41	0·24 (0·04–1·42)	0·116	− 1·01 ± 0·52	4·07	0·043*
CattleMSR	− 0·004 ± 0·001	0·12 (0·03–0·44)	0·001***	− 0·005 ± 0·002	7·84	0·005**
CattleBuff	0·08 ± 0·03	3·15 (1·43–6·94)	0·005**	0·09 ± 0·03	7·55	0·006**

#Variables are mean temperature of the warmest month (PreTemMax) and mean precipitation in driest month (PreRainMin) in the preceding year, mammal species richness (MSR), percentage of the area occupied by buffalo (Buffalo), the interaction terms CattleD × MSR (CattleMSR) and CattleD × Buffalo (CattleBuff).
* $P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

percentage of areas with a bTB fade-out was 22% (persistence percentage was thus 88%).

Risk factors for bTB persistence

Both the stepwise selection approach and removal approach showed that cattle density was positively correlated to bTB persistence, while the interaction of cattle density and MSR was negative ([Table 3](#)). Only one of the investigated maintenance hosts, buffalo, played a significant role in bTB persistence, as indicated by the positive interaction with cattle density in both approaches. Removal approach also detected a positive main effect of buffalo. In addition, the mean precipitation of the driest month in the preceding year (PreRainMin) showed a negative relationship with bTB persistence in both approaches, and the mean temperature of the warmest month (PreTemMax) was negatively correlated with bTB persistence in the stepwise selection approach.

Risk factors for bTB recurrence

For bTB recurrence, the stepwise selection approach and removal approach generated similar results

([Table 4](#)). In contrast to bTB persistence, bTB recurrence was found to be correlated with a different set of predictors ([Tables 3](#) and [4](#)), highlighted by the positive main effect of the area occupied by Buffalo and the absence of climatic effects for bTB recurrence. Similar to bTB persistence, cattle density had a positive effect on bTB recurrence and there was a significant negative interaction between cattle density and MSR.

DISCUSSION

Despite extensive efforts to investigate the influences of wildlife on bTB transmission, the understanding of the impacts of livestock-wildlife interactions and wildlife community structure remains limited (Corner, [2006](#); Renwick *et al.* [2007](#); Humblet *et al.* [2009](#)). Here, we demonstrated that wildlife species play a substantial role in both the persistence and recurrence of bTB, and moreover, that these two distinct phases are correlated with different sets of risk factors.

In line with previous studies (Gilbert *et al.* [2005](#); Humblet *et al.* [2010](#)), our results showed that a higher cattle density facilitates both persistence and

Table 4. *Summary statistics (regression coefficient b ± s.e.; Adjusted Odds Ratio, AOR and 95% CI, calculated from the first and third quartiles, and P-value) for the predictors correlated with bTB recurrence using a stepwise selection procedure and a removal approach (some non-significant variables in the removal approach were not listed)*

Variables	Stepwise selection approach			Removal approach		
	b ± s.e.	AOR (95% CI)	*P*-value	b ± s.e.	$\Delta - 2LL$	*P*-value
Cattle density	0·059 ± 0·016	2·47 (1·49–4·09)	<0·001***	0·076 ± 0·030	7·54	0·006**
MSR	0·006 ± 0·015	1·11 (0·65–1·88)	0·686	0·006 ± 0·02	0·09	0·762
Buffalo	0·68 ± 0·20	4·44 (1·87–10·55)	<0·001***	0·67 ± 0·24	7·34	0·007**
CattleMSR	− 0·0013 ± 0·0005	0·38 (0·18–0·77)	0·007**	− 0·0018 ± 0·0007	7·19	0·007**

#Variables are mammal species richness (MSR), percentage of the area occupied by buffalo (Buffalo), the interaction term CattleD × MSR (CattleMSR).
*$P<0.05$; **$P<0.01$; ***$P<0.001$.

recurrence of bTB. This can be explained by the manner of bTB transmission, which is mainly through aerosol transmission (Renwick *et al.* 2007; Skuce *et al.* 2012), a density-dependent transmission (Huang *et al.* 2013*b*). Increasing host densities can lead to higher encounter rates of susceptible and infectious hosts, thereby promoting persistence and spread of the pathogen (Lloyd-Smith *et al.* 2005; Brooks-Pollock and Keeling, 2009).

Recently, the influence of species diversity on disease dynamics has attracted great interest (Keesing *et al.* 2006). A well-known hypothesis is described as the 'dilution effect', which states that high species diversity can reduce disease risk (Keesing *et al.* 2006). The negative interaction between cattle density and MSR in our study indicates the occurrence of a dilution effect in this bTB disease system. High MSR can reduce the positive effect of cattle density on both bTB persistence and recurrence. This dilution effect is possibly explained by 'encounter reduction', in that the addition of alternative hosts may decrease the risk of pathogen transmission by reducing encounter rates between susceptible and infected hosts (Keesing *et al.* 2006). Many mammal species that can be infected by bTB are spillover or dead-end hosts and do not transmit the pathogen efficiently (Corner, 2006; Renwick *et al.* 2007). The presence of these non-competent wildlife species might act as barriers to herd movement of cattle and reduce encounter rates among herds, which leads to decreased probabilities of bTB persistence and recurrence in cattle. A few previous studies indicated that herbivores may forage in limited areas in the presence of other species, especially predators (Howery and DeLiberto, 2004). However, the understanding of effects of wildlife on livestock movements is still lacking and needs more studies. In addition, we cannot exclude the possibility that the dilution effect we found might be caused by some other predictors correlating with MSR. For example, higher mammal species might occur in nature reserves where fences are frequently

used to prevent contact between wildlife and livestock. These fences are also able to interfere with cattle movements and thus lead to a 'pseudo' dilution effect.

Buffalo was found to have a positive identity effect on both bTB persistence and recurrence in cattle. The positive interaction between buffalo and cattle density in bTB persistence indicates that the positive effect of cattle density on bTB persistence was amplified under high buffalo occurrence. Theoretical studies suggested that the probability of pathogen persistence is indeed positively related to host density (Lloyd-Smith *et al.* 2005). As a maintenance host, buffalo can increase the effective encounter rates among cattle herds by frequently contacting different cattle herds, especially because they have similar habitat and dietary requirements, and thereby increase the effect of cattle density on pathogen persistence. For bTB recurrence, the positive association between buffalo and bTB recurrence might be caused by buffalo that spread the pathogen from infected regions to pathogen-free regions. Also, as a reservoir species, buffalo could preserve the pathogen and transmit it to cattle in the regions without cattle infection, triggering bTB recurrence in cattle. Previous studies suggested that maintenance hosts are more likely to remain in the community with decreased biodiversity (Johnson *et al.* 2012; Huang *et al.* 2013*a*), which indicated that the positive effect of a maintenance host might also be underlain by the dilution effect. In this study, however, we did not find a significant negative correlation between MSR and buffalo occurrence, suggesting the independence of the identity effect from the dilution effect. For greater kudu, neither bTB persistence nor recurrence was correlated with the presence of greater kudu, which might indicate that greater kudu is not a maintenance host for *M. bovis*.

Climate plays a role in the epidemiology of bTB through affecting the survival of *M. bovis* (Wint *et al.* 2002; Rhodes *et al.* 2007). Extreme temperatures and

precipitation (i.e. mean temperature of the warmest month and mean precipitation in driest month in the preceding year) were found to be correlated with bTB persistence. This is probably because hot and dry weather precludes long-time survival of *M. bovis* (Wint *et al.* 2002; Rhodes *et al.* 2007; Humblet *et al.* 2009, 2010). However, we did not find any significant relationship between climatic variables and bTB recurrence, which indicates that climate might exert little effect on pathogen re-establishment in cattle at this scale of analysis.

In summary, our study showed that wildlife substantially influences regional patterns of bTB persistence and recurrence. Mammal species richness was negatively correlated with bTB persistence and recurrence, suggesting the existence of a dilution effect, while buffalo as the maintenance host species had a positive identity effect. Our study also underlines the relevance of different ecological/climatic factors in determining bTB risk, and suggests that bTB persistence and recurrence are correlated with different sets of risk factors. These results are relevant for more effective control strategies and better targeted surveillance measures in bTB.

SUPPLEMENTARY MATERIAL

To view supplementary material for this article, please visit http://dx.doi.org/S0031182013002357

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