



Original Contribution

Synergistic Effects of Grassland Fragmentation and Temperature on Bovine Rabies Emergence

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Abstract: In 2007, common vampire bats were the source of the first outbreak of paralytic bovine rabies in Uruguay. The outbreak coincided in space and time with the fragmentation of native grasslands for monospecific forestry for wood and cellulose production. Using spatial analyses, we show that the increase in grassland fragmentation, together with the minimum temperature in the winter, accounts for the spatial pattern of outbreaks in the country. We propose that fragmentation may increase the connectivity of vampire bat colonies by promoting the sharing of feeding areas, while temperature modulates their home range plasticity. While a recent introduction of the virus from neighboring Brazil could have had an effect on outbreak occurrence, we show here that the distribution of rabies cases is unlikely to be explained by only an invasion process from Brazil. In accordance with previous modeling efforts, an increase in connectivity may promote spatial persistence of rabies virus within vampire bat populations. Our results suggest that land use planning might help to reduce grassland fragmentation and thus reduce risk of rabies transmission to livestock. This will be especially important in the context of climatic changes and increasing minimum temperatures in the winter.

Keywords: Spatial autoregressive models, Geographically weighted regression, *Desmodus rotundus*, Minimum mean temperature, Spillover, Uruguay

INTRODUCTION AND PURPOSE

The combination of landscape change and increasing anthropogenic food availability for wildlife may influence wildlife demographics, foraging behavior, and immune responses, affecting the spatial and temporal dynamics of infectious diseases (Gottdenker et al. 2014; Becker et al. 2015). Species' behavioral responses to landscape change in particular may be bounded by their ability to adapt phys-

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ologically to changing environmental conditions (Weiner 1992; Wong and Candolin 2015). In particular, low temperatures and associated heat loss might limit the energy budget of species and their ability to respond plastically (Weiner 1992). Hence, populations living close to the limit of the species distribution could exhibit lower plasticity to respond to various environmental changes.

In Latin America, vampire bats (*Desmodus rotundus*) have replaced dogs as the main source of rabies infection, following successful control campaigns of canine rabies in many countries (Vigilato et al. 2013; Velasco-Villa et al. 2017). Vampire bats feed on vertebrate blood (primarily mammals), and this foraging ecology facilitates transmission of rabies virus through saliva. In 2007, an explosive outbreak of paralytic bovine rabies (i.e., 200 cattle deaths within two weeks) was detected for the first time in Uruguay (Botto Nuñez et al. 2019). Vampire bats were confirmed as the source of infection through virus isolation and evident feeding on livestock, and the outbreak cost the country ~ USD 2 million in immediate vaccination expenses (Guarino et al. 2013; Botto Nuñez et al. 2019). Bovine rabies outbreaks have continued to occur sporadically in the northeast region of the country (Fig. 1), suggesting that the virus continues to circulate. The last outbreak was recorded in March 2017 (Botto Nuñez et al. 2019). Rabies has not spread to other areas of Uruguay, despite abundant livestock and the presence of vampire bats throughout the country (Botto Nuñez et al. 2019). Uruguay presents a novel case-study as vampire bat-borne rabies spilled over into a livestock population that has robust surveillance. Given the conditions of the country, it is unlikely that a rabies outbreak would go undetected by animal health authorities, suggesting that the outbreak in 2007 was likely the first introduction of the virus (Botto Nuñez et al. 2019).

Uruguay, in contrast with most other Latin American countries, has experienced an increase in forest cover over the past 30 years (Ministerio de Ganadería Agricultura y Pesca 2012; Hansen et al. 2013). However, rather than reforestation efforts, this change has been caused by monospecific exotic forestry for wood and cellulose production replacing highly diverse native grasslands (Silveira and Alonso 2009). This commercial exotic forestry fragments the native grasslands, replacing them with habitat that provides little or no food for vampire bats. Fragmentation of natural ecosystems has been often associated with pathogen emergence, persistence, and spillover (Schneider et al. 2001; Schneider et al. 2009; Gottdenker et al. 2014; de

Thoisy et al. 2016; Rulli et al. 2017; Faust et al. 2018; Mastel et al. 2018). However, grassland fragmentation is under-represented in the fragmentation literature (Fardila et al. 2017). Forest fragmentation has been associated with pathogen spillover through increased contact between reservoir and recipient hosts (e.g., edge effects) or by changes in abundances and diversity of reservoir species (e.g., dilution effects) (Rulli et al. 2017; Faust et al. 2018). However, the effects of fragmentation on reservoir host movement and subsequent disease dynamics have been less studied (Gottdenker et al. 2014). Moreover, habitat fragmentation is predicted to have strong effects on host movement and infection dynamics, particularly in highly mobile hosts such as bats, but quantifying such changes in natural systems is challenging (Hess 1996; Plowright et al. 2011; Becker et al. 2017; Becker et al. 2018c; Kessler et al. 2018). Thus, this grassland system provides an opportunity to test different effects of land-use change on pathogen spillover.

Commercial forestry in the 2007 outbreak area increased more than tenfold in the previous 17 years (from 17,967 ha in 1990 to 256,874 ha in 2007 in Rivera and Tacuarembó Departments), and this is now the most forested territory in the country (Ministerio de Ganadería Agricultura y Pesca 2012). During the same period, livestock production in the area also increased (Dirección de Estadísticas Agropecuarias 2011; Dirección de Estadísticas Agropecuarias 2014a). Owing to this simultaneous increase in forestry area and livestock herds, domestic animals, the primary food source of vampire bats (Voigt and Kelm 2006a; Streicker and Allgeier 2016), are now concentrated in increasingly scattered grassland habitat patches. This increase in livestock density may have driven an increase in size of vampire bat colonies, as demonstrated in previous work in Latin America (Streicker et al. 2012; Delpietro et al. 2017; Becker et al. 2018a), while the concentration of this food source in fewer, separated patches could alter vampire bat foraging patterns and population connectivity. Specifically, this shifted distribution of livestock could increase foraging times of bats roosting within forest patches and facilitate more overlap of bats in these shared feeding patches between colonies (Delpietro et al. 2017; Botto Nuñez et al. 2019).

While rabies virus has typically been considered an epizootic pathogen that travels in spatial waves (Delpietro and Nader 1989; Johnson et al. 2014; Benavides et al. 2016), longitudinal studies of vampire bats in Perú suggest that the pathogen instead persists enzootically within this reservoir host (Streicker et al. 2012). Previous data-driven

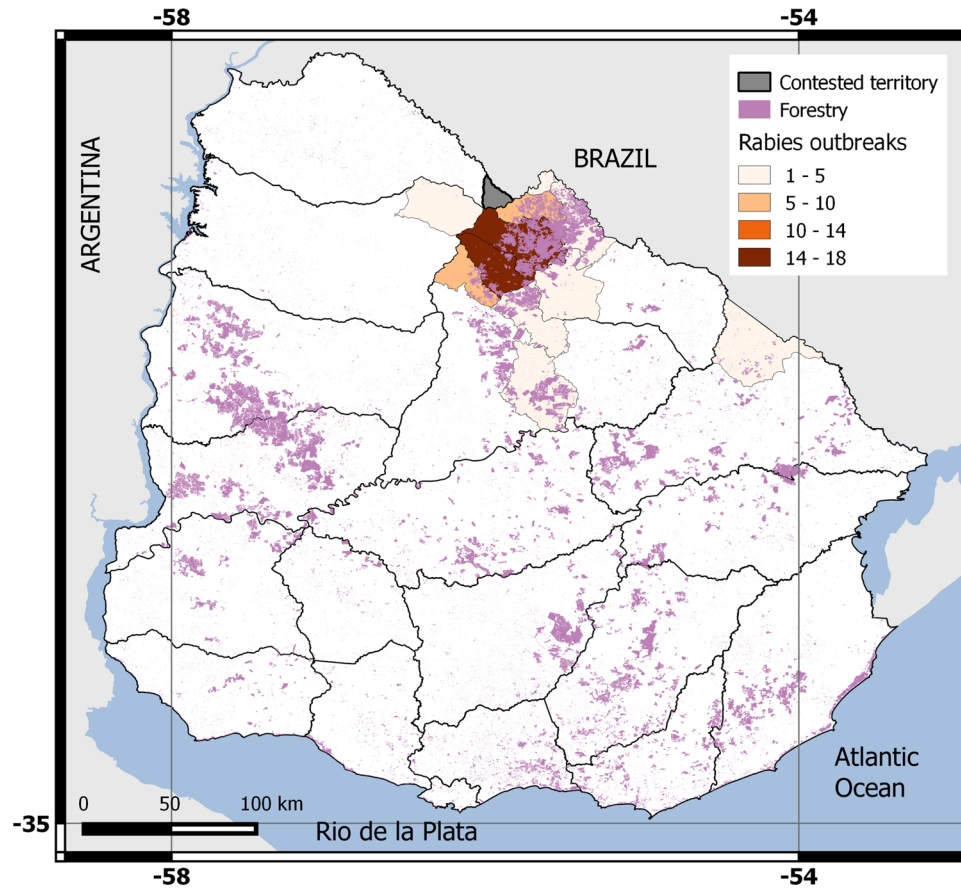


Figure 1. Distribution of ranches with bovine rabies cases in Uruguay from 2007 to 2017, and distribution of exotic forestry areas in 2011. Data from the Uruguayan Ministry of Livestock, Agriculture and Fisheries (MGAP) and the Uruguayan National Environment Office (DINAMA).

mathematical models from Perú also accordingly suggest that rabies cannot persist in isolated populations of vampire bats. Asynchronous connectivity and metapopulation dynamics facilitate persistence of rabies virus alongside frequent (non-lethal) immunizing exposures (Blackwood et al. 2013). Thus, increases in population connectivity and inter-colony interactions at shared feeding sites driven by these shifts in livestock distribution in Uruguay could facilitate rabies persistence.

The plasticity of changing foraging times, in response to changes in livestock distribution, could be constrained by temperature, as heat loss limits bat flight times (McNab 1973; Weiner 1992; Wong and Candolin 2015). Hence, the effects of changes in livestock distribution need to be disentangled from the effects of climate variables. Particularly, minimum temperature of the coldest month has been identified as an important limiting factor for the distribution of vampire bats (McNab 1973; Zarza et al. 2017; Hayes and Piaggio 2018). This finding has two main explanations: lowest temperatures in roost sites determine the energy

expenditure necessary to maintain body functions, and air temperature determines heat loss during flight, limiting its duration and foraging distances (McNab 1973).

Here, we used an extensive and spatially explicit dataset from Uruguay to describe the spatial structure of rabies outbreaks across the country and to test the spatial association between rabies outbreaks and landscape transformation. Specifically, we aimed to examine how the distribution of bovine rabies outbreaks was associated with the fragmentation of grazing areas, the density of commercial afforestation, the concentration of livestock, and temperature. We predicted that (a) outbreak densities of rabies would be higher in more fragmented landscapes where livestock is concentrated in separated patches and (b) vampire bats' ability to respond to fragmentation of livestock rearing areas would be limited by minimum winter temperatures.

METHODS

Study Area

Uruguay is located in the southern cone of South America (Fig. 1). The climate is temperate with an annual rainfall of 1300 mm and mean temperature of 17°C, with latitudinal variations across the country (20°C and 1600 mm in the north, and 16°C and 985 mm in the coast) (PNUMA 2008). Uruguay is generally flat, with a median elevation of 104 meters above sea level, and with a maximum altitude of 514 m. Uruguay is included in the Uruguayan biogeographic region—a landscape that is dominated by sub-tropical grasslands, modified by agricultural activities in varying degrees (Evia and Gudynas 2000; PNUMA 2008).

Spatial Data

We obtained the distribution of 2007–2017 rabies outbreaks from the Uruguay Ministry of Livestock, Agriculture and Fisheries. We aggregated the rabies data to the counts of rabies-quarantined ranches (i.e., an individually owned livestock-rearing facility) per police precinct, which are the geostatistical units used in Uruguay (Uruguay Census and Statistics Bureau, INE).

Spatial data on the distribution of livestock were obtained from the National Agricultural Census, which is performed regularly (at least every 10 years) by the Uruguay Ministry of Livestock, Agriculture and Fisheries. The information is publicly available for 2011 at the scale of census tracts (Dirección de Estadísticas Agropecuarias 2011; 2014a; 2014b). The total number of cattle, horses, and sheep were recorded for each agricultural census tract, as these species are common prey of vampire bats (Bohmann et al. 2018) and are raised mostly free roaming in ranches, and so their density can be calculated for large areas. We did not include poultry in this analysis, as these are generally exploited as a secondary food source to domestic herbivores (Bobrowiec et al. 2015). As livestock species vary in size and thus blood available for vampire bats, we used livestock biomass to approximate prey availability (Becker et al. 2018a). Total livestock biomass was obtained by summing species counts multiplied by mean body mass (kg; Jones et al. 2009).

The distribution of forestry and grassland areas was obtained from the National Environment Bureau (Dirección Nacional de Medio Ambiente - DINAMA) for the years 2000 and 2011 (Alvarez et al. 2015; DINAMA 2017),

based on interpretation of Landsat TM and ETM+ images following the Land Cover Classification System (Alvarez et al. 2015; Di Gregorio 2016). We used the categories Natural Herbaceous (He), Shrubs (Ar), Palm Groves (Pa), and Naturally Flooded Areas (ANi) as areas compatible with livestock rearing (see Supplementary Table S1 for the Land Cover Classification System legend used in Uruguay and the categories selected). We used the category Forestry Plantations (PF) to indicate non-native forests. Spatial data on average minimum temperature for the coldest month (BIO6) were obtained from WorldClim database version 2 (Fick and Hijmans 2017). All spatial data were projected using the WGS84 / UTM 21S (EPSG 32721) coordinate system and converted into rasters with cell sizes of $\sim 100 \text{ km}^2$ and then incorporated into a hexagonal grid of 500 km^2 cells based on weighted averages. Although these data on spatial covariates range from 2000 to 2011 (and rabies data range from 2007 to 2017), the vast majority of rabies cases in Uruguay occurred through 2010 (Figure S1). Following processing spatial data, all analyses were conducted in R (R Core Team 2016).

Fragmentation Analysis

For each land-cover layer (years 2000 and 2011), we created one spatial variable for livestock areas and another for non-native forests. Four cell-based metrics were used to assess fragmentation of livestock areas, both for 2000 and 2011: proportion of landscape (pl), number of patches (n), mean patch size (mps), and effective mesh size (ems) (Jaeger 2000; Baldi et al. 2006; Baldi and Paruelo 2014). For each cell c of the grid, we used the following formulas:

$$pl_c = \frac{1}{A_c} \sum_{i=1}^n A_{ic}$$

$$mps_c = \frac{1}{n_c} \sum_{i=1}^n A_{ic}$$

$$ems_c = \frac{1}{A_c} \sum_{i=1}^n A_{ic}^2$$

where A_c is the area of the grid cell c , and A_{ic} is the area of each of the n_c grassland polygon inside the cell c . For non-native forests, we calculated the number of patches (fnp) and proportion of landscape (fpl) both for 2000 and 2011. We also calculated the recent change in the four fragmentation variables (i.e., n , pl , mps , ems) and the two forestry variables (i.e., fnp , fpl) from 2011 to 2000. As fragmentation

variables exhibited collinearity (Figure S2), we performed a principal component analysis (PCA) with the 12 variables of livestock area fragmentation, for 2000, 2011 and the change between 2000 and 2011 (Table S2). The PCA was performed over the correlation matrix, as the scale of the variables included varied significantly, using the function *princomp* from the *stats* package. Using the spectral decomposition (i.e., using *prcomp*) rather than the singular decomposition (i.e., *princomp*) gave similar results, with only inverted loadings on the second component (Figure S4).

Autocorrelation Analysis and Spatial Modeling

To explore the existence of simple spatial trends and to test for spatial stationarity needed to assess spatial autocorrelation, we fit a linear model for rabies outbreak density with the x and y coordinates of the centroids of the grid cells and the xy interaction, as the predictors. As a significant effect was detected, residuals were then used as the response variable for all remaining analyses.

Because rabies data could show spatial autocorrelation (i.e., nearby areas have similar outbreak densities), we calculated a global index on the model residuals via Geary's *C* using the *spdep* package (Bivand et al. 2013; Bivand and Piras 2015; Brunsdon and Comber 2015). This analysis used a Monte Carlo randomization to assess statistical significance and row-standardized spatial weights for the neighbors list.

To next test how landscape changes were associated with the distribution of rabies outbreaks, we fit a spatial autoregressive model (SAR) (Brunsdon and Comber 2015) for the residuals of the linear model, using the *spdep* package, because an ordinary least squares linear model is not appropriate for spatially autocorrelated data (Bivand et al. 2013; Bivand and Piras 2015). We included livestock biomass, the amount of fragmentation in livestock areas, the recent changes in fragmentation, non-native forest land cover, and the mean minimum temperature of the coldest month as predictors. We used a forward selection process, including one variable in each step, based on the improvement of Akaike's information criterion (AIC). We used a difference of two units in AIC as the minimum improvement to include a variable (Burnham and Anderson 2002) and used an intercept-only model as a null model. We assessed the degree of spatial dependence in the model by estimating the value of λ in the fitted model using the *spdep* package (Bivand et al. 2013; Bivand and Piras

2015; Brunsdon and Comber 2015). To assess whether the model accounted for autocorrelation, we tested the residuals for Geary's *C* (Jetz et al. 2005; Brunsdon and Comber 2015).

To investigate the local variation of the effect of the environmental variables, we next fit a geographically weighted regression (GWR) (Lichstein et al. 2002; Jetz et al. 2005) for the residuals of the linear model, using the *spgwr* package (Bivand and Yu 2017) and the same predictors used for the SAR model (i.e., recent changes in fragmentation, non-native forest land cover, and the mean minimum temperature of the coldest month). This method allows estimating coefficients that vary across space. The varying coefficients can account for local effects not included in the model. Again, we followed a forward selection process (and considered an intercept-only model), but to avoid overfitting, we considered the AIC value for the global model (i.e., with stationary coefficients for each variable) for the selection. We also tested residuals for Geary's *C* to assess whether the top model accounted for autocorrelation.

To obtain the final predictions from the spatial modeling, we added the predictions from the linear regression to the predictions of each of the spatial models (i.e., fitted(LM) + fitted(SAR) and fitted(LM) + fitted(GWR), as both SAR and GWR were fitted using the residuals of the linear regression as the response variable. All data and R scripts to reproduce our analyses are available in a Zenodo repository: <https://doi.org/10.5281/zenodo.3735667>

RESULTS

Fragmentation Analysis

The first principal component (*pc.frag1*) explained the 46.74% of the total variance (Figure S3) and was related to fragmentation status. *pc.frag1* increased with the increase in number of patches or with the decrease in proportion of landscape covered by livestock areas, the mean patch size, and the effective mesh size. The second principal component (*pc.frag2*) explained the 20.94% of the total variance and was associated with recent change in fragmentation. Negative values in the *pc.frag2* are indicative of increased fragmentation from 2000 to 2011. Both components showed positive and significant spatial autocorrelation, being greater for the second component (*pc.frag1*: $C = 0.25$, p value < 0.01 ; *pc.frag2*: $C = 0.52$, p va-

lue < 0.01). Fragmentation was more intense in the western and southwestern region (related to intensive crop production, mainly soybean, wheat, corn, and sorghum) and in the northeastern region (related to commercial afforestation) (Fig. 2a, b). Recent changes in forest coverage were related to increased fragmentation in the northeastern region (Fig. 2a–d).

Autocorrelation Analysis and Spatial Modeling

The density of ranches with rabies cases (Fig. 3a) was significantly predicted by longitude, latitude, and their interaction in our initial linear model (adjusted $R^2 = 0.19$, $p < 0.01$, Table S3). Fitted values suggested an underlying northeast-to-southwest gradient in bovine rabies outbreaks, with higher expected values in the northeast and decreasing values in the northeast-to-southwest direction (Fig. 3B, Figure S5). We accordingly found positive and significant autocorrelation ($C = 0.38$, $p < 0.01$) in the detrended residuals (Figure S6, S7). This suggests additional spatial structure in the outbreaks beyond the latitudinal–longitudinal gradient where areas with higher density of cases are clustered. In subsequent spatial models, we used these residuals as our response variable.

We next fitted a SAR model to the detrended density of ranches with rabies cases (linear model residuals). The final model included the change in number of forestry patches (*c.fnp*) and the mean minimum temperature of the coldest month (*temp_jul*; $w_i = 0.98$). This model showed an improvement from the model containing only the change in number of forestry patches (*c.fnp*; $\Delta AIC = 8.22$, $w_i = 0.02$; Table 1) and showed a discrete but significant positive spatial effect ($\lambda = 0.88$, $p < 0.01$). Residuals showed no significant spatial autocorrelation ($C = 0.96$, $p = 0.15$, Figure S8), implying that spatial structure was accounted for by the SAR. Combining the fitted values from the SAR and the linear model for simple trends accounted for a large portion of the variability in the original density of ranches with rabies cases ($R^2 = 0.76$; Fig. 3, A and C, Figure S12 A, Table S5).

The final GWR model included the first component of the fragmentation PCA (*pc.frag1*), the change in number of commercial forestry patches (*c.fnp*), the change in proportion of landscape covered by forestry (*c.fpl*), and mean minimum temperature of the coldest month (*temp_jul*) (Table 2, Figure S9). The differences in AIC and Akaike weights were much larger when evaluating the weighted models than when comparing the global regression models:

the Akaike weights were 0.78 and 1.00 for the best model in the global regression and the weighted regression, respectively (Table 2). There was no trend in the values of the fitted coefficients in relation to the values of each variable (Table S4, Figure S10). A trend in the fitted coefficients would have suggested an unaccounted process, linking the explanatory variable with the disease density. While there was some spatial heterogeneity in the distribution of residuals, these were not concentrated in the area of the outbreaks. Residuals again showed no significant spatial autocorrelation ($C = 1.13$, $p = 0.99$, Figure S11). When combined with the predictions from the linear model, the GWR offered a better prediction of the distribution of the density of ranches with rabies cases (Figure 3, A and D; $R^2 = 0.94$, Figure S12 B, Table S5).

DISCUSSION

Rabies virus has been present in the regions neighboring Uruguay (i.e., southern Brazil and northern Argentina) for more than a century, yet vampire bat rabies was not detected in Uruguay until 2007 (Botto Nuñez et al. 2019). Given robust surveillance and historical records of vampire bats, the absence of rabies spillover in Uruguay cannot be explained by failure to detect the disease nor by the absence of the bat reservoir; a recent historical review suggests that contemporary changes in the ecology of rabies may better explain this recent phenomenon of emergence (Botto Nuñez et al. 2019). The largest expansion of commercial afforestation in the northeast region of the country coincides with the emergence of rabies in the area in space and time and could potentially explain the recent outbreaks, which we tested in our spatial analyses.

We hypothesized that concentration of livestock in separated patches might increase contact of previously unconnected vampire bat colonies, increasing pathogen transmission and facilitating pathogen persistence (Botto Nuñez et al. 2019). We in turn quantified the process of patch isolation, as represented by the mesh size and the number of patches, rather than more commonly used measures in epidemiological studies such as edge size, which is important as a proxy for the rate of contact between patches and matrix (Olivero et al. 2017; Rulli et al. 2017; Faust et al. 2018). Fragmentation metrics are diverse, and usually the effects of habitat loss and changes in habitat configuration are not disentangled (Fahrig 2003). In our system, contact rates between the reservoir host (vampire

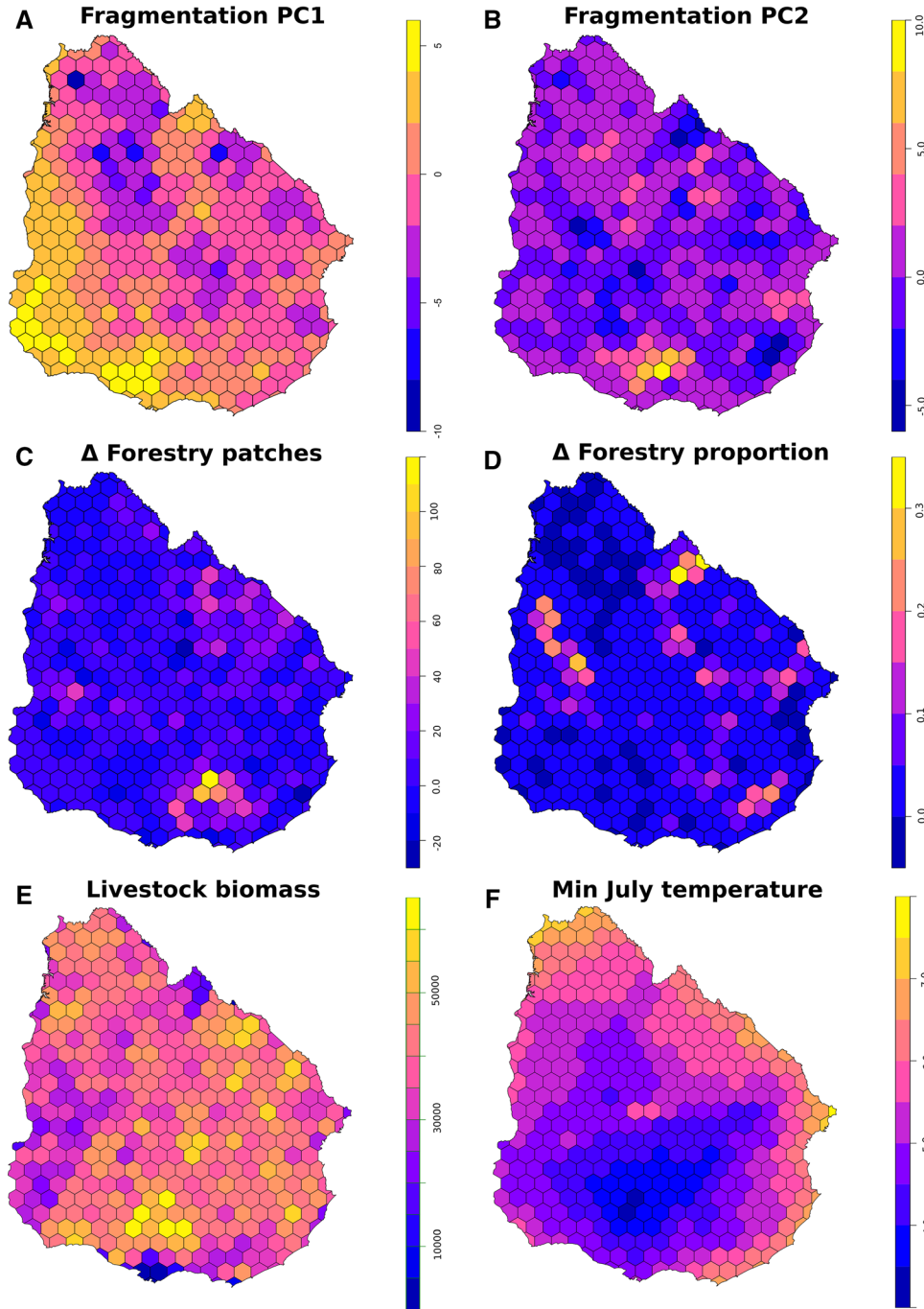


Figure 2. Spatial distribution of predictive variables used for modeling the density of ranches with rabies cases. **A.** Fragmentation PC1 (*pc.frag1*), positive values indicate higher fragmentation of livestock areas. **B.** Fragmentation PC2 (*pc.frag2*), recent changes in fragmentation of livestock areas, negative values indicate increased fragmentation from 2000 to 2011. **C.** Δ forestry patches (*c.fnp*), change in number of exotic forestry patches between 2000 and 2011. **D.** Δ forestry proportion (*c.fpl*), change in proportion of landscape covered by exotic forestry between 2000 and 2011. **E.** Livestock biomass (*liv.biom*), considering cattle, horses, and sheep. **F.** Minimum Jul temperature (*temp_jul*), average minimum temperature of the coldest month,

bats) and the recipient hosts (livestock) are not driven by edge length, as vampire bats are already using livestock as their main (and perhaps, in many areas, only) food source (Voigt and Kelm 2006b; Bobrowiec et al. 2015; Becker et al.

2018b; Bohmann et al. 2018; Botto Nuñez et al. 2019). In contrast with other studies of the relationship between infectious disease emergence and habitat fragmentation, fragmentation of livestock rearing areas in our system is not

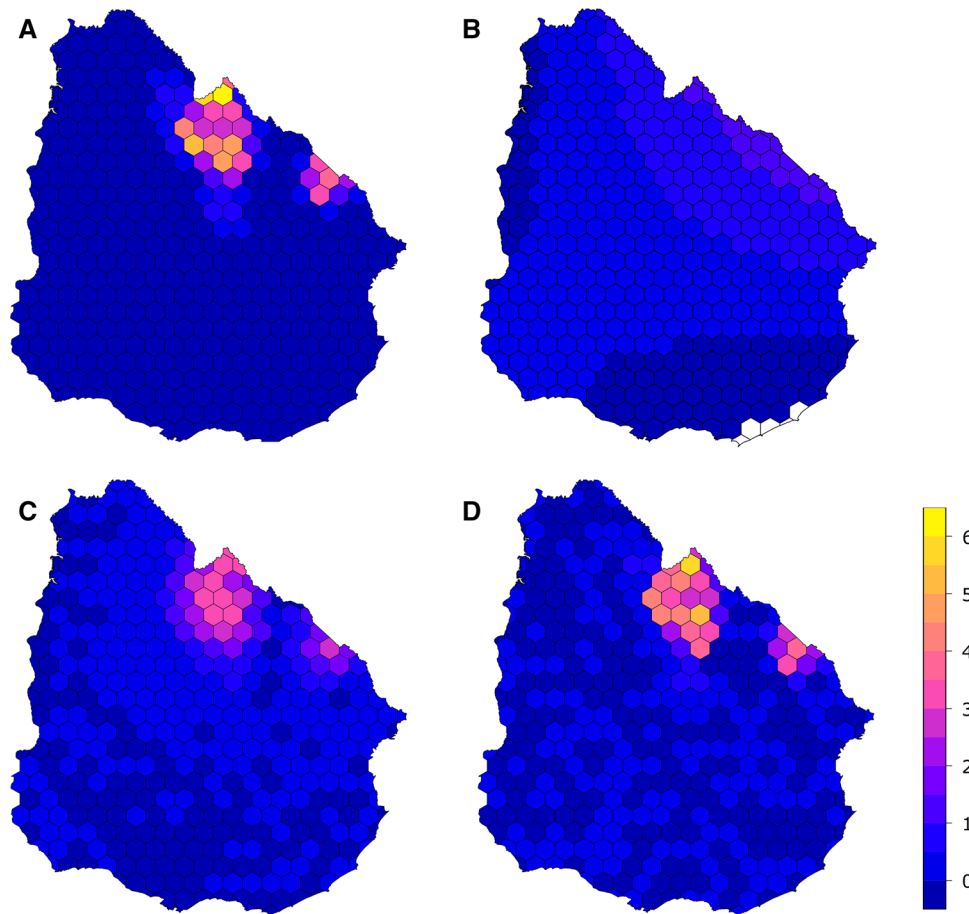


Figure 3. Measured and estimated rabies density: **a** Calculated density of ranches with rabies cases in the regular grid, from the data from official veterinary services. **b** Distribution of fitted values from the linear regression showing a northeast-to-southwest trend on the density of ranches with rabies cases. There are higher expected densities in the northeastern region of the country and decreasing values in the northeast-to-southwest direction (see also Figure S5 for an enhanced color scale for these predicted values). **c** Predicted density of ranches with rabies cases in the regular grid, combining the predictions of the simultaneous autoregressive model and the linear model. **d** Predicted density of ranches with rabies cases in the regular grid, combining the predictions of the Geographically Weighted Regression and the Linear model. Color scale is the same for the four maps.

related to decreased availability or abundance of food or roosts (Olivero et al. 2017; Rulli et al. 2017; Faust et al. 2018). Instead, the direct effect of fragmentation in our system is a change in the spatial distribution of food sources, impacting the foraging strategies of bats and hence the connectivity and contacts between colonies. Thus, a novel approach to fragmentation (in relation to emergence of infectious diseases) was implemented to represent this different proposed mechanism.

We summarized the livestock area fragmentation process in two principal components that described overall fragmentation and recent changes in fragmentation. Both components showed significant spatial structure. Western and southwestern fragmentation areas were mainly related to cropland intensification (particularly soybean produc-

tion), while northern areas were related to commercial afforestation (Fig. 2a), which has increased recently (more negative values of *pc.frag2*, Fig. 2b) (PNUMA 2008). The commercial afforestation process was highly stimulated by policies promoting and providing economic incentives to forestry ventures (PNUMA 2008).

We detected a spatial trend likely related to invasion of rabies from Brazil, as higher predicted values of rabies outbreaks were observed close to the northeastern border and decreased in the southwestern direction; however, this did not fully explain the spatial distribution of rabies cases (Fig. 3a, b). While an introduction of the virus from Brazil is likely, as outbreaks north of the border have been occurring for more than a century (Teixeira et al. 2008; Barbosa de Lucena 2009), this alone does not explain why

Table 1. Forward selection process for the SAR models. Estimated coefficients and p values (p) are presented for each variable (starred p values are significant at 0.05 level), and differences in Akaike information criteria values in comparison with the best ranking model (Δ AIC), and Akaike weights (w_i) are shown for each model. The first step, considering an intercept-only model, is used as null model.

Variables	Estimate	p	Δ AIC	w_i
Step 1: <i>detrended_residuals</i> ~ 1			14.44	0.00
<i>Intercept</i>	0.00			
Step 2: <i>detrended_residuals</i> ~ <i>c.fnp</i>			8.22	0.02
<i>Intercept</i>	− 0.04			
<i>c.fnp</i>	0.01	* < 0.01		
Step 3: <i>detrended_residuals</i> ~ <i>c.fnp</i> * <i>temp_jul</i>			0.00	0.98
<i>Intercept</i>	− 0.27			
<i>c.fnp</i>	− 0.04	* < 0.01		
<i>temp_jul</i>	0.04	0.68		
<i>c.fnp:temp_jul</i>	0.01	* < 0.01		

cases in Uruguay only occurred in this area, why they only occurred after 2007, and why pathogen transmission has not expanded since 2007. Rabies cases in Uruguay probably occurred in two independent invasions, both close to the Brazilian border (Figs. 1, 3a), but neither expanded south, despite the presence of bats and livestock throughout Uruguay (Botto Nuñez et al. 2019). This could be further confirmed by phylogeographic analyses if sequences from both foci are made available.

One important spatial measure missing in our study is the local abundance of vampire bats, which is currently unavailable for Uruguay. Although presence and absence data can often be useful for estimating occupancy (which can serve as a surrogate for abundance in some contexts; MacKenzie and Nichols 2004), vampire bats are habitat generalists (Greenhall et al. 1983) and are present throughout Uruguay (González and Martínez-Lanfranco 2010). In lieu of spatial data on vampire bat abundance, livestock abundance might be a useful approximation, as livestock biomass indicates food availability that, along with roosts, limits vampire bat colony size. There is an ongoing survey of vampire bat roosts in Uruguay, but surveillance is higher in or near areas where rabies outbreaks have occurred. Mark–recapture studies would also be useful to estimate vampire bat colony sizes and connectivity.

The SAR model was able to capture the spatial structure of the rabies outbreaks, as the residuals from the model did not show spatial autocorrelation (Figure S8). The positive and significant λ estimate also showed positive spatial dependence in the rabies outbreaks with the two predictive variables included in the final model: the recent change in proportion of landscape occupied by forestry and the average minimum temperature in the coldest month. It is interesting to note that rabies outbreaks did not occur in areas with the largest livestock populations (Botto Nuñez et al. 2019). Livestock populations in Uruguay are large enough to sustain large populations of vampire bats, even in the relatively low-density areas; this could explain the lack of a significant effect of livestock in our analysis (González and Martínez-Lanfranco 2010; Botto Nuñez et al. 2019). In contrast, the minimum temperature in the winter had significant effects (both SAR and GWR models, Tables 1 and 2). While temperature variation is moderate within the country, Uruguay is on the edge of the limit of the tolerance range for the species (McNab 1973; Greenhall et al. 1983). Winter temperatures might influence the length of foraging flights, affecting the ability of vampire bats to modify their home ranges in response to resource's fragmentation.

The GWR model was used mainly as a descriptive analysis to explore the effect of allowing regression coefficients to vary spatially. The results showed significant effects of fragmentation level, the recent changes in forestry, and the coldest temperatures. Allowing spatial variation in the coefficients allowed splitting the regional effects and accounted for unobserved variables, such as the potential influx of the virus from the north. While the fitting process for the GWR model does not guarantee that the model accounted for the global spatial autocorrelation in the response variable, the final model fitted showed no spatial structure in the residuals (Figure S11).

Temperature is a major determinant of the distribution of vampire bats due to their poor thermoregulatory capacity and low tolerance for periods of fasting. Lacking fat storage, vampire bats cannot deal with a series of cold nights where energy invested in foraging flight is not compensated by energy obtained from feeding (McNab 1969; McNab 1973; Greenhall et al. 1983). Uruguay is in the southern limit of the species' distribution, and while *Desmodus rotundus* is present throughout the country, the cold temperatures might limit the distance they can fly to feed in the winter. For instance, if food sources become patchier, vampire bats roosting in higher temperatures could modify

Table 2. Forward variable selection process for the GWR models. The global component of the four fitted GWR is shown. Differences AIC values and Akaike weights (w_i) are shown for each model, in comparison with the best ranking model, both from the global regression ($\Delta AIC[GR]$; $w_i [GR]$) and from the GWR model ($\Delta AIC[GWR]$; $w_i [GWR]$). Global estimated coefficients are presented for all included variables, along with the p values (p; starred p values are significant at 0.05 level). Response variable: residuals from the linear model (*detrended_residuals*). The first step, considering an intercept-only model, is used as null model.

Variables	Estimate	p	$\Delta AIC [GR]$	$w_i [GR]$	$\Delta AIC [GWR]$	$w_i [GWR]$
Step 1: <i>detrended_residuals</i> ~ 1			35.41	1.60×10^{-8}	162.46	5.28×10^{-36}
Intercept	0.00					
Step 2: <i>detrended_residuals</i> $\sim pc.frag1$			15.09	4.13×10^{-4}	282.37	4.83×10^{-62}
Intercept	0.00					
<i>pc.frag1</i>	0.08	* < 0.01				
Step 3: <i>detrended_residuals</i> $\sim pc.frag1 + c.fnp$			7.14	0.02	255.74	2.92×10^{-56}
Intercept	- 0.06					
<i>pc.frag1</i>	0.08	* < 0.01				
<i>c.fnp</i>	0.01	* < 0.01				
Step 4: <i>detrended_residuals</i> $\sim pc.frag1 + c.fnp + c.fpl$			2.75	0.20	228.05	3.02×10^{-50}
Intercept	- 0.10					
<i>pc.frag1</i>	0.08	* < 0.01				
<i>c.fnp</i>	0.01	* < 0.01				
<i>c.fpl</i>	1.92	*0.01				
Step 5: <i>detrended_residuals</i> $\sim pc.frag1 + c.fnp + c.fpl + temp_jul$			0.00	0.78	0.00	1.00
Intercept	- 0.62					
<i>pc.frag1</i>	0.08	* < 0.01				
<i>c.fnp</i>	0.01	* < 0.01				
<i>c.fpl</i>	1.95	*0.01				
<i>temp_jul</i>	0.10	*0.03				

(expand) their home ranges. By contrast, those colonies roosting in places with lower temperatures during winter nights might exhibit limited plasticity in home ranges, as the energy needed for foraging is inversely related to temperature. Thus, colder temperatures in the winter might modulate the effect of patchiness of food sources on connectivity. The area where the outbreaks occurred has recently fragmented livestock areas as well as the highest minimum temperatures in the winter (Fig. 2). During the 20th century, there was an overall increase of 0.8°C, where minimum temperatures increased all year round (PNUD 2007). A regional study also concluded that in the period 1960–2000 and based on daily minimal temperatures, there was a consistent trend of increase in temperature of coldest nights and an increase in the number of warm nights (Vincent et al. 2005). This trend is more evident in coastal areas (Vincent et al. 2005). For the next decades, the temperature is expected to keep rising with a total increase of 1.0–2.5°C for 2050 (in relation to the 2000) (Vincent

et al. 2005). In this context, and combined with increased land use change and fragmentation of native grasslands (Baldi and Paruelo 2014), understanding how temperature affects plasticity of wildlife to respond to other environmental changes is crucial for predicting potential pathogen spillover risks.

In this work, we showed that the spatial distribution of rabies outbreaks can be explained by a combination of landscape fragmentation and climatic conditions. The recent changes in landscape structure in Uruguay, explained by changes in land use practices, can explain the occurrence of recent outbreaks in the early 2000 s. However, temperature might limit the expansion of rabies into other areas of Uruguay. Our results show that an understudied fragmentation process, such as grassland fragmentation, might have an important effect on the dynamics of infectious diseases. Processes that affect movement of individuals across roosts, such as culling activities, have been proposed to facilitate persistence of rabies virus in vampire bat co-

lonies (Streicker et al. 2012; Blackwood et al. 2013). Similarly, changes in the distribution of food sources can facilitate persistence by increasing contact among colonies. Our results also suggest that physiological limits imposed by temperature affect how species respond to landscape change, modulating how fragmentation may affect the spatial spread of pathogens. More work is needed to disentangle the effects of temperature from the effects of habitat fragmentation. In particular, field studies on how vampire bat home ranges vary across fragmentation and temperature gradients are needed to understand the effects of both variables on vampire bat connectivity and ultimately on rabies virus persistence and spillover risk. Such work would also link habitat and disease data on identical timescales and provide greater inference into associations between environmental change and rabies dynamics in bats and livestock.

CONCLUSION

The effects of temperature in combination with fragmentation are major factors in determining the spatial pattern of rabies outbreaks in Uruguay. Even when the effects of virus invasion were removed, fragmentation and temperature explained the spatial structure of disease. These results are consistent with our hypotheses that fragmentation could enhance connectivity among vampire bat colonies and promote viral persistence by increasing the rate of immigration of infected individuals. This increased ability of the virus to persist would likely facilitate virus transmission to livestock. The congruence between the conceptual results from both models provided stronger support for the effects of fragmentation on disease emergence. While more experimental support is needed for causal inference and directing policy (such as field-based estimations of vampire bat home ranges across a gradient of fragmented areas), our results suggest that land use planning might help to reduce fragmentation of livestock rearing areas when planning new forestry ventures to help reduce the risk of rabies to livestock. In particular, incorporating metrics of fragmentation of natural grasslands into environmental impact assessment would account for habitat disturbance. Given our results, future work should also analyze landscape fragmentation in the context of climate change, as temperature modulates the responses bat behavior to the fragmentation of food sources.

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