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Research paper

Landscape epidemiology in urban environments: The example of rodent-borne *Trypanosoma* in Niamey, Niger

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ABSTRACT

Trypanosomes are protozoan parasites found worldwide, infecting humans and animals. In the past decade, the number of reports on atypical human cases due to *Trypanosoma lewisi* or *T. lewisi*-like has increased urging to investigate the multiple factors driving the disease dynamics, particularly in cities where rodents and humans co-exist at high densities. In the present survey, we used a species distribution model, Maxent, to assess the spatial pattern of *Trypanosoma*-positive rodents in the city of Niamey. The explanatory variables were landscape metrics describing urban landscape composition and physiognomy computed from 8 land-cover classes. We computed the metrics around each data location using a set of circular buffers of increasing radii (20 m, 40 m, 60 m, 80 m and 100 m). For each spatial resolution, we determined the optimal combination of feature class and regularization multipliers by fitting Maxent with the full dataset. Since our dataset was small (114 occurrences) we expected an important uncertainty associated to data partitioning into calibration and evaluation datasets. We thus performed 350 independent model runs with a training dataset representing a random subset of 80% of the occurrences and the optimal Maxent parameters. Each model yielded a map of habitat suitability over Niamey, which was transformed into a binary map implementing a threshold maximizing the sensitivity and the specificity. The resulting binary maps were combined to display the proportion of models that indicated a good environmental suitability for *Trypanosoma*-positive rodents. Maxent performed better with landscape metrics derived from buffers of 80 m. Habitat suitability for *Trypanosoma*-positive rodents exhibited large patches linked to urban features such as patch richness and the proportion of landscape covered by concrete or tarred areas. Such inferences could be helpful in assessing areas at risk, setting of monitoring programs, public and medical staff awareness or even vaccination campaigns.

1. Introduction

In 2014, 54% of the world's population was urban, a proportion that is expected to reach 66% by 2050 (United Nations, 2014) making urban areas management one of the most important challenges of the 21st century. In Africa, cities represent ca. 40% of the population and still grow fast, currently showing a rate of nearly 3.4% per year, the highest in the World (Anderson et al., 2013). Many of these fast-growing cities involve unplanned areas of dense and impoverished slums with inadequate infrastructures, basic services, medical facilities or public amenities (Simon et al., 2006), often resulting in a marked spatial heterogeneity in terms of population health (Pacione, 2009). As such, they correspond to an intermediate situation between western cities in which the main sources of morbidity and mortality arise from chronic degenerative conditions linked to older adulthood, and underdeveloped rural areas where pandemics of infections and parasitic and dietary diseases are the chief causes of death (see the epidemiological transition concept Omran, 1971). Although health resources are usually concentrated in cities and scarce in rural areas, they often do not beneficiate to the inhabitants living in slums and shantytowns (Brockerhoff and Brennan, 1998), leading to the notion of “urban penalty” (Pacione, 2009) and “urban double burden” (Agyei-Mensah and de-Graft Aikins, 2010). From another perspective, the intra-urban contrasts in health led to the development of the inverse care law which stipulates that the availability of good medical care is inversely proportional to the need for it (Hart, 1971). This phenomenon is well documented (Oni et al., 2016; Timæus and Lush, 1995) and might be further amplified by climate change (Sverdlik, 2011). This puts emphasis on the urgent need of developing accurate tools to better understand and anticipate health hazards in spatially explicit urban frameworks.

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Spatial epidemiology is the study of spatial variation in disease risk or incidence and the ecological and/or socio-economic factors that shape it (Brooker, 2007; Ostfeld et al., 2005). The presence of human infectious diseases, particularly of host- and/or vector-borne ones, depends on multiple factors, a critical one being the existence of suitable conditions for the maintain of host and vector species of epidemiological significance (Hartemink et al., 2015). Species distribution models (SDM) are widely used in ecology and conservation biology to depict species geographical distributions in relation to environmental data (Franklin, 2009; Peterson, 2011). These tools are also increasingly being used to predict the potential distribution of large-scale disease and/or associated hosts/vectors spatial patterns, both at present or under various climate change scenarios. They have proved very useful in veterinary epidemiology (Alkhamis and VanderWaal, 2016; Escobar et al., 2014; Escobar et al., 2015) and medicine (Ben-Ari et al., 2012; Colacicco-Mayhugh et al., 2010; Costa et al., 2014; Kulkarni et al., 2010; Otranto et al., 2006). Species distribution models are often based on climatic descriptors that do not vary much at the scale of a city the size of Niamey (several km). As a consequence, they offer limited explanatory power in the context of more focused studies, such as city-centered surveys, since urban environments are, by essence, strongly human- and physically-modified environments. In the case of cities, landscape composition and physiognomy appear pertinent factors as they directly reflect habitat availability for reservoirs and hosts hence pathogens, as well as the probability of contact between them (Hartemink et al., 2015; Lambin et al., 2010). Landscape ecologists have developed numerous mathematical indices (i.e. the landscape metrics) that capture spatial attributes such as composition or physiognomy of natural landscapes or agro-ecosystems (Romme, 1982; Turner et al., 2001) and urbanized areas (Clifton et al., 2008; Luck and Wu, 2002). Fitting SDM with landscape metrics is therefore a possible way to account for landscape features in modeling species distribution. Importantly, a critical issue of landscape description is scale dependency (Wu, 2004). Indeed, landscape metrics may strongly vary according to the size of the buffer zone surrounding the focus point used in the computations. For that particular reason, it has been emphasized that using a set of different buffer size appears to be a reasonable strategy (Barve et al., 2011).

We here present a survey that focuses on the spatial epidemiology of rodent-borne *Trypanosoma*, especially *T. lewisi* in the city of Niamey, Niger. *Trypanosoma lewisi* is a worldwide distributed kinetoplastid protozoa that essentially parasites rodents, especially Rattini species (i.e. *Rattus* and allies Tatard et al., 2017), and that is transmitted by fleas through their excreta. Although it is usually considered as non-pathogenic for humans, transient and lethal infections have been documented in humans from Asia and Africa (Howie et al., 2006; Kaur et al., 2007; Sarataphan et al., 2007; Truc et al., 2013; Verma et al., 2011). Furthermore, *T. lewisi* is now considered as potential infective in humans since this parasite was found to be resistant to normal human serum, like the congeneric species *T. brucei* and *T. cruzi* responsible for sleeping sickness and Chagas disease, respectively (Lun et al., 2015). Although the risk of emergence remains to be demonstrated (Brun, 2005), *T. lewisi* receives more and more attention as a new potential threat for human health (Lun et al., 2015; Maia da Silva et al., 2010; Truc et al., 2013). This has urged to investigate the multiple factors driving the disease dynamics, particularly in cities where rodents and humans co-exist at high densities (Pumhom et al., 2015).

Created *ex nihilo* at the very end of the nineteenth century by French colonizers (Motcho, 2010; Salifou, 2010; Sidikou, 2011) Niamey is an illustrative example of the rapid urban population growth typical of colonial African cities with a population increasing from > 30,000 in the late 1950s, to > 1,200,000 inhabitants today (Adamou, 2012; Institut National de la statistique, 2012; Motcho, 2010; Sidikou, 2011). Population expansion at low density has led to urban sprawl and development of informal settlements with weak governance structure, high levels of poverty and limited infrastructure and service deliveries (Diop, 2008; Olvera et al., 2002). The purpose of our study is to address the relationships between the spatial distribution of rodent-borne *Trypanosoma* and both the composition and the physiognomy of the urban landscape across the city of Niamey using SDM. To achieve this, we have characterized urban landscape using the metrics developed in landscape ecology and explored their relationships with the occurrences of trypanosomes using the maximum entropy method (Maxent) (Elith et al., 2011; Phillips et al., 2006). In addition, we provide maps of landscape suitability depicting the citywide risk of being exposed to the pathogen. The identification of such areas is an important prerequisite achievement for the set up of new researches and sampling campaigns, for public awareness as well as public health management purposes.

2. Materials and methods

2.1. Study site: the city of Niamey

Niamey is the capital city of Niger and lies on the Niger River in a typical semi-arid Sahelian region. The climate is characterized by high temperatures (monthly average temperatures range between 22 and 36 °C) and low rainfalls (ca. 540 mm per year) with a single rainy season usually occurring between May and September (Adamou, 2012). Since its creation ca. 120 years ago, the city has experienced a continuous though recently accelerated demographic growth associated with a spectacular spatial expansion. As commonly observed in the developing countries, the rapid urbanization of Niamey is accompanied by the appearance of numerous informal settlements, thus leading to a marked socio-economical variability across the city (Diop, 2008; Olvera et al., 2002). The present survey relies on a Geographic Information System (GIS) of Niamey implemented from a SPOT satellite image (scene reference number 506 132 308 121 010 151 32 T; CNES 2008, resolution of 2 m) using 8 land-cover categories: Niger river, ponds, bare soils, tarred areas, concrete areas, trees, other greenings and sheet steel-made roofs (Fig. 1). The satellite image was converted into a raster map of 2 m by 2 m resolution for landscape analyses (see below). The EPSG projection is 32631 - WGS 84/UTM zone 31N (http://spatialreference.org).

We encountered a peculiar problem due to the traditional use of unfired ground as a building material (referred to as “banco”) in Niamey. When used to construct the roof, this indigenous building material led to a spectral signature nearly identical to that of bare soil leading to a sole land-cover class and, as a consequence, some settlements were mistaken for bare soil. Fortunately, these “banco”-made roofs are more and more often replaced by sheet steels and nowadays mostly occur in two underprivileged and old districts named Gamkaleye and Karadjé (Fig. S1, Supplementary material).

2.2. Pathogens and hosts: sampling and identification

Rodent assemblages in Niamey have been described previously (Garba et al., 2014) on the basis of molecular and chromosomal data, thus allowing us to unambiguously identify each specimen at the species level. In total, > 14,000 night-traps were placed in 52 localities of Niamey, allowing us to capture 987 rodents (see Fig. 2 in Tatard et al., 2017). Two groups of species were collected: one rural-like group (i.e. *Arvicanthis niloticus*, *Cricetomys gambianus*, *Mus nannomys hausa* and *Taterillus gracilis*) that inhabits rice fields and market-gardens occurring within the city, and a group of strictly commensal species (i.e. *Mastomys natalensis* and the invasive *Mus musculus* and *Rattus rattus*) associated with the human infrastructures of the core city. Furthermore, within the commensal species, the native *M. natalensis* almost strictly segregated spatially from the two invasive species, namely *Mus musculus* (house mouse) and *Rattus rattus* (black rat) (Garba et al., 2014).

Among the 987 rodents trapped, 896 individuals originating from 184 georeferenced sites were captured alive and could thus be monitored for the presence of *Trypanosoma* as described in details elsewhere

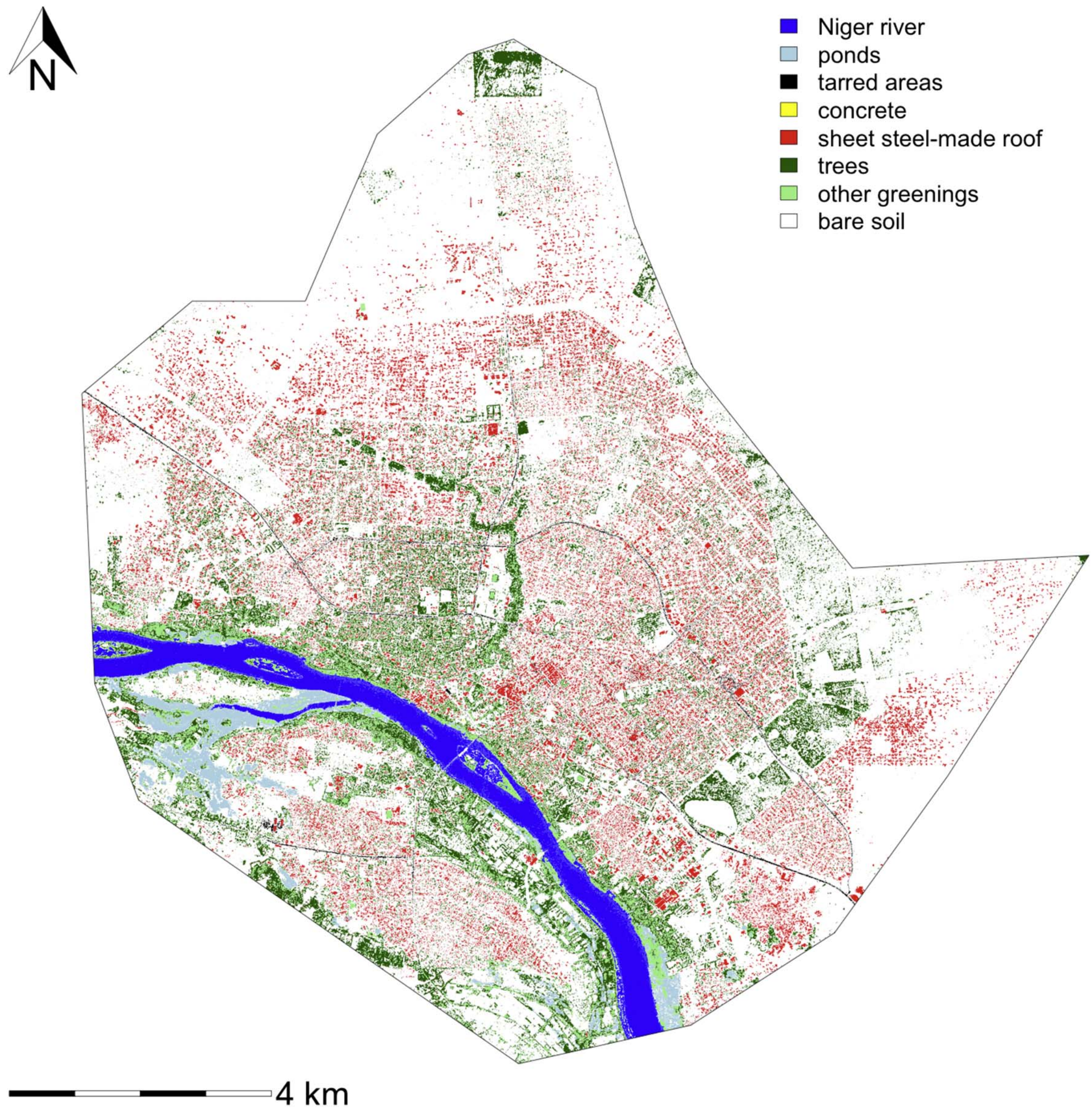

Fig. 1. Map of the city of Niamey (Niger). Eight land-cover classes are represented (see text for details).

(Dobigny et al., 2011; Tatard et al., 2017) and used for the present study. They belonged to *Cricetomys gambianus* (n = 12), *Taterillus gracilis* (n = 2), *Mus N. hausa* (n = 1), *Arvicanthis niloticus* (n = 65), *Mastomys natalensis* (n = 599), *M. musculus* (n = 64) and *R. rattus* (n = 153). *Trypanosoma*-carrying rodents were searched using a qPCR approach that targets a 131 bp long fragment of the 18S rDNA gene (Dobigny et al., 2011; Tatard et al., 2017). *Trypanosoma* species hosted by qPCR-positive rodents were then investigated using PCR and sequencing of a 400 bp long fragment of the kinetoplastid SSU rDNA gene (Dobigny et al., 2011; Tatard et al., 2017). Rodents were sampled in 2009 and 2010. For some sampling locations, the pathogen was searched but was not found. We did not interpret these negative results as true absences since they may be explained by different factors other than habitat unsuitability sensu stricto (e.g., host that has not been in contact with the pathogen yet; infection under detection threshold) (Peterson, 2011).

2.3. Landscape analysis

The urban landscape of Niamey was characterized by means of class and landscape level metrics calculated using the software FRAGSTATS (McGarigal et al., 2012). The term 'landscape metrics' refers to indices developed for categorical maps describing landscapes. They are used with the aim to capture some of the synoptic features of landscapes such as composition and physiognomy. Class metrics focus on one land-cover class (e.g. bare soil, trees…) while landscape metrics consider all classes simultaneously (Turner et al., 2001). We used one class metrics reflecting landscape composition (PLAND) and 4 landscape metrics listed in Table 1 (see details in Turner et al., 2001). It must be noted that class and landscape metrics are derived from the same categorical map which implies that many metrics are correlated or collinear and provide partially redundant information (McGarigal et al., 2012). For that reason we have limited the number of metrics used in the models and focused on landscape composition (PLAND), richness and diversity measures (PRD, SIEI) as well as contagion and edge density estimations (CONTAG, ED). The metrics were computed for circular buffers of increasing radii (20 m, 40 m, 60 m, 80 m and 100 m) so as to capture landscape features at different spatial scales (i.e. for different resolutions). We positioned buffers on each pixel of the raster map displayed in Fig. 1 and computed the metrics on the local landscapes thus delimited. Such method is referred to as moving window strategy in landscape analysis (McGarigal et al., 2012). The resulting values were

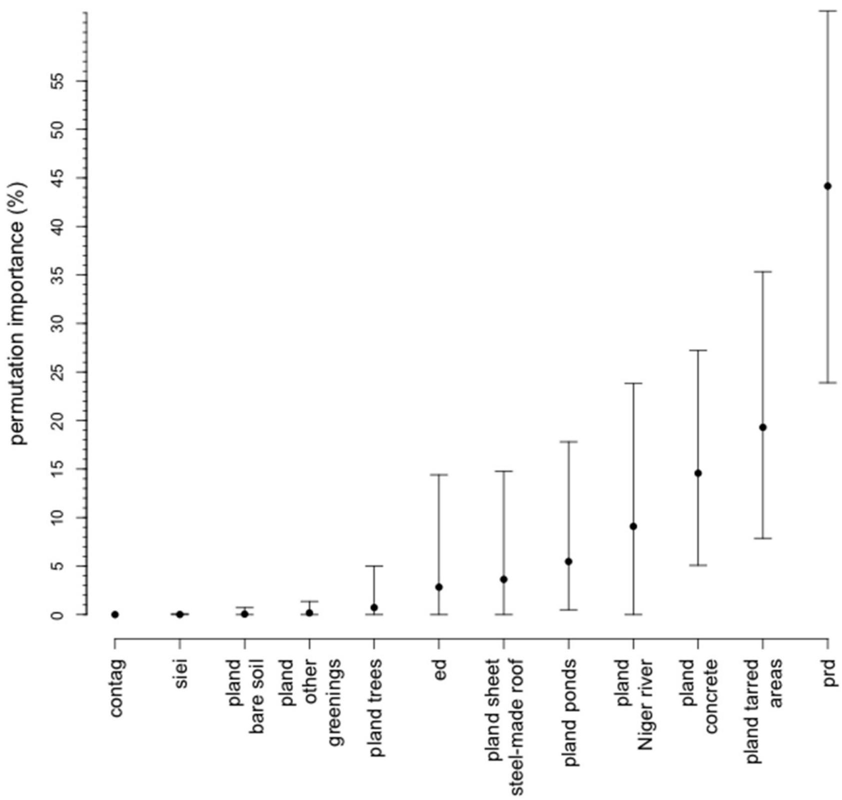

Fig. 2. Average permutation importance of the landscape descriptors involved in the Maxent models (n = 350) for buffers of 80 m radius over 350 runs. Error bars indicate the quantiles for p = 0.025 and p = 0.975. PLAND: Percentage of landscape, CONTAG: Contagion index, ED: Edge density, PRD: Patch richness density, SIEI: Simpson's evenness index. See Table 1 for metric definition.

returned to the centre cell thus yielding a raster maps for each metric (examples are given in Fig. S2). Points where *Trypanosoma* was recorded were associated to the descriptors of the cell they fall in. These raster maps also provided background data for model calibration and citywide prediction (see below).

2.4. Modeling framework

We modeled the distribution of *Trypanosoma*-positive rodents by means of Maxent, one of the most commonly used presence-only methods (Elith et al., 2006; Phillips et al., 2006). Maxent uses occurrence and background data in conjunction with environmental descriptors (here landscape metrics) to make a correlative model of the environmental conditions that best reflect the species' ecological requirements. In our case, the number of occurrences was small (114) and the outputs of the model were expected to be affected by the random partitioning of the data used in the fitting and evaluation. We therefore considered a batch of 350 models for each buffer size and summarized the outputs by a map depicting the frequency of models predicting the presence of *Trypanosoma*-positive rodents (see details below and in Fig. S3). We adopted a two steps strategy to build the model corresponding to each of the 5 spatial resolutions explored. First we assessed the optimal parameters for the Maxent model using the full dataset and second, we used these parameters to fit and evaluate Maxent models using random partitioning of the dataset.

Because species' responses to environmental constraints are often complex, it is usually useful to fit nonlinear functions (Elith et al., 2006) and for that reason the parametrization of Maxent involves choosing which kinds of transformations (referred to as feature classes or FCs) of original environmental descriptors are to be used (i.e. linear, quadratic, product, hinge and threshold: Phillips and Dudik, 2008). The parametrization of Maxent also involves a regularization multiplier (RM) introduced to reduce overfitting (Merow et al., 2013). There is a growing body of evidences showing that the default settings of Maxent may not be optimal in all situations and might lead to poorly performing models in some cases (Radosavljevic et al., 2014; Shcheglovitova and Anderson, 2013). It is therefore advised to search for the best parameters given the dataset at hand (Radosavljevic et al., 2014). We built models with RM values ranging from 0.5 to 4 with increments of 0.5 and 6 FC combinations (L, LQ, H, LQH, LQHP, LQHPT with L = linear, Q = quadratic, H = hinge, P = product and T = threshold) using the R package ENMeval (Muscarella et al., 2014). This led to 48 different models. For each spatial resolution, these models were fitted using all the occurrence points and 10,000 background points. The optimal settings corresponded to the models giving the minimum AICc values (see Muscarella et al., 2014, for details). We

Table 1
Metrics used to describe the urban landscape in the city of Niamey (adapted from McGarigal et al., 2012). Level indicates if the metrics are computed for land-cover classes or for landscape as a whole.

Acronym	Name	Level	Description	Unit
PLAND	Percentage of landscape	Class	PLAND is a measure of landscape composition: how much of the landscape is comprised of a particular land-cover	Percent
CONTAG	Contagion index	Landscape	CONTAG measures the overall clumpiness on categorical map.	Percent
ED	Edge density	Landscape	Edge density (ED) quantifies the edge length in a per unit area basis.	Meters per hectare
PRD	Patch richness density	Landscape	PRD measures richness as the number of different land-covers in a landscape in a per area basis.	Number per 100 ha
SIEI	Simpson's evenness index	Landscape	SIEI expresses the evenness component of diversity by controlling for the contribution of richness to the diversity index	None

evaluated the performance of the AICc-selected models using the AUC metric (Fielding and Bell, 1997) and the Boyce index (Hirzel et al., 2006). The Boyce index is a reliable presence-only evaluation measure that varies between −1 and +1. Positive values indicate a model which predictions are consistent with the distribution of the presences in the evaluation dataset. The Boyce index was calculated using the R package ecospat (Broennimann et al., 2016).

Having assessed the best FC and RM values for each resolution (i.e. buffer size) we run 350 independent models using the R package dismo (Hijmans et al., 2016). In each case, the Maxent model was set up using the optimal RM and FC values, a training dataset constituted by a random subset of 80% of the occurrences and 10,000 background points. Each model was used to predict the landscape suitability across the city of Niamey using the logistic output of MaxEnt (Phillips and Dudik, 2008). Suitability values were transformed into presence/absence binary maps by applying the threshold at which the sum of the sensitivity (true positive rate) and specificity (true negative rate) was the highest (Liu et al., 2005). The 350 resulting binary maps were summarized by computing, for each pixel, the proportion of models predicting the presence of rodent-borne *Trypanosoma* (details are given in Fig. S3). For each model, the permutation importance of the environmental descriptors was assessed by randomly permuting (jackknife) the predictors' values between presence and background points and examining the change in the AUC (Phillips, 2017).

3. Results

3.1. Rodent sampling and prevalence of rodent-borne Trypanosoma

Although this is not within the scope of the present paper, our results of molecular screening of rodent-borne *Trypanosoma* in Niamey are briefly recalled below (for details, see Tatard et al., 2017). In total, qPCR allowed us to identify 114 (12.6%) *Trypanosoma*-positive rodents, with the highest prevalence observed in *C. gambianus* (6 positive individuals out of 12; 50%) and *R. rattus* (45/153; 29.4%), followed by *M. musculus* (6/64; 9.3%), *M. natalensis* (52/599; 8.7%) and *A. niloticus* (5/63; 7.9%), while no positive were found in the very poorly sampled *T. gracilis* (N = 2) and *M. n. hausa* (N = 1). *Trypanosoma* sequences could be retrieved only from 33 *Trypanosoma*-positive animals: 31 sequences (all obtained from *R. rattus*) corresponded to *T. lewisi* or *T. lewisi*-like, while 2 sequences (both from *C. gambianus*) were similar to *T. microti*. Although this may cast some doubt on the species-specific identification of *Trypanosoma* parasiting some of the rodents in Niamey, it is highly probable that most of them belong to *T. lewisi* or *T. lewisi*-like (Tatard et al., 2017). However, for the purpose of the present paper, we chose to remain stringent, and to consider rodent-borne *Trypanosoma* spatial distribution as a whole.

3.2. Maxent parametrization

The regularization multiplier and the feature class of the models selected with AICc are given in Table 2. The values of the AUC ranged from 0.70 for a resolution of 20 m to 0.79 for a resolution of 80 m. The Boyce index was positive and ranged between 0.82 and 0.90. Both metrics indicated that model fitted to the landscape data measured with buffers of 80 m performed better (larger AUC and larger Boyce index). The 350 independent models fitted using the latter FC and RM values yielded AUC values ranging from 0.55 to 0.85 indicating a high variability in model performances. Again, the resolution of 80 m led to the best performing models.

3.3. Importance of the environmental descriptors

The Fig. 2 shows the average permutation importance of each landscape metric over the 350 models for the resolution of 80 m and the corresponding quantiles for p = 0.025 and p = 0.975. The patch richness density was the most important variable although its permutation importance varied markedly from one run to another as indicated by its statistical envelope. Various composition metrics also contributed to a lesser extent to the model. They reflected the proportion of landscape covered by tarred areas and concrete as well as the Niger river (see also the maps of these metrics in Fig. S2, Supplementary material).

Table 2
Optimal feature classes and regularization parameters and two evaluation metrics for Maxent models linking urban landscape features computed for 5 different spatial resolutions to the occurrences of *Trypanosoma*-positive rodents in the city of Niamey (Niger). L = linear, Q = quadratic, H = hinge and P = product. In a first step, the Maxent models were fitted with the full dataset to determine the optimal feature class and regularization multiplier (one model per spatial resolution). The AUC (full dataset) and the Boyce index were computed for these models. The optimal RM and FC values were then used to fit 350 independent models with a training dataset constituted by a random subset of 80% of the occurrences and 10,000 background points. The right-column gives the range of the AUC values for these models.

Resolution	Feature classes (FC)	Regularization multiplier (RM)	AUC (Full dataset)	Boyce index	AUC (range)
20 m	LQHP	3.5	0.70	0.85	0.55–0.77
40 m	LQHP	3.5	0.75	0.82	0.60–0.82
60 m	LQHP	3.5	0.76	0.90	0.43–0.78
80 m	LQH	3.5	0.79	0.94	0.63–0.85
100 m	L	3	0.75	0.92	0.59–0.81

3.4. Models prediction

An example of the prediction (logistic output of Maxent) yielded for one of the 350 models fitted for buffers of 80 m can be seen in Fig. S4 (Supplementary material). Habitat suitability changed across the city and reached very high values in some localized hotspots. When converted into binary values using the threshold at which the sum of the sensitivity and specificity is maximum, those hot spots were easily identifiable (Fig. S4). Pixels considered as suitable for rodent-borne *Trypanosoma* formed more or less coalescent small to large patches. Aggregating the logistic outputs of the 350 models run for 80 m radius buffers yielded the maps displayed in Fig. 3: it shows the areas (in red) where a large proportion of models predict suitable environmental conditions for the pathogen. Applying the arbitrary frequency level of 95% led to the map displayed at the bottom of Fig. 3 where pixels in red are predicted as suitable for *Trypanosoma*-positive rodents in at least 95% of the model runs. We obtained a similar map for the resolution of 40 m and 60 m while buffers of 20 and 100 m led to more homogeneous map (Fig. S5, Supplementary material). The frequency threshold of 95% used in Fig. 3 was changed to yield maps for the values of 50%, 75% and 90% (Fig. S6, Supplementary material). Such maps reflect different perceptions of the risk associated to *Trypanosoma*-positive rodents.

4. Discussion

4.1. Mapping areas at risk in the city of Niamey

Risk maps associated to new potential zoonotic threat for human health are appealing because they provide a direct view of areas where efforts (e.g. host or vector monitoring and control, public awareness, environmental management actions, medical diagnostic and care) could be put in priority. As such, they constitute a major tool of health geography (Peterson, 2008). For instance, SDM predictions were recently implemented to map H7N9 risk in China (Xu et al., 2016). In the same manner, the modeling of the past, current and future distributions of *Aedes albopictus* (vector for dengue, chikungunya, zika, etc.) in Southern France has shown that the mosquito progression was faster and faster every year, but also that long-distance dispersals were poorly successful (Roche et al., 2015), thus suggesting that population control should

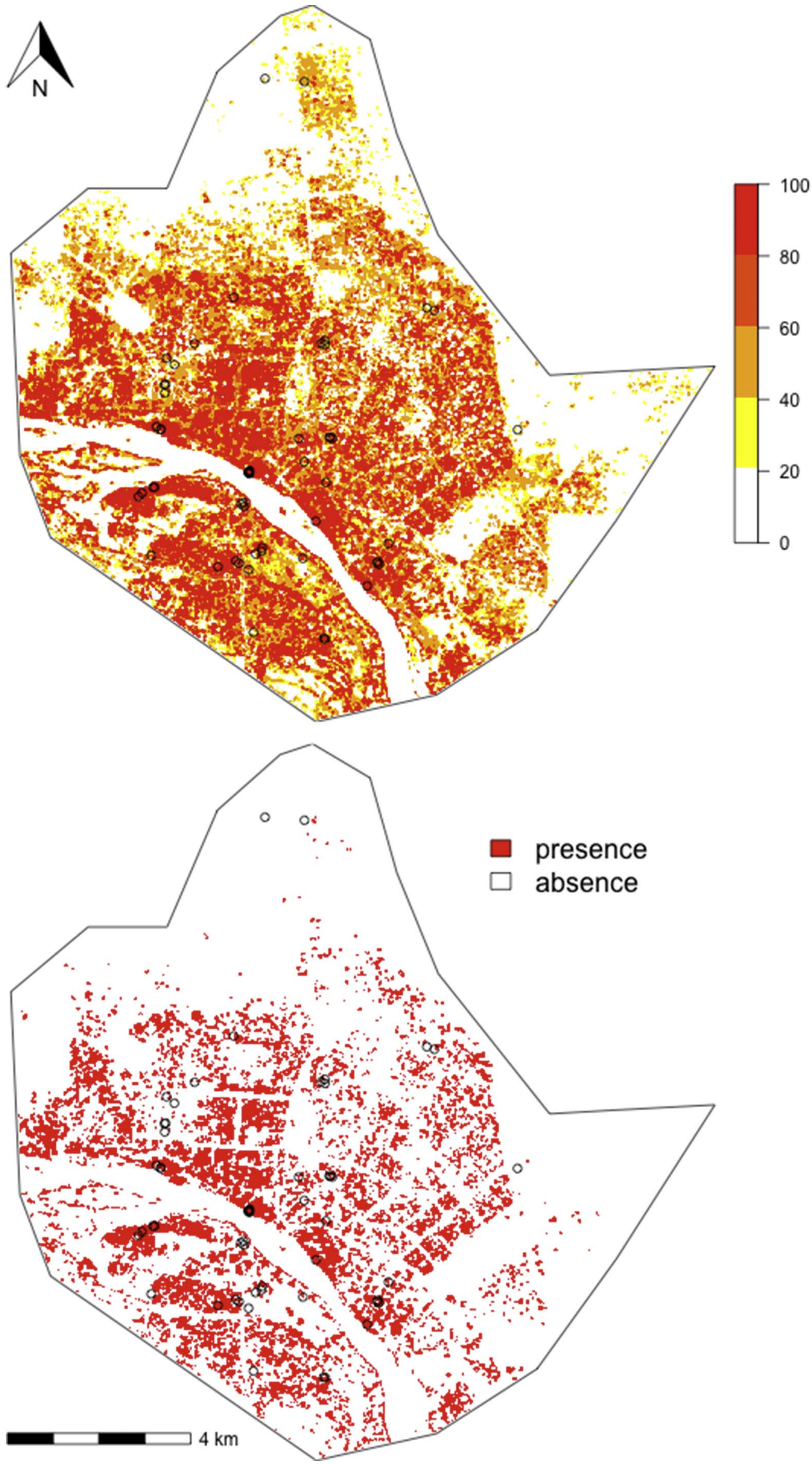

Fig. 3. Risk maps for the presence of *Trypanosoma*-positive rodents in the city of Niamey (Niger). Top: map of the frequency of models considering a given pixel as suitable for the *Trypanosoma*-positive rodents. Bottom: map showing the pixels considered as suitable in at least 95% of the Maxent models. The analysis is based on local landscapes corresponding to circular buffers of 80 m radius. Open circles indicate sampling locations where *Trypanosoma*-positive rodents were recorded. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

essentially be performed around the invasion front. Such models and risk maps are also precious to design long-term surveys and identify ecological and possibly socioeconomic factors that drive host and parasite spatio-temporal dynamics in urban settings. Changing the threshold frequency as we did in Fig. S6 (Supplementary material) adds certain flexibility in the interpretation of the results by allowing local authorities to decide what level of risk they are prepared to take.

The maps produced in the present survey revealed that areas at risk for rodent-borne trypanosomes are scattered across most of Niamey but with higher intensity along the Niger River course (Fig. 3). The spatial distribution of pixels predicted as suitable for *Trypanosoma*-positive rodents are not distributed as a few large patches but rather as many more or less coalescent small aggregates which density decreases with the distance from the Niger River. There is no obvious link with land-covers such as urban greenings or irrigated gardens that were shown to play an important role in maintenance and circulation of rodent-borne *Toxoplasma gondii* (Mercier et al., 2013) and pathogenic *Leptospira* (Dobigny et al., 2015). The percentage of landscape covered with the Niger River was found to have a moderate importance (ca. 10%) which could not be reliably interpreted. The importance of tarred areas and concrete was stronger but remains difficult to interpret in terms of causal relationships since the landscape metrics used in the study are inherently highly correlated. The difficulty in interpreting our results in terms of which variables matter most for the organism being modeled is discussed below.

The areas at risk identified using the models do not match with the areas colonized by *R. rattus* identified in Garba et al. (2014) although this species is a privileged reservoir for *T. lewisi* (Tatard et al., 2017). This may reflect the fact that *T. lewisi* is also largely hosted by other rodent species in Niamey but our molecular data cannot discard the presence of different species of *Trypanosoma* infecting several rodent species (see discussion in Tatard et al., 2017). Interestingly, our results show no obvious effect of the age of the district upon the risk since the models predict high level of risks both in the northern part of the city (oldest part of the city) and the right bank of the Niger River, which have been recently urbanized (mid 70s) (Motcho, 2004). Finally the risk maps produced in this survey do not match with the spatial pattern of poverty in the city of Niamey (see map p. 115 in Clément, 2000). Apart from the areas located in the vicinity of the Niger River, the localities where the risk is the greatest includes some advantaged neighborhoods such as Yantala Plateau (where, unfortunately, no rodent monitoring was organized).

4.2. Quantifying urban pattern with landscape metrics

This survey showed that the landscape metrics primarily developed to characterize natural or semi-natural landscapes provided acceptable predictors of *Trypanosoma*-positive rodent occurrences in an urban environment. This suggests that the form and the structure of urban landscape drive the providing of suitable habitats for the pathogen and its hosts, and/or impact the processes implied in its differential dispersion over space. The metrics from the different types of land-cover that were considered here (river, trees, sheet steel, tarred areas…) proved to be relevant to our modeling objective, but other helpful information could probably be added to the analysis. Indeed, the land-use data (e.g., residential, commercial, storage, industrial…) as well as the very local features (e.g., sanitary indoor conditions, construction types, food storage,…) would also be precious because they strongly affect the rodent community as well as rodent abundance within the urban habitats (Advani, 1995; Bradman et al., 2005; Dehghani et al., 2012; Garba, 2012; Langton et al., 2001; Murphy and Marshall, 2003; Omudu and Ati, 2010; Promkerd et al., 2008). Consequently, these factors are also expected to impact rodent-borne pathogen circulation hence transmission to human. We therefore believe that, when available, both land-cover and land-use data should be used to derive landscape metrics and to identify those associated with zoonotic risks, something that we were not able to do here because land-use data lacked. This study highlighted the effect of the spatial resolution used to compute the landscape metrics (also referred to as buffer size) upon model results. The model performances varied according to the scale considered and it was possible to identify one buffer size for which Maxent performed better. Such observations were also reported in agro-ecology (Rusch et al., 2011) or biodiversity (Rossi and van Halder, 2010) studies and definitely confirms the need for multiscale analysis to adequately characterize landscape heterogeneity including urban landscapes.

4.3. The problem of data scarcity

The number of occurrences of *Trypanosoma*-positive rodents is relatively low in this study and this prevented us from analyzing the distribution of the parasite for each rodent species separately. As stated earlier, in Niamey, rodent species differ in their habits and use of urban landscape, with one rural group of species (*A. niloticus*, *C. gambianus* and *T. gracilis*) on the one hand, and one native (*M. natalensis*) and two invasive (*M. musculus* and *R. rattus*) species strictly linked to human infrastructures on the other. Garba et al. (2014) showed a clear spatial segregation between these two species assemblages as well as between commensal native and invasive rodents. Such a segregation may be explained by the respective species-specific ecological affinities and the spatial pattern of their preferred habitats across the city as well as by a possible ongoing replacement of native species by the recently introduced black rats and domestic mice (Garba et al., 2014). Taking these elements into consideration, there is little doubt that analyzing each rodent species epidemiology would have allowed us to better characterize the landscape-host/parasite relationships and would have yielded much more precise risk estimation. Species-specific risk maps could be combined to yield a global risk appraisal based on the same principle as the ensemble forecasting in species distribution modeling (Araújo and New, 2007). A recurrent problem with epidemiological studies in developing countries is the lack of biological data or the scarcity of contextual information (e.g. here, the map of land-use) which limits the power of the analyses and models. This is all the more regrettable since third world cities and peri-urban areas are the places where such risk assessments are the most urgently needed. Nonetheless, the results presented in this paper show that it is possible to analyze small data sets and to obtain useful results.

4.4. Predictive vs. explanatory models

Predictive modeling can be defined as the process of applying a statistical model or data mining algorithm to data for the purpose of predicting new or future observations (Shmueli, 2010). The present study lies in the frame of empirical prediction, and it aims at producing maps of potential spatial distribution of *Trypanosoma*-positive rodents. As underlined by Shmueli (2010), predictive models have only slight and indirect relation to causal explanation. In our case, putative causal explanation would start by ranking and further testing the relationships between the landscape variables contributing to the model. Beyond the small size of our dataset and the fact that our explanatory variables are inherently collinear or correlated, it is the complex relationships in the biological system at hand that make it difficult to hypothesize and to construct a causal model. For instance, we have very poor knowledge of the impact of landscape at the local scale upon the ecology of each rodent species, of the parasite(s) and almost no piece of information about the flea vectors. In the same line, we know almost nothing about rodent/flea/trypanosomes/human interactions in the field, something that is yet pivotal to a good understanding of transmission dynamics. Of course, such a matter of fact precludes any cause-consequence hypothesis, hence explanatory modeling sensu Shmueli (2010). The landscape that exhibited the higher importance in the models was the patch richness density. It conveys very different sources of structuration such as city history, large scale features (e.g., the Niger River) and some local and/or recent features linked to urban planning and changes (e.g., the development of urban gardens) (Guèye et al., 2009). Two composition metrics also contributed to the model though to a lesser extent: the percentage of local landscape covered with tarred areas on the one hand, and covered with concrete on the other. These metrics may reflect the presence of resources for certain rodents and/or flea vectors (shops, storage areas) as well as environmental conditions favourable to rodent/flea/human transmission of trypanosomes. However, the measure of variable importance must be handled with extreme caution in particular because of the high level of correlation or the co-linearity between landscape metrics that complicates the interpretation of explanatory variables (see Dormann et al., 2013).

5. Conclusions

The SDM approach that we presented here aimed at mapping the distribution of a host-borne zoonotic agent, *Trypanosoma* spp., within the city of Niamey, Niger. Although they require quite a time-consuming fieldwork, we show here that such inferences could be helpful in the design of some environmental health strategies. In particular, it should lead to a better assessment of risk areas, and could thus be useful for the setting of monitoring programs, public and medical staff awareness or even vaccination campaigns. In some instances, SDM-based analysis could also point towards causal and testable hypotheses about disease maintaining, circulation and transmission to humans, thus providing new research guidelines.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.meegid.2017.10.006.

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