A R T I C L E

A REVIEW OF OTTER DISTRIBUTION MODELING: APPROACH, SCALE, AND METRICS

Ana L. QUIÑÓNEZ C.[1], Todd K. FULLER[1]*, and Timothy O. RANDHIR[1]

[1]Department of Environmental Conservation, University of Massachusetts,
Amherst, MA 01003, USA
e-mail: aquinonezcam@eco.umass.edu, randhir@eco.umass.edu, tkfuller@eco.umass.edu
**Corresponding author*

(Received 13th July 2017, accepted 11th January 2018)

ABSTRACT: All otter species are of conservation concern and are used both as flagship species for conservation and as indicators of watershed health; consequently, identifying and understanding their distribution is a basic necessity. We reviewed the published literature to identify otter distribution modeling efforts worldwide and then compiled information on the different metrics/variables used, what information is commonly available and what may be required, what different results can be obtained with different models, and model limitations. We identified 29 studies of 8 species that used 4 main methods of modeling otter distribution across a given area or the relationship between otter species and certain environmental factors. The studies modeled distribution across a variety of scales, including local, regional, country, continental, and at the geographic extent of the species. We cataloged 301 different environmental metrics used in otter models, which we then sorted into six main categories: anthropogenic disturbance, climate, terrestrial, aquatic, and biological interaction. Food, water availability and quality, and anthropogenic influences are all regularly identified as important variables correlating with otter distribution, but they are often measured in a variety of ways, or identified in models by proxy or surrogate variables because relevant data availability is low or absent. Scale, approach, and metric selection all need to be carefully considered for each study, but understanding measurement issues and model shortcomings identified by others should help improve otter modeling in the future. Review of information in this review paper can inform future efforts in modeling processes, data types used, data gathering methods, and variables/metrics to include. This information should still be carefully evaluated for use to specific study areas, species of interest, and as a basis for developing innovative, and more effective methods.

KEYWORDS - climate, habitat, landscapes, *Lontra*, *Lutra*, water

INTRODUCTION

All of 13 otter species in the world are on the International Union for Conservation of Nature Red List (IUCN Otters Specialist Group, 2013). They often are used as flagship species for conservation and are considered indicators of healthy watershed habitats (Kruuk, 2011; Stevens et al., 2011). Other than the two marine species (*Enhydra lutris* and *Lontra felina*), otters live in a variety of freshwater habitats, though some species may also be found along marshes, rocky coasts, and mangroves (Kruuk, 2006). In general, aquatic habitat requirements for otters include rivers that contain deep pools that retain water during the winter and dry seasons, dense vegetation surrounding the river for protection, rivers with sandy banks, and a substantial prey density (Pardini, 1998; Ruiz-Olmo et al., 2001; Kruuk, 2006; Sánchez, 2007). As apex predators, otters have an important role within their local food chain, feeding on fish, crustaceans, amphibians, and even birds, reptiles, and mammals (Pardini, 1998; Kruuk, 2006). Unfortunately, as semi-aquatic top predators, they also are highly vulnerable to habitat degradation, as well as to direct removal for the protection of other species and human livelihoods (e.g., fisheries and domestic fowl) and because of the value of their furs (Kruuk 2006, 2011; Scorpio et al., 2016).

Studying otters can be challenging because they are scarce, elusive, can be nocturnal, sometimes live in difficult-to-access habitats, and have fairly large territories and home ranges (Kruuk, 2011). Because of these factors, data collection can be expensive and labor-intensive (Kruuk, 2011). Consequently, the presence of some otter species is largely unknown over large geographic areas, population declines are nearly impossible to detect (Kruuk, 2011), and many questions about their biology, population sizes, and distribution remain unanswered (Foster-Turley et al., 1990; Kruuk, 2006). Thus, it is very challenging to try to ameliorate threats that affect otter persistence, since factors such as population and range size can affect their vulnerability (Brodie et al., 2013).

In the face of a biodiversity crisis, efforts are increasing to improve our understanding of species declines and conservation efforts (Marcelli and Fusillo, 2009). Understanding the factors that drive the distribution of species is important for their conservation and determining their ecological requirements (Lopes Rheingantz et al., 2014). Scientific studies can answer several questions about potential species distributions and species conservation, but can be prohibitive for mammals with large ranges due to cost and amounts of effort required (Lopes Rheingantz et al., 2014). Species distribution modeling is becoming an essential tool for the management of ecosystems and species conservation, as it gives a geographical perspective that can be used as context for future studies (Barbosa et al., 2003). By studying over time, these models can allow tracking of occurrence patterns and changes in population in order to focus conservation efforts in areas that require it the most.

Many modeling approaches exist that accommodate a varied number of data types to estimate species distributions. Therefore, we classified the modeling approaches found, based on the type of data that was used for the model's development and the statistical process used. When there is lack of information of otter presence or when studying over a large range, common environmental factors related to the species, in general, can be used. Deductive habitat suitability models do not require otter presence data as they use conceptual knowledge about the species-habitat relationships based on expert opinion, literature, and research (Ali et al., 2010). Presence-only models use incomplete information (presence-only data) to represent the ecological niche of a species from the analysis of several variables to define their distribution across an area (Santiago-Plata, 2013; Gomez et al., 2014; Bieber, 2016). In an occupancy model analysis, presence/absence data is used with different variable combinations to choose the model that best accounts for the probability of an individual occupying a site and being detected in a survey (Bennett, 2014). Finally, phenomenological models used presence/absence data to find relationships or correlation between species presence and a variety of factors, sometimes defining whether these relationships are negative or positive. Due to information gaps and the diverse habitat and resource use among the different otter species, much effort has been invested in modeling otter distribution and discovering more about the correlations between their presence and their surrounding habitats and conditions (Barbosa et al., 2001; Park et al., 2002; Nel and Somers, 2007; Sepúlveda et al., 2009; Ali et al., 2010; Jeffress et al., 2011; Lopes Rheingantz et al., 2014; de Oliveira et al., 2015).

In this paper, we assess models constructed for otter species in order to inform future efforts. We compile information on the different variables used to model the distribution of otters, what information is commonly available and what may be required, what different results can be obtained with different models, and model limitations. This should make future modeling of otter distribution easier and more efficient by providing insights as to what is necessary to make successful and useful models, thus improving our conservation efforts. This will also help disseminate knowledge to non-scientists about important factors that can affect the distribution of otter species.

RESULTS

We found 29 publications containing different modeling methods for assessing otter distributions and correlating distribution with environmental factors. Most of the articles found were related to *Lutra lutra,* and were from studies across its range in the Tyne catchment (England), Abruzzo region (Italy), southern Italy, Molise region (Italy), Soraksan Nacional Park (Korea), Spanish provinces, the Iberian Peninsula (Spain and Portugal), Hungary, Switzerland, Italy and across Europe. For *Lontra canadensis,* we identified studies in Maine, the Midwest, New Jersey and Nebraska in the U.S. For *Lontra longicaudis,* we located studies in Ibera Lake (Argentina), central México, Rio San Juan (Costa Rica), Parana River Delta (Argentina), Pueblo Nuevo (México) and across its geographical range, and for *Lontra provocax* in Nahuel Huapi National Park (Argentina) and Chile. Studies of *Aonyx capensis* were from South Africa, *Pteronura brasiliensis* from the northern Brazilian Amazon, *Lutrogale perspiccillatea* from the Indus plains of Pakistan, and *Enhydra lutris* from Glacier Bay, Alaska (see Appendix A1 for Tables A1-A8 that summarize the variables used for each species). Species such as *Lontra provocax*, *Aonyx capensis, Pteronura brasiliensis,* and *Lutroale perspicillata* are relatively underrepresented. These results also highlight unrepresented species, such as *Aonyx cinereus, Aonyx congicus, Lontra feline*, *Hydrictis maculicollis,* and *Lutra sumatrana.*

Among these studies there were four main modeling approaches for defining otter distribution across a given area or the relationship between otter species and certain environmental factors (Table 1). These included deductive habitat suitability models, presence-only models, occupancy model analysis, and presence-absence phenomenological models/variable correlation. The use of these different methods could have been influenced by the availability of modeling techniques at the time, the availability of information, the objectives of the study or analysis, and the extent and/or type of area being used or described (see Appendix A2 for information on advantages and disadvantages for each modeling approach, according to articles reviewed).

There were also differences in the scales of the modeling efforts (Table 2), including local, regional, country, continental, and at the geographic extent of the species. The use of different scales was likely due to the information need/gaps for the different species and the objectives of the study or analysis, such as species status in an area or reintroduction efforts (see Appendix A3 for Tables A9-A13 that summarize the metrics used at each scale).

When we cataloged all of the different environmental metrics used in the otter modeling literature, we identified a total of 301 metrics which we then sorted into six main categories: anthropogenic disturbance, climate, terrestrial, aquatic, and biological interaction (Table 3). These metrics were used by authors in different combinations and with different methods in an attempt to better understand the relationship between otters and their habitat, and here we describe them in more detail and, in particular, identify those that were deemed to significantly correlate with otter distributions.

Table 1. Model types used to assess otter distribution

Model type	No. of References	References
Presence-only models	8	Sepúlveda et al., 2009 Cianfrani et al., 2010; 2011 Santiago-Plata, 2013 Cirelli and Sánchez-Cordero, 2009 Gomez et al., 2014 Lopes Rheingantz et al., 2014 Bieber, 2016
Occupancy model analysis	4	Santiago-Plata, 2013 Jeffress et al., 2011 Bennett, 2014 Bieber, 2016
Deductive Habitat Suitability	5	Ottino et al., 1995 Loy et al., 2009 Ottaviani et al., 2009 Ali et al., 2010 Gomez et al., 2014
Presence-Absence phenomenological models/variable correlation	19	Dubuc et al., 1990 Kemenes and Demeter, 1995 Thom et al., 1998 Barbosa et al. 2001; 2003 Park et al., 2002 Aued et al., 2003 Gori et al., 2003 Nel and Somers, 2007 Sepúlveda et al., 2009 Marcelli and Fusillo, 2009 Cianfrani et al., 2010; 2011; 2013 Gomez et al., 2014 Carone et al., 2014, de Oliveira et al., 2015 Cruz et al., 2017 Williams et al., 2017

Anthropogenic Disturbance variables

Anthropogenic disturbance variables are significant contributing factors to negative effects on otter presence and habitat quality, and are the result of human population growth and human behaviors (de Oliveira et al., 2015). Freshwater habitats are highly impacted by anthropogenic activity, such as pollution and water diversion and use, which affect water quality and quantity, and riparian vegetation (Kemenes and Demeter, 1995; Barbosa et al., 2003; Nel and Somers, 2007; Sepúlveda et al., 2009; Cianfrani et al., 2010). Roads have an effect on otters via habitat fragmentation, high sedimentation of watercourses, and increased human disturbance due to greater access to otter habitat (Barbosa et al., 2003).

Table 2. Scales used to model otter distributions

Scale	No. of References	References
Local	9	Dubuc et al., 1990 Thom et al., 1998 Park et al., 2002 Aued et al., 2003 Gori et al., 2003 Santiago-Plata, 2013 Gomez et al., 2014, Cruz et al., 2017 Williams et al., 2017
Regional	10	Ottino et al., 1995 Cirelli and Sánchez-Cordero, 2009 Loy et al., 2009 Cianfrani et al., 2010 Ali et al., 2010, de Oliveira et al., 2015

		Jeffress et al., 2011 Bennett, 2014 Carone et al., 2014 Bieber, 2016
Country	8	Kemenes and Demeter, 1995 Barbosa et al., 2001; 2003 Nel and Somers, 2007 Sepúlveda et al., 2009 Marcelli and Fusillo 2009 Ottaviani et al., 2009 Cianfrani et al., 2013
Continent	1	Cianfrani et al., 2011
Geographic range	1	Lopes Rheingantz et al., 2014

Table 3. Factors considered relevant to otter distribution and their classification into different types of variables. There are two metrics under the name of "other" that are not included in this table because they represent metrics of different categories under one single name.

Categories and subcategories of variables	No. of Metrics	References
Anthropogenic Disturbance Roads Population Tourism Contaminants Land use Others	**80** 15 13 6 4 30 12	Dubuc et al., 1990 Kemenes and Demeter, 1995 Ottino et al., 1995 Barbosa et al., 2001 Park et al., 2002 Aued et al., 2003 Barbosa et al., 2003 Nel and Somers, 2007 Loy et al., 2009 Marcelli and Fusillo, 2009 Ottaviani et al., 2009 Sepúlveda et al., 2009 Ali et al., 2010 Cianfrani et al., 2010; 2011 Jeffress et al., 2011 Cianfrani et al., 2013 Santiago-Plata, 2013 Bennett, 2014 Gomez et al., 2014 Lopes Rheingantz et al., 2014 de Oliveira et al., 2015 Bieber, 2016
Climate factors Air humidity Evapotranspiration Temperature Precipitation Other	**46** 3 4 16 18 5	Barbosa et al., 2001 Aued et al., 2003 Barbosa et al., 2003 Cirelli and Sánchez-Cordero, 2009 Sepúlveda et al., 2009 Cianfrani et al., 2011; 2013 Santiago-Plata, 2013 Lopes Rheingantz et al., 2014
Terrestrial characteristics Vegetation variables Elevation Others	**70** 55 9 6	Dubuc et al., 1990 Kemenes and Demeter, 1995 Ottino et al., 1995 Thom et al., 1998, Barbosa et al., 2001, 2003 Park et al., 2002 Aued et al., 2003 Gori et al., 2003 Nel and Somers, 2007 Cirelli and Sánchez-Cordero, 2009 Loy et al., 2009 Marcelli and Fusillo 2009 Ottaviani et al., 2009 Sepúlveda et al., 2009 Ali et al., 2010 Cianfrani et al. 2010; 2011; 2013 Jeffress et al., 2011 Santiago-Plata 2013 Bennett 2014

		Carone et al., 2014 Gomez et al., 2014 Lopes Rheingantz et al., 2014 Bieber, 2016 Cruz et al., 2017
Aquatic features Water body characteristics River Hierarchy Others	**92** 54 36 2	Dubuc et al., 1990 Kemenes and Demeter 1995 Ottino et al., 1995 Park et al., 2002 Aued et al., 2003 Gori et al., 2003 Nel and Somers, 2007 Loy et al., 2009, Marcelli and Fusillo, 2009 Ottaviani et al., 2009 Sepúlveda et al., 2009, Ali et al., 2010 Cianfrani et al., 2010; 2011 Jeffress et al., 2011 Santiago-Plata, 2013 Bennett, 2014 Gomez et al., 2014 Lopes Rheingantz et al., 2014 de Oliveira et al., 2015 Bieber, 2016 Cruz et al., 2017 Williams et al., 2017
Interspecies interactions Competition Resource availability Food	**11** 1 5 5	Dubuc et al., 1990 Thom et al., 1998 Aued et al., 2003 Gori et al., 2003 Nel and Somers, 2007 Sepúlveda et al., 2009 Cianfrani et al., 2010 Bennett, 2014

The variables most commonly used were roads, population density/distribution, and land use. Metrics significantly affecting otter presence were distance to roads (Park et al., 2002), number of visitors to a park (Park et al., 2002), human settlements (Aued et al., 2003), water use and pollution (Nel and Somers, 2007), roads (Sepúlveda et al., 2009), agriculture/livestock adjacent areas (Marcelli and Fusillo, 2009), proportion of urban areas (Marcelli and Fusillo, 2009), distance from industrial areas (Marcelli and Fusillo, 2009), human population density (Lopes Rheingantz et al., 2014; Marcelli and Fusillo, 2009), distance from surface excavations (Cianfrani et al., 2010), distance from productive areas (Cianfrani et al., 2010), proportion of area comprised of cropland (Jeffress et al., 2011), location of fishing nets (de Oliveira et al., 2015), location of homes (de Oliveira et al., 2015), and distance to the nearest otter release site (km)(Bieber, 2016).

Sometimes, using anthropogenic disturbance variables can be complex since their effect on otter presence is variable. Otters have been found to have high resistance to disturbance factors and can be found in areas that we normally consider too disturbed to be ideal for their use (e.g. Kemenes and Demeter, 1995; Bennett, 2014). Human density or development may have a negative effect on otter distribution, but this may vary at a regional scale or with habitat quality (Bennett, 2014). The effect of disturbance factors may be direct, causing otters to avoid certain areas, or indirect through changes inhabitant conditions (Bennett, 2014).

Terrestrial variables

For otters, vegetation could be important as a source of refuge (Gori et al., 2003), as resting and breeding sites, for providing water quality, and for increasing fish productivity (Cianfriani et al., 2010, 2011, 2013; Carone et al., 2014). Riparian vegetation is commonly correlated with high water quality, high primary productivity, high fish biomass, and high availability of alternative prey species (Ottaviani et al., 2009). Altitude/elevation is limiting when considering that there is more food availability at lower and medium river sections than in headwaters (Barbosa et al., 2003). Acclivity (upward slope) may be considered important because very steep river banks have been considered good indicators of areas inaccessible to humans, and as optimal sites for otter holts/dens and couches/resting sites (Ottaviani et al., 2009). Mean altitude has been used as a surrogate of otter habitat quality and its variation (Marcelli and Fusillo, 2009). Slope and topographic convexity are variables that may influence the hunting opportunities (Kruuk, 2006; Cianfrani et al., 2013). Soil permeability is a factor that may affect otter presence in a negative way due to its effect on superficial freshwater availability (Barbosa et al., 2003).

Vegetation and elevation were the variables most commonly used. Metrics found significant for otter presence were percent of forested land composed of birch-aspen (Dubuc et al., 1990), percent of forested land composed of mixed hardwood-softwood (Dubuc et al., 1990), sum of the areas of all water bodies characterized by emergent herbaceous vegetation (Dubuc et al., 1990), density of bank vegetation (Kemenes and Demeter, 1995), soil permeability (Barbosa et al., 2001), mean longitude (Barbosa et al., 2001), coarse scale extra-riparian CORINE (Coordination of Information on the Environment, Land Cover database developed by project of Commission European of the European Union) land cover (Park et al., 2002), vegetation type of stream bank zone (Gori et al., 2003), vegetation complexity (Aued et al., 2003), elevation (Aued et al., 2003), semi-dense riparian vegetation (Sepúlveda et al., 2009), proportion of survey area buffer comprised of woodland (Jeffress et al., 2011), and proportion of survey area comprised of grassland (Jeffress et al., 2011).

Sometimes using terrestrial variables can be complex, since their effect on otter presence is variable. For example, Lopes Rheingantz et al. (2014) describe how elevation was not found to influence their model as it did in other studies, and that vegetation cover had little influence on the model. Variables such as elevation, slope, and density of bank were identified as significant in some studies, but not in others.

Aquatic variables

Water availability is crucial for otters (Cianfrani et al., 2011), a semi-aquatic species that spends a large part of its time in aquatic environments. Water bodies are also a source of fish, which is the most common otter food. Water availability and water quality should have an influence on otter distribution and presence (Kemenes and Demeter, 1995; Cianfrani et al., 2013). Otters appear sensitive to reduction of water depth (Kemenes and Demeter, 1995), as well as stream order and its variation (Marcelli and Fusillo, 2009). Hierarchy of tributaries is used as a proxy of water flow (Ottaviani et al., 2009). If otters are forced to find food sources out of the water or too close to the shore, they may become more vulnerable to terrestrial predators, in turn affecting their survival rates (Ruiz-Olmo and Jimenez, 2009).

In modeling efforts, water body characteristics and river hierarchy were the variables most commonly used. Metrics found significant for otter presence included mean shoreline diversity index (shape; Dubuc et al., 1990), total stream length, over all stream orders (Dubuc et al., 1990), water depth (Kemenes and Demeter, 1995; Nel and Somers, 2007), river/stream width (Park et al., 2002), bottom structure of stream (Park et al., 2002), bank (shore) type (Gori et al., 2003), current type (Nel and Somers, 2007), anastomosed (two or more interconnected channels that enclose flood basins) river length (Sepúlveda et al., 2009), sum of the waterbody perimeters/sum of waterbody areas for entire watershed (Jeffress et al. 2011), sum of stream (3rd order) km within the watershed/watershed area (Jeffress et al., 2011), number of waterbodies within the watershed/watershed area (Jeffress et al., 2011), river water level (de Oliveira et al., 2015), long-term median flow rate of the river (ft^3/s) (Bieber, 2016), flow zone (Cruz et al., 2017), total dissolved solids (Cruz et al., 2017) and pH (Cruz et al., 2017).

Sometimes using aquatic variables can be a challenge, since the characteristics that need to be measured for their effect on otter presence are not easily defined. Water fluctuations can have a negative effect on fish abundance and size; therefore, floods and droughts can cause otters to abandon areas (Ruiz-Olmo et al., 2001), though this reaction seems to vary from species to species, and from area to area. In some areas, species such as *Lutra lutra* are able to live in dry rivers during the summer, as long as there are pools that provide enough fish to eat throughout the season (Ruiz-Olmo et al., 2001; Prenda et al., 2001). For other species, like *Aonyx capensis* in South Africa, freshwater availability is more important than prey availability (Van Niekerk et al., 1998). Also, variability in the metrics presented shows how difficult it is to define which characteristics of a water body can affect otters. Sometimes the scale of the study could be what affects the effect of the metrics; river/stream width was considered a significant variable by Park et al. (2002; local scale), but in Nel and Somers (2007) it was not (country scale) (Appendix A3, Tables A9-A13).

Climate variables

Climate mostly influences distributions of species at macroscales (Cianfrani et al., 2011). Climate factors at large scales have high potential as surrogates for local freshwater availability, and water warming could affect fish species diversity and abundance (Cianfrani et al., 2011). Floods can increase the deposit of suspended solids, which tend to bury potential denning areas, as well as decreasing food availability for fish and otters (Ruiz-Olmo et al., 2001). Droughts may also increase mortality, because with a drought comes diminishing food availability which may trigger an increase in territoriality among individuals (Prenda et al., 2001).

In the models we looked at, temperature and precipitation where the climate variables most commonly used. Significant metrics affecting otter presence included relative humidity in January (Barbosa et al., 2001) and annual temperature (Lopes Rheingantz et al., 2014). Lopes Rheingantz et al. (2014) also found that annual precipitation was the most relevant climatic metric for neotropical otter (*Lontra longicaudis*) distribution within its geographic range.

Using climatic variables can have its difficulties, such as finding the information at an appropriate scale for the study. The common use of macroscale global climatic data, even in local studies, is a clear example of this. The effect of climatic variables on otters has not been directly measured, so many studies use variables that are assumed to be most significant to the species and/or were used in previous mammal studies (e.g., Lopes Rheingantz et al., 2014).

Biological interaction variables

Food availability has been found to be the factor of most importance for otter presence (Kruuk, 2006; Nel and Somers, 2007; Cianfrani et al., 2013). Mink (*Mustela vison*) are considered a potential competitor for resources (Aued et al., 2003), and beaver (*Castor canadensis*) presence has been found to be a predictor of otter presence (Dubuc et al., 1990; Bennett, 2014). The metrics found significant for otter presence were: percent of all wetlands with active or inactive beaver sign (Dubuc et al., 1990), food availability (Nel and Somers, 2007), and freshwater crab and crayfish abundance (Sepúlveda et al., 2009).

Disadvantages of using biological interaction variables include how costly and time consuming it is to define food availability, which is considered as the most important factor affecting otter distribution. In many cases, it is easier to use surrogate variables for food availability rather than measure actual food presence and abundance, but this could cause overprediction, may not be as accurate, and makes it riskier to interpret the data (Sepulveda et al., 2009).

DISCUSSION

The reliability of modeling efforts may be influenced by the modeling scale (i.e., ecological scale or the extent of the landscape under consideration) used, measuring issues, and several other shortcomings that we are forced to face as we work with such complex ecosystems (cf. Elith and Graham 2009). Some of the complications found or mentioned in the reviewed articles are as follows:

Influence of modeling scale

The importance of scale is very often underestimated or not accounted for in many ecological studies (Thom et al., 1998). Using course resolution in an analysis can make it complicated to assess land use and connectivity during the analysis (Cianfrani et al., 2011). In addition, scale mismatch between data and ecological process is a major problem in ecological modeling. Fine-scale data is important for modeling some species, including otters, because characteristics such as riparian vegetation cover may not be well represented in coarser data layer such as land cover (Loy et al., 2009). Habitat variables that might be effective to predict species response at one scale might not be as effective other scales (Ali et al., 2010); unfortunately, the resolution of variables usually depends on data available. HIS models are used under the assumption that habitat-wildlife relationships are consistent at all scales (Ali et al., 2010). Environmental data for freshwater bodies (water temp, depth, water velocity, etc.) is usually not spatially accurate to be used in models (Cianfrani et al., 2013).

Otter habitat is complex, consisting of a narrow strip of an aquatic and riparian ecosystem, and though individuals may move several hundred meters from this area, their activity mostly occurs close to this strip (Ruiz-Olmo et al., 1998; Ottaviani et al., 2009). Therefore, fine-scale modeling is appropriate to measure decreasing habitat suitability as one considers habitats away from a waterway, as well as the effects of land use as it moves towards riparian habitat (Ottaviani et al., 2009). It is not easy to obtain useful large-scale information of habitat suitability based on fine scales habitat linearity (Ottaviani et al., 2009). Relevant information such as fish abundances, water flow, hunting pressure, and water pollution are rarely available or reliable at large spatial scales, particularly since they fluctuate a lot within time and space. Also, survey techniques are difficult to standardize at large scales for some species in some systems; therefore, proxies are commonly used (Ottaviani et al., 2009; Cianfrani et al., 2013). Large-scale efforts need to be refined with local data such as pollution, food availability, and human disturbance when you want to apply them in local conservation plans, or else only be used for large scale conservation strategies (Ottaviani et al., 2009).

Fine-scale models are limited in their application and evaluation of potential habitat at a larger scale (Park et al., 2002). Sometimes one has to use a larger, less accurate scale to identify the fine scale of microhabitat (Lopes Rheingantz et al., 2014); this is because the fine-scale data are usually not available over large areas.

Measurement issues

Sparse otter occurrence may lead to overestimated range sizes when including areas of sporadic occurrences (Marcelli and Fusillo, 2009). Some areas where otters are observed are used only to move from one site to a better one, and they do not necessarily represent an area that the otter regularly inhabits. Using the characteristics of these rarely used areas as basis for defining habitat suitability can cause for overestimating the areas that are used by the species. Also, insufficient numbers of data points may not provide enough information to use independently for validation and calibration, therefore performance could be overestimated (Sepúlveda et al., 2009). In general, overprediction and underprediction can affect results for distribution ranges and for conservation efforts; therefore, making different types of models and then overlaying them may be a good way of reducing this effect, but there are definitely pitfalls to avoid (Cade, 2015). Optimization methods in modeling fitting and testing for such deviations in predictive ability should be useful way forward in model selection (e.g., Elith and Leathwick, 2009; Merow et al., 2014)

Sometimes it is difficult to measure the time in which a track was made or when spraints were deposited, usually due to their location; therefore, there may be discrepancies with the actual environmental conditions in which they were made (Kemenes and Demeter, 1995). Weather (snow and rain) and water level variations may affect the ability to detect indirect signs of otter presence, and therefore affect the results of our models, so monitoring should be done consistently during drier seasons (de Oliveira et al., 2014; Bieber, 2016).

The use of more detailed variables will allow a better understanding of actual relationships between otter and their surrounding habitat (species or types of vegetation for example). Fish population estimates at each site might not be representative of the population of the full stretch of habitat/river (Thom et al., 1998), though obtaining a more representative estimate might be impractical due to financial and time constraints.

In most of the work related to absence/presence data there is a possibility of being biased due to "false absences". It is difficult to know *a priori* which absences are reliable and which ones are not since species distribution is usually a snapshot in time of a system that is dynamic (Cianfrani et al., 2010). Sometimes the species may be considered as absent in an area, but in reality, it was just not detected (Jeffress et al., 2011; Ruiz-Olmo et al., 2001). There is also always a possibility of errors when using multiple/inexperienced observers.

Sometimes when using data collected over time, methods might not be comparable between the surveys (e.g. difference in grid system or lack there off, surveying one or both bank sides; Marcelli and Fusillo, 2009). Information (scat census or density and vegetation cover) used may not always be from the same time periods, and may have changed since the time the information was produced (outdated), affecting the relationships found within the model and therefore the accuracy the results. Usually when using data from different time frames and projects, the geographic extent of the surveys is not the same (Marcelli and Fusillo, 2009).

The information available for modeling efforts can come from different sources such as scientific collections, museums, herbariums and online databases (Table 4). This information might have several issues: there may only be presence data, the species might not have been classified, the data might not be correctly georeferenced, and data are usually collected for different reasons, without a standardized methodology, therefore representing a biased distribution of the species (Santiago-Plata, 2014).

Table 4. Types of data collected in reviewed articles

Data collection	Frequency	Article/Thesis Authors
track /foot prints	12	Dubuc et al., 1990, Ottino et al., 1995 Kemenes and Demeter, 1995 Gori et al., 2003, Nel and Somers, 2007 Sepúlveda et al., 2009 Santiago-Plata, 2013, Gomez et al., 2014 Jeffres et al., 2011 Bennett, 2014 de Oliveira et al., 2015 Bieber, 2016
camera-traps	2	Gomez et al. 2014 Bieber 2016
observations	9	Dubuc et al., 1990 Nel and Somers, 2007 Sepúlveda et al., 2009 Ali et al., 2010 Santiago-Plata, 2013 Bennett, 2014 de Oliveira et al., 2015 Bieber, 2016, Williams et al., 2017,
latrine/spraints/scats	16	Dubuc et al., 1990 Ottino et al., 1995 Kemenes and Demeter, 1995 Thom et al., 1998 Gori et al., 2003 Nel and Somers, 2007 Sepúlveda et al., 2009, Marcelli and Fusillo, 2009 Cianfrani et al., 2010, Jeffres et al., 2011, Santiago-Plata, 2013, Gomez et al., 2014 Bennett, 2014, de Oliveira et al., 2015, Bieber, 2016 Cruz et al., 2017
burrows	1	Gomez et al., 2014
skins	1	Gomez et al., 2014
interviews/questionnaires	3	Nel and Somers, 2007 Santiago-Plata, 2013 Gomez et al., 2014,
anal secretions	3	Ottino et al., 1995 Thom et al., 1998 Gori et al., 2003
published maps /information of previous otter surveys	9	Barbosa et al., 2001 Barbosa et al., 2003, Aued et al., 2003, Loy et al., 2009, Marcelli and Fusillo, 2009 Ottaviani et al., 2009 Ali et al., 2010, Cianfrani et al., 2011 Carone et al., 2014

literature	2	Nel and Somers, 2007 Rheingantz et al., 2014
researcher's records	3	Nel and Somers, 2007 Cianfrani et al., 2013, Lopes Rheingantz et al., 2014
ecological indicators of species presence	2	Cirelli and Cordero-Sanchez, 2009 Cianfrani et al., 2013
scrapes/scratches	2	Gori et al., 2003 de Oliveira et al., 2015
dens	3	Gori et al., 2003 Santiago-Plata, 2013 de Oliveira et al., 2015
slides	3	Dubuc et al., 1990 Gori et al., 2003 Bennett, 2014
rolling places	2	Gori et al., 2003 Santiago-Plata, 2013
Otter trace/signs	1	Park et al., 2002
camp sites	1	de Oliveira et al., 2015
food remains historical records	1 1	Gori et al., 2003 Bieber, 2016

Shortcomings

It is common to lack enough data points for the range being modeled, or for there to be areas that are unrepresented by available data. When working with data from different time frames, usually one of the observation times has a limited dataset (Carone et al., 2014). Fish density (when available) is usually not measured evenly within the otter's range.

The level of productivity of rivers varies, being usually low in the headwater, increasing in the middle reaches and peaking in the lower reaches (Nel and Somers, 2007). Therefore, considering all of a river as suitable or with the same suitability is not adequate or realistic. Temporal, spatial, or quantitative variation in negative or positive effects of factors on the species may be case specific (Marcelli and Fusillo, 2009). Lack of observed influence of some variables could be due to their low variability through study area (Jeffress et al., 2011, Cruz et al., 2017). Using different climate scenario for future predictions can cause discrepancies in the models (Cianfrani et al., 2011).

Spraint numbers are not sensitive to changes in otter distribution in relation to changes in prey distributions (Thom et al., 1998). Location of spraint and spraint sites might sometimes interfere with their relationship to the periods of feeding activity, and in some sites, they might last longer (Thom et al., 1998).

Sometimes the lack of information on local water fluctuations will force one to downgrade the suitability of certain areas such as smaller streams and areas located at certain altitudes (Ottaviani et al., 2009). It is common to ignore water regimes of different watercourses in the modeling process, even though it affects their carrying capacity at several levels (Ottaviani et al., 2009).

It is not a simple task to determine if you have been able to choose all relevant factors that affect otter presence and distribution (Barbosa et al., 2003), particularly because of surrogate variables and the extent to which they may correlate to other variables used. Using regional bioclimatic variables (representing annual tendencies, stationarity, and extreme factors) without taking into account that some of them might not have a relationship with the species being modeled may generate instability in the models generated (Santiago-Plata, 2014). Selection of variables may lead to randomness in the predictions (Cianfrani et al., 2010). Reliability of models also depends on the species ability to adaptation and the environment's temporal and spatial variability (Cianfrani et al., 2010). Pseudo-absence data will affect distribution modeling efforts, no matter how minimized their effect is (Carone et al., 2014).

Additional considerations

Sometimes, as in the case of Aued et al. (2003), the lack of otter presence in an area within the study cannot be defined quantitatively, therefore you can infer what factors can qualitatively be causing this absence. These inferences cannot be statistically demonstrated, but perhaps further research will provide the information needed.

There are also cases in which there are too many variables to consider or factors that cannot be accounted for directly, and in order to make the analysis less complex or to include other possibilities, a single variable of "other" is used. This is a complicated decision to make, since the effect of these compound variables is not being clearly defined, and since any of the many options included could be responsible for it. Also, the extent to which each variable is responsible for affecting the otter species is difficult, if not impossible, to measure. This highlights the need for more careful attention to model choice and model fitting, for which there is a vast literature (e.g., Burnham and Anderson, 2003; Johnson and Omland, 2004; Guisan et al., 2017).

Many of the variables that are important in determining otter abundance are affected by climate change. Temperature and precipitation ranges and distribution are the main factors affected directly by climate change. Though their direct effect on species is usually unknown, their effect through freezing, drought and flooding could have negative consequences on otter populations. These two variables have a huge impact on other variables such as vegetation, food availability, and waterbody-related variables. Vegetation community assemblages are expected to vary due to climate change (Brodie et al., 2013), and vegetation is considered an important variable because it is commonly used as a proxy for refuge and food resources.

Though climate change studies are more common for terrestrial species, we found one paper related to climate change and otters (Cianfrani et al., 2011). The main focus of this research was identifying the effects of temperature and precipitation on otter distribution. Precipitation is expected to have an important role in water availability and distribution. Temperature on the other hand, is expected to affect fish assemblages as water warms up. Results indicated that climate change may cause a profound reshuffling in the potential otter distribution across Europe, though there was some variation in outcomes across the range. Even when vulnerability to climate change and conservation status seem to be correlated, their relationship is not perfect, as other factors may affect their degree of correlation (Brodie et al., 2013).

CONCLUSIONS AND RECOMENDATIONS

As apex predators, otters have an important role in ecosystems, but their dependence on aquatic habitats makes them vulnerable. This dependency on water sources and the food and shelter they provide makes freshwater species more vulnerable, with higher extinction rates, than terrestrial species (Scorpio et al., 2016). Otters are considered among the most threatened mammals in the world (Kruuk, 2006; Scorpio et al., 2016) and prey and water availability seem to be the two most important factors that limit otters (Prenda and Granado-Lorencio, 1996; Prenda et al., 2001; Ruiz-Olmo et al., 2001).

Otters are difficult to study, and thus large information gaps exist for many of the species (see Kruuk, 2011 for species-specific research recommendations based on information gaps). Defining otter distribution, even with the advances in software and technology today, is a complicated process given the gaps in important information. There are several factors that have been deemed important for otter distribution, based on the studies reviewed, such as anthropogenic disturbance, climatic, terrestrial, aquatic and biological interaction variables. Unfortunately, we are still uncertain on how many of the factors are directly or indirectly affecting otters or whether they have the adaptability to deal with changes within them. The relationship between otters and some of these factors are simple to interpret, but other relationships are still unclear. Sometimes a variable deemed as important in one study is considered unimportant in another. Even when a variable is known to be important, it may be hard to measure. Most research had focused on *Lutra lutra*, though based on the differences between their life histories and geographic ranges with other otters, the results can often not be extrapolated to predict impacts on other species. Even if the results of species-specific studies cannot often be extrapolated, the processes and data types used, the data gathering methods, and the variables/metrics considered can still provide guidance for future research. Researchers should still be careful in considering what really applies to their study areas and species of interest.

We still need to have a better understanding of the relationships among many factors and otter distribution, as well as their varying effects on different otter species, and articles cited in this review provide many useful suggestions for improved modeling. Modeling should be considered a dynamic process in order to progressively improve the quality of the predictions, and adequate evaluation indexes should be used when evaluating model quality (Cianfrani et al., 2010). Robust spatially explicit models for identifying and hierarchically assessing areas for otter conservation and restoration can be achieved with sequential implementation of methods combining species modeling and place prioritization (Cirelli and Sánchez-Cordero, 2009). The use of multiple survey methods, data sets and analysis methods to allow a better representation of the areas of interest and the direct comparison between the methods being used (Bieber 2016).

With respect to the type of model being used, accuracy of presence data is important for calibrating habitat suitability models (Cianfrani et al., 2013), as is definition of the cut-off point above which the presence of a species is more likely than expected at random, since it can be used to correct the established thresholds that are used to separate unsuitable from suitable areas (Ali et al., 2010). When the species-environment equilibrium assumption (this assumption presumes that a species occupies all suitable habitat that is available) is not met (e.g. recolonization and expansion), habitat suitability models' predictions should be assessed carefully (Cianfrani et al., 2010). Prior to employing environmental niche models, an important step is to test for environmental similarity (Cianfrani et al., 2013). When dealing with species with unstable spatial equilibrium, presence-only models may be a better option than presence–absence methods for making reliable predictions of suitable areas for expansion (Cianfrani et al., 2010).

Using the same variables at different scales may have different effects on populations, and therefore should be analyzed the most appropriate scale (Thom et al., 1998). Unfortunately, there are many variables whose information is not usually available at different scales. Studies of regional-scales processes are an important complement for local-scale studies, providing a broader geographic perspective that can be seen as context in local studies, and allowing us to take into account factors that have an effect on a larger scale (Barbosa et al. 2003).

Better research on direct factors affecting otter distribution is needed, since proxy variables, and even seemingly direct habitat characteristics, sometimes indicate the opposite of expectations (Kemenes and Demeter, 1995). In considering the shifting dynamics over time and how factors effect on species distributions may vary (Sépulveda et al., 2009), radio-telemetry may provide the best data for the analysis of habitat choice and use by otters (Nel and Somers, 2007). Despite being difficult to quantify, additional emphasis should be placed on water quality and prey availability, given their importance. Finding better ways of integrating these factors into analyses will allow results to be more reliable. Distribution studies could be directed towards areas where there is previous information available regarding other important factors, such as water quality assessment (Bennett, 2014) and food availability, in order to help include this critical but hard to obtain information within the studies. PCB contamination and fish density are necessary in a spatially explicit way, and therefore should be a priority for future research (Cianfrani et al., 2013). When trying to build models on the effect of environmental variables, the results from field surveys should always be compared with water quality data (Kemenes and Demeter, 1995).

Also, it is important to collect long-term site occupancy data and to use modeling procedures that account for imperfection in detectability (Marcelli and Fusillo, 2009). Avoiding the concentration of data points in a particular area over another (i.e., having an equal distribution of data along the area of study) is needed to prevent bias in the probability of distribution of the models (Santiago-Plata, 2014). It also is important to obtain data on trends over time from periodic survey of factors such as water quality, land use, anthropogenic disturbance changes, and vegetation.

We need to have a better understanding of the relationship between otters and the variables that are commonly used to describe their habitats, especially water quality and prey availability, as these seem to be the most important but the hardest to quantify. Ultimately, to gain a more accurate and meaningful understanding of otter survival, we need to focus on finding better ways of integrating measurable variables into our analyses.

After considering the modeling approaches used in the papers reviewed, a few suggestions come to mind. Williams et al. (2017) applied a Bayesian approach for the first time in these modeling efforts while calculating sea otter occupancy and abundance; it would be interesting to try these methods on other otter species, as well as other methods such as simulations and mission learning tools. Advances in technology and science open the door for the use of new tools for our conservation efforts; thus, we need to keep an eye on these advances and an open mind to distribution studies made for other species.

Acknowledgements - The authors would like to thank Brian Gerber for very helpful review comments and insights.

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RÉSUMÉ

SYNTHÈSE BIBLIOGRAPHIQUE DES MODÈLES DE LA DISTRIBUTION DE LA LOUTRE: DÉMARCHE, ÉCHELLE ET MÉTRIQUES

Toutes les espèces de loutre sont concernées par la conservation et sont utilisées comme espèce parapluie pour la conservation et comme indicateur de la santé des bassins versants; En conséquence, l'identification et la compréhension de leur distribution est une nécessité élémentaire. Nous avons passé en revue la littérature publiée afin d'identifier un modèle de distribution de la loutre dans le monde et la compilation de données sur différentes métriques/variables utilisées: quelle information est communément disponible et peut être requise? Quels résultats distincts peuvent être obtenus avec différents modèles et limitations de modèle? Nous avons identifié 29 études sur 8 espèces qui utilisaient principalement 4 méthodes de modélisation de distribution de la loutre à travers une région déterminée ou la relation entre les espèces de loutre et certains facteurs environnementaux. Les études ont été modélisées sur base d'une distribution à différentes échelles, incluant l'extension géographique locale, régionale, nationale et continentale. Nous avons catalogué 301 métriques environnementales différentes utilisées dans les modélisations que nous avons ensuite classées en 6 catégories principales : perturbation anthropogénique, climat, interactions terrestre, aquatique et biologique. L'alimentation, la disponibilité en eau et sa qualité, ainsi que les influences anthropogéniques sont régulièrement identifiées comme variables importantes corrélées avec la distribution de la loutre, mais sont souvent mesurées de différentes façons, ou identifiées dans des modèles par des variables indirectes ou de substitution parce que la disponibilité des données pertinentes est insuffisante ou absente.

L'échelle, la démarche, et la sélection des métriques, tout cela demande à être envisagé avec précaution pour chaque étude. Cependant, la compréhension des problèmes de dimensionnement et des lacunes de modélisation identifiées par d'autres devraient permettre d'améliorer ce type de modélisation dans le futur. L'examen du contenu de cet article de synthèse bibliographique peut fournir des indications sur les efforts ultérieurs dans les processus de modélisation, les types de données utilisées, les méthodes de collecte des informations, et des variables/métriques à inclure. Cette information doit encore être évaluée avec précaution pour une utilisation sur des zones d'études spécifiques, des espèces dignes d'intérêt, et comme base de développement de méthodes innovantes et plus efficaces.

RESUMEN

REVIEW DEL MODELADO DE DISTRIBUCIÓN EN NUTRIAS: ENFOQUE, ESCALA Y MÉTRICA

Todas las especies de nutrias son de preocupación de conservación, y son utilizadas tanto como especies-bandera para la conservación, así como indicadores de salud de cuencas; consecuentemente, identificar y entender su distribución es una necesidad básica. Revisamos la literatura publicada para identificar esfuerzos de modelado de distribución, en todo el mundo, y luego compilamos información sobre distintas métricas/variables usadas, qué información está comúnmente disponible y qué se puede requerir, qué distintos resultados se pueden obtener con diferentes modelos, y limitaciones de los modelos. Identificamos 29 estudios sobre 8 especies que utilizaron 4 métodos principales para modelar distribución de nutrias en una determinada área, o la relación entre las especies de nutria y ciertos factores ambientales. Los estudios modelaron distribución a través de una variedad de escalas, incluyendo la local, regional, nacional, continental, y de toda la distribución de la especie. Catalogamos 301 diferentes métricas ambientales usadas en los modelos, que luego clasificamos en seis categorías principales: disturbios antropogénicos, clima, interacciones terrestres,

acuáticas y biológicas. El alimento, disponibilidad y calidad del agua, y las influencias antropogénicas todas fueron regularmente identificadas como variables importantes que se correlacionan con la distribución de nutrias, pero son a menudo medidas en una variedad de maneras, o identificadas en los modelos mediante variables proxy ó sucedáneas, porque la disponibilidad de los datos relevantes fue escasa o ausente. La escala, el enfoque, y la selección de métricas, todas necesitan ser cuidadosamente consideradas para cada estudio, pero entender los temas de medición y las limitaciones identificadas en los modelos, deberían ayudar a mejorar el modelado de nutrias en el futuro. La revisión de información de este paper de review puede ayudar a futuros esfuerzos respecto de procesos de modelado, tipos de datos usados, métodos de recolección de datos, y variables/métricas a incluir. Esta información debería de todos modos ser cuidadosamente evaluada antes de usarse en áreas de estudio o especies específicas, y como una base para desarrollar métodos innovadores y más efectivos.

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Appendix A1 – Variables used for different otter species

Table A1 - Factors use for modeling *Lutrogale perspicillata.* Many studies do not consider variable significance in their analysis.

Article/thesis name	Factors	Scale
Ali et al., 2010	roads, population, vegetation, water body characteristics	regional

Table A2 - Factors use for modeling *Aonyx capensis.* Factors in **bold** where found to be significant for this species.

Article/thesis name	Factors	Scale
Nel and Somers 2007	land use**, water body characteristics, water use, pollution, food resources,** vegetation	country

Table A3 - Factors use for modeling *Lontra provocax.* Factors in **bold** where found to be significant for this species.

Article/thesis name	Factors	Scale
Aued et al., 2003	competition (mink), water body characteristics, **elevation, vegetation, population**, precipitation, roads	local
Sepúlveda et al., 2009	**Food resources, water body characteristics, vegetation,** temperature, **roads**	country

Table A4 - Factors use for modeling *Pteronora brasiliensis.* Factors in **bold** where found to be significant for this species.

Article/thesis name	Factors	Scale
de Oliveira et al. 2015	**population, fishing nets, water body characteristics**	regional

Table A5 - Factors use for modeling *Lontra canadensis.* Factors in **bold** where found to be significant for this species. Many studies do not consider variable significance in their analysis.

Article/thesis name	Factors	Scale
Dubuc et al., 1990	roads, population, **vegetation, water body characteristics, river hierarchy, resource availability (beavers)**	local
Bieber, 2016	**distance to the nearest otter release site (km)**, vegetation, **water body characteristics**, resource availability	local
Jeffress et al., 2011	Local: **vegetation,** river hierarchy, water body characteristics, land use Landscape**:** land use, vegetation, ***river hierarchy**,* roads	regional
Bennett, 2014	land use, vegetation, water body characteristics, competition (mink), resource available (beaver), other (ecosystem types and land uses)	regional

Table A6 - Factors use for modeling *Enhydra lutris*. Many studies do not consider variable significance in their analysis.

Article/thesis name	Factors	Scale
Williams et al., 2017	water body characteristics	regional

Table A7 - Factors use for modeling *Lutra lutra*. Factors in **bold** where found to be significant for this species. Many studies do not consider variable significance in their analysis.

Article/thesis name	Factors	Scale
Thom et al., 1998	vegetation and food resources **(no relationship found)**	local
Park et al., 2002	**water body characteristics, vegetation, road, tourism**	local
Ottino et al., 1995	vegetation, water body characteristics, disturbance	regional
Loy et al., 2009	population, elevation, vegetation	regional
Cianfrani et al., 2010	vegetation, **land use**, population, elevation, water body characteristics, food resources	regional
Carone et al., 2014	vegetation, elevation	regional
Kemenes and Demeter 1995	**land use, other possible factors (variable, e.g. pollution, dry section in water body), water body characteristics, vegetation**	country
Barbosa et al., 2001	**longitude, soil permeability, air humidity, roads,** latitude, precipitation, insolation, solar radiation, evapotranspiration, run-off, bioclimatic belts, temperature, phytogeographic sectors, population, tourism, land use, vegetation	country
Barbosa et al., 2003	run-off, soil permeability, latitude and longitude, elevation, precipitation, insolation, solar radiation, frost days, evaporation, temperature, air humidity, population, roads	country
Marcelli and Fusillo, 2009	population, land use, roads, river hierarchy, elevation	country
Ottaviani et al., 2009	roads, vegetation, elevation, water body characteristics	country
Cianfrani et al., 2013	bioclimatic model: temperature, precipitation regional environmental model: land use, elevation, population, vegetation	country
Cianfrani et al., 2011	Roads, population, precipitation, river hierarchy, land use, vegetation, water body characteristics, elevation	continental

Table A8 - Factors use for modeling *Lontra longicaudis.* Factors in **bold** where found to be significant for this species. Many studies do not consider variable significance in their analysis.

Article/thesis name	Factors	Scale
Gori et al., 2003	**vegetation, water body characteristics, resource availability**	local
Santiago-Plata, 2013	**species distribution model:** **land use**, **roads**, population, river hierarchy, **elevation**, **precipitation** and temperature. Occupancy model: Local variables: vegetation, water body characteristics, elevation, human (impacts) landscape variables: vegetation, **land use**, roads, **river hierarchy**	local
Gomez et al., 2014	elevation, water body characteristics, population, polder cover (%), boat traffic, vegetation, land use, contaminants	local
Cruz et al., 2017	**water body characteristics**, vegetation	local
Cirelli and Sánchez-Cordero, 2009	vegetation, elevation, precipitation, temperature	regional
Lopes Rheingantz et al., 2014	precipitation, temperature, elevation, population, vegetation, water body characteristics	geographic extent

Appendix A2 – Advantages and disadvantages of modeling approaches

Presence-Absence phenomenological models/variable correlation *methods*

Advantages

The variety of tools available for this method (e.g. artificial neural networks, generalized linear models, generalized boosting models, generalized additive models, classification tree analysis, multi-adaptive regression splines, univariate and multivariate logistic regressions, stepwise discriminant analysis, flexible discriminant analysis, analyses for correlation, linear tend surface equation, partial regression analyses, piecewise linear functions, random forests, nearest-neighbor analyses, bootstrapping, variable transformations, correlation tests), allow us to take into consideration the information that is available and the selection of the most appropriate tools for the type of analysis that is being considered.

Can assess the relative importance of spatial, environmental and human factors that influence otter distribution (Barbosa et al., 2001).

Can be used to specify how much of the variance of the distribution of otters is due to different types of factors (variance partitioning), due to interactions between factors, and due to the combinations of factors (Barbosa et al., 2001).

These methods allow the establishment of negative or positive correlations, statistical significance of the relations found, and the level of confidence in the results obtained (Marcelli and Fusillo, 2009; Nel and Sommers, 2007).

Can be used to stablish ranges (thresholds) upon which the presence of certain factors exerts a greater influence (negative or positive) on the probabilities of observing a species (Marcelli and Fusillo, 2009; Nel and Sommers, 2007).

Distribution models based on presence probabilities, allow a more detailed knowledge of a species potential distribution when they are extrapolated to scales of finer resolution (Barbosa et al., 2003).

The sighting data used can take many forms, including presence-absence, sighting rate (de Oliveira et al. 2015), number of signs (Gori et al., 2013), proportion of positive sights (Barbosa et al., 2001), and frequency distribution (Thom et al., 1998).

These methods can be used to create habitat suitability maps, distribution of probability of occurrence maps, and presence-absence prediction maps which can be used to define action plans for conservation efforts (Gomez et al., 2014).

Disadvantages

Causal relationships among variables that are shown through the use of statistical regressions are not necessarily direct. A variable used could be an indicator or surrogate for a different unmeasured variable that does have an influence on the dependent variable (Barbosa et al.,2001; Barbosa et al., 2003).

It is important to understand that some of the factors we would like to consider can be correlated, and therefore the understanding of their individual effect may not be easy to interpret or define.

The variables chosen can provide randomness in the predictions made (Cianfrani et al., 2010; Santiago-Plata, 2013).

The quality of presence-absence HSM models should be carefully revised when the species-environment equilibrium assumption is not met (i.e. as in the case of species recolonization or expansion) (Cianfrani et al., 2010).

Since these methods use species presence/absence data for the analysis, false-positive, and false negative observations can affect the results obtained (Marcelli and Fusillo, 2009; Cianfrani et al., 2010).

Since the habitat suitability for otter species can be restricted to a 150m buffer around rivers or water bodies, it is important for the presence data to have high locational accuracy, particularly when calibrating the model (Cianfrani et al., 2013).

It is important to have enough otter presence/absence data to use some of the information in the calibration of the model and the other part in the validation of the model. If the same information is used for both processes, the model performance can be overestimated (Sepúlveda et al., 2009.)

Deductive Habitat Suitability methods

Advantages

In habitat suitability models, the classification of suitable and unsuitable areas can be made deductively based on the information known of the species of interest. A GIS overlay is a commonly used method (Ottaviani et al., 2009; Loy et al., 2009).

By providing information on overall habitat quality, HSMs provide an important base for determining potential habitats for species of interest (Ali et al., 2010).
Habitat suitability maps don't require otter sighting data, but it can be used to validate the models (Loy et al., 2009).

Disadvantages

When choosing areas for conservation prioritization based solely on ecological niche and habitat models, there is a high probability of including areas of low presence likelihood for the species of interest; i.e., overprediction (Cirelli and Cordero-Sanchez, 2009).
Wildlife habitat selection is affected by many factors and therefore no single theory is suitable for every animal since other factors that are not being considered or that have not been measure or determined could be limiting their distribution (Ali et al., 2010).
Because HSM are usually build based on the information that is available, they are commonly used under the assumption that wildlife-habitat relationships are consistent throughout different scales (Ali et al., 2010).
The variables chosen can provide randomness in the predictions made (Cianfrani et al., 2010; Santiago-Plata, 2013).

Occupancy methods

Advantages

Occupancy models use presence/absence data and the attributes of each site to define species-habitat relationship that are described as the probability of occupancy by a species (Santiago-Plata, 2014; Bieber, 2016).
To improve their assessment of species distribution and species-habitat relationships, occupancy models are now developed to account for mistakes in species detection by including estimates of detection probability. Detection probability reduces bias issues and allows for stronger inferences about species-habitat relationships (Jeffress et al., 2011; Bieber, 2016).
There are tools that are already developed for occupancy modeling, such as PRESENCE software and single season models.
One can assess the results obtained from the PRESENCE software with other statistical analyses to choose best model and define direction and relative effect size of variables used (Jeffress et al., 2011).
This approach can create ranges of occupancy estimates (Bieber, 2016).

Disadvantages

Requires more visits within the same site (like river stretch), which are necessary to allow for spatial replication, in order to determine the detection probability (Jeffress et al., 2011)
Substrate type can affect the detection probability (Jeffress et al., 2011).
In occupancy models, when the surveys for calculating detection probability are not the same day, it is recommended to survey the sites 3 or more times if the probability is > 0.5 (Bieber, 2016).

Presence-only methods

Advantages

These methods use incomplete information (presence-only data) to represent the ecological -niche of a species from the analysis of several variables and as a result produces a map of a species distribution probability (potential distribution) or habitat suitability within an area of interest (Santiago-Plata, 2013; Bieber, 2016).
There are tools that are already developed to create habitat suitability models, such as ENFA (Ecological Niche Factor Analyses), GARP, and MAXENT (Maximum entropy algorithm). These programs require presence data and thematic maps of the variables being considered.
Maxent includes the possibility using analyses that examine relative impact of each environmental variable (Jackknife test) and measures the fitness of the model (test of the area under the curve (AUC) in the receiver operating characteristic (ROC) plot) (Santiago-Plata, 2013; Bieber, 2016). It also has a generative approach, rather than a discriminative one, which prevents the over adjustment of the model when there is a reduced number of values (Santiago-Plata, 2013)
ENFA models compares the environmental characteristics of the sites occupied by the species to the characteristics of the whole area of interest (Cianfrani et al., 2010).

Absences may prevent models identifying areas that are suitable for a species to spread into. Therefore, when working with species that have an unstable distribution (recolonization a or expansion) presence-only models are more reliable (Cianfrani et al., 2010).

Distribution models based on presence probabilities, allow a more detailed knowledge of a species potential distribution when they are extrapolated to scales of finer resolution (Barbosa et al., 2003).

Disadvantages

Maxent does not have a rule of minimum of maximum number of data values require for it to provide an adequate analysis, therefore there is still some discrepancy regarding these values (Santiago-Plata 2013). It is also sensible to the location of the presence data values; therefore, it may underestimate in areas where there are no observations registered, even when the region has suitable characteristics (Santiago-Plata, 2013).

Maxent produces three possible types of outputs: raw, log, and cumulative. This should be considered when choosing an output and interpreting the results (Santiago-Plata, 2013; Bieber, 2016).

When using Maxent for occupancy estimation, it may produce more liberal results than when using other occupancy estimation methods (Bieber 2016). The estimates obtained through Maxent can vary a lot based on the occupancy threshold that is established (Bieber, 2016).

There is no limit to the variables used in these models, therefore one must be very careful with variables that are selected, since the quality of the model will depend on the quality of the predictors considered (Cianfrani et al., 2010; Santiago-Plata, 2013).

These methods function based on incomplete information, therefore underestimation and overestimation are still possible, depending on the quality of the data available. The results will be better when the presence data represents a wider variety of environmental condition under which the species can be found (Cianfrani et al., 2010).

Appendix A3 – Metrics used at each scale

Table A9 - Metrics used at the local scale. Metrics in **bold** where found to be significant at this scale. Many studies do not consider variable significance in their analysis.

Classification	Variables	Metrics
Disturbance variables	Roads	distance to roads, number of major roads, park roads and paved roads crossing the watershed, number of dirt roads crossing the watershed, roads, total highway and roads density, **range distance to road**
	Population	distance to towns, total number of human residences within 500 m of the watershed occupied year-round, total number of homes within 500 m of the watershed occupied on a seasonal basis, settlement density, **human settlements**
	Tourism	**number of visitors**
	Contaminates	suspended solids, nitrates, phosphates, coliforms, dissolved oxygen
	Land use	grazing area, crops, land use, floodplain area (%), protected area (%), urban use
	Others	total number of times a footpath(s) crossed the stream, total length of footpath(s) within 25 m of the watershed, boat traffic (2), impact(human), polder cover (%)
Climate variables	Temperature	temperature
	Precipitation	precipitation
Terrestrial variables	Vegetation variables	**vegetation type of stream bank zone**, **vegetation type**, **vegetation complexity**, plant cover(%), riverbank vegetation (types), forest, tree cover(%), forestry(%), % of forested land area within 100 m of all streams and water bodies, % of forested land composed of mixed softwood, **% of forested land composed of birch-aspen**, **% of forested land composed of mixed hardwood-softwood**, % of forested land composed of "wetland softwood", % of forested land composed of northern-hardwoods, sum of the areas of all water bodies characterized by alder-willow, sum of the areas of all water bodies characterized by emergent herbaceous vegetation/ sum of the area (ha) of all water bodies, sum of the areas of all water bodies characterized by floating-leaf vegetation, **sum of the areas of all water bodies characterized by emergent herbaceous vegetation**, sum of the areas of all water bodies characterized by ericaceous vegetation, herbaceous cover, shrub cover, canopy cover, tree density sclerophylous, visual obstruction between 0 - 0.50 m, visual obstruction between 0.50 - 1.0 m, visual obstruction between 1.0 - 1.50 m
	Elevation	elevation, **slope**

Aquatic Variables	Water body characteristics	**water depth**, river length, stream velocity, **river/stream width**, average width of river, **bottom structure of stream**, **mean shoreline diversity index(shape)**, **bank types (shore type)**, average width of bank, number of pools, number of tree logs, area lake, tributary presence, sum of the perimeters of all water bodies, sum of the area (ha) of all water bodies, sum of all open water areas of all water bodies, average stream gradient over the entire watershed, **total dissolved solids**, **pH**, **flow zones**, water temperature, distance to shore, bottom slope, shoreline complexity
	River Hierarchy	distance to rivers of high hierarchy(3,4, 5), distance to rivers of low hierarchy(1,2), rivers(hierarchy), sum of the perimeters of all water bodies, sum of the area (ha) of all water bodies, sum of all open water areas of all water bodies, total length of all first-order stream, total length of all second-order stream segments, total length of all third-order stream segments, **total stream length over all stream orders**, total point-to-point length of all first-order streams, total point-to-point length of all second-order streams, total point-to-point length of all third-order streams, total point-to-point stream lengths over all orders, ratio1 (total length of all first-order stream / total point-to-point length of all first-order streams), ratio2 (total length of all second-order stream segments / total point-to-point length of all second-order streams), ratio3 (total length of all third-order stream segments/ total point-to-point length of all third-order streams), ratiot (total stream length over all stream orders/ total point-to-point stream lengths over all orders) average stream gradient over all first-order streams, average stream gradient over all second-order streams, average stream gradient over all third-order streams
Predator - Prey/Competition variables	Competition	mink presence
	Resource availability	**refuge availability**, % of all wetlands with active beaver sign, **% of all wetlands with active or inactive beaver sign**

Table A10 - Metrics used at the regional scale. Metrics in **bold** where found to be significant at this scale. Many studies do not consider variable significance in their analysis.

Classification	Variables	Metrics
Disturbance variables	Roads	distance to roads, sum of road km within the watershed/watershed area
	Population	distance from cities, distance to towns, human population density, **location of homes**
	Land use	**proportion of survey area comprised of cropland**, proportion of watershed comprised of cropland, frequency of dry herbaceous cropland in a 5-km radius, frequency of arboreal cropland in a 5-km radius, frequency of heterogeneous agricultural areas in a 5-km radius, high intensity development, low intensity development, proportion of watershed comprised of urban, (commercial, industrial, transportation, and recreation), **distance from surface excavation**, **distance from productive areas**
	Others	the site was a reservoir, **location of fishing nets (5.1 km sections),** disturbance, stream distance of site to nearest of border line for either Missouri or Oklahoma, **distance to the nearest otter release site (km)**
Climate variables	Temperature	mean annual temperature, minimum daily temperature, maximum daily temperature
	Precipitation	mean annual precipitation, mean daily precipitation, maximum daily precipitation
Terrestrial variables	Vegetation variables	riparian vegetation cover, land cover, bankside fine scale land cover, coarse scale extra-riparian CORINE land cover, vegetation type, distance from riparian vegetation, **proportion of survey area buffer comprised of woodland**, proportion of watershed comprised of woodland, frequency of deciduous forest in a 5 km radius, frequency of sclerophylous vegetation in a 5 km radius, **proportion of survey area comprised of grassland,** proportion of watershed comprised of grassland, upland natural, non-coastal wetlands, dominant vegetative land cover, amount of non-river channel wetland area
	Elevation	elevation, slope, aspect, convexity (hunting efficiency)
Aquatic Variables	Water body characteristics	water depth, bank height, bankfull height, bank slope, river/stream width, survey segment sinuosity, flow accumulation, **river water level**, water quality, AMNET/FIBI water quality, AMNET/FIBI habitat quality, the waterbody is 303(d) impaired, distance from water (rivers), distance to the closest lake/pond, freshwater, long-term median flow rate of the river (ft^3/s), last five year-dry history
	River Hierarchy	the site was a 3rd order stream, the site was a 4th order stream, the site was a 5th order stream, the site was a 6th–7th order stream, sum of all open water

		areas of all water bodies, **sum of the waterbody perimeters/sum of waterbody areas for entire watershed**, **sum of stream (3rd order) km within the watershed/watershed area**, **number of waterbodies within the watershed/ watershed area**
Predator - Prey/Competition variables	Competition	mink presence
	Resource availability	beaver presence, probability of beaver occupancy
	Food resources	fish biodiversity
Other		Cemetery, managed wetlands, schools, flats, tidal areas, bays, among others

Table A11 - Metrics used at the country scales. Metrics in **bold** where found to be significant at this scale. Many studies do not consider variable significance in their analysis.

Classification	Variables	Metrics
Disturbance variables	Roads	distance to the nearest highway, number of major roads, park roads and paved roads crossing the watershed, national road density, secondary road density, roads, total highway and roads density, presence of valley roads within 1 km, **main roads**, secondary roads, **highway density**, density of habitat cells (%of cell in the neighborhood occupied by roads)
	Population	distance to the nearest town with more than 100,000 inhabitants, distance to the nearest town with more than 500, 000 inhabitants, distance to small urban settlement, distance to large urban settlement, human population density, **mean density of human population**
	Tourism	hotels per km, vehicles per km, vacancies in tourist apartments per km, total tourist vacancies per km, vacancies in camping sites per km
	Land use	**agriculture**, percentage of agricultural area, relative pasture area, relative cropland area, agricultural/livestock as adjacent area, **proportion of agriculture area**, land use, percentage of urban area, **proportion of urban area**, no vegetation as adjacent area, **distance from industrial areas**, distance from mines, nearest distance from dam reservoirs
	Others	**water use**, **pollution**
Climate variables	Air humidity	**mean relative air humidity in January**, mean relative air humidity in July, annual relative air humidity range
	Evapotranspiration	annual potential evapotranspiration, annual actual evapotranspiration, mean annual potential evapotranspiration, mean annual actual

	Temperature	mean temperature in January, mean temperature in July, mean annual temperature, annual temperature range, average monthly mean temperature, average monthly minimum temperature, average monthly maximum temperature, daily temperature range, maximum temperature of the warmest month, minimum temperature of the coldest month
	Precipitation	mean annual number of days with precipitation, average monthly precipitation, mean annual precipitation, maximum precipitation in 24h, relative maximum precipitation, precipitation seasonality, annual days of precipitation, precipitation of the driest month, precipitation of the wettest month, pluviometric irregularity
	Others	mean annual insolation, mean annual solar radiation, mean annual number of frost days, mean daily solar radiation, number of bioclimatic belts
Terrestrial variables	Vegetation variables	**density of bank vegetation**, land cover, diversity of density of riparian vegetation (Simpson index), riparian vegetation width < 20 m, open riparian vegetation, dense riparian vegetation, riparian vegetation width>20 m, **semi-dense riparian vegetation**, forestry (%), relative woodland area, temu pitra swamp forest, exotic forest plantations as adjacent area, native vegetation as adjacent area, absence of riparian vegetation, upland natural, non-coastal wetlands, number of phytogeographic sectors
	Elevation	elevation/altitude, slope, aspect, mean altitude, minimum altitude, maximum altitude, altitude range, convexity (hunting efficiency), acclivity
	Others	mean annual run-off, **soil permeability**, west coordinate, south coordinate, mean latitude, **mean longitude**
Aquatic Variables	Water body characteristics	**water depth**, river slope, **anastomosed river length**, **current type**, narrow river, medium river, wide river, river/stream width, straight river, meandric river, shore type, streams, habitat type, average river elevation, total watercourses, hydrographic network
	River Hierarchy	stream order, first order rivers, second order rivers, third order rivers, fourth and fifth order rivers
Predator - Prey/Competition variables	Food resources	**freshwater crab**, **freshwater crayfish**, **food availability**
Others		other possible factors e.g. pollution, dry section of water body

Table A12 - Metrics used at the continental scale. Many studies do not consider variable significance in their analysis.

Classification	Variables	Metrics
Disturbance variables	Roads	roads, distance to roads
	Population	distance to the nearest town with more than 100,000 inhabitants, human population density
	Land use	industrial areas
Climate variables	Precipitation	annual precipitation, mean precipitation driest quarter, mean precipitation wettest quarter
Terrestrial variables	Vegetation variables	forest
	Elevation	elevation/altitude
Aquatic Variables	Water body characteristics	% lake
	River hierarchy	% rivers 1-2 Strahler order, % rivers 3–5 Strahler order, % rivers 6–9 Strahler order

Table A13 - Metrics used at the geographic extent scale. Metrics in **bold** where found to be significant at this scale. Many studies do not consider variable significance in their analysis.

Classification	Variables	Metrics
Disturbance variables	Population	**human population density**
Climate variables	Temperature	**annual temperature**, temperature standard, isothermality
	Precipitation	annual precipitation, precipitation of the driest months, precipitation seasonality, precipitation of the warmest quarter
Terrestrial variables	Vegetation variables	vegetation cover
	Elevation	elevation/altitude
Aquatic Variables	Water body characteristics	percentage of water bodies