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MODELLING SPECIES DISTRIBUTIONS TO MAP THE ROAD TOWARDS CARNIVORE CONSERVATION IN THE TROPICS

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ABSTRACT. — Knowing the distribution of species and the factors which determine it is a basic requirement for conservation efforts and developing management plans. Species distribution modelling (SDM) is a speedy and cost-effective tool for predicting species distributions, particularly for species in remote and inaccessible areas. This technique can be applied for example for poorly known small carnivore species in Southeast Asia, a biodiversity hot spot for mammals. SDM is used to gain ecological insights about the environmental factors that determine species distribution, and helps to identify the areas where a species can occur and where conflicts may arise. However, recent advances in statistical theory and computer processing have made SDM a somewhat complex, diverse, and confusing area of research. This review presents an overview over the different techniques of species distribution modelling, and databases needed to answer applied questions in carnivore conservation, particularly in the tropics. We guide the ecologist through different methods which have become established approaches in the scientific literature and through freely available resources on abiotic data (environmental layers) for conducting such studies. We summarise the steps involved in predictive species distribution modelling, where the (carnivore) occurrence data come from different resources (such as museum records, voluntary surveys, systematic surveys, etc.). Finally, we explore the applications of such predictions in carnivore conservation.

KEY WORDS. — carnivore conservation, small carnivores, Southeast Asia, species distribution model, tropics

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INTRODUCTION

With biodiversity in the tropics being in turmoil, mitigation of human-mediated impacts such as shifting land use or wildlife exploitation continues to be a clear focus for tropical conservation biology (Bradshaw et al., 2009). Carnivores and ungulates are a special target of conservation in the tropics and can serve as effective primers for designing conservation landscapes and management measures at the human-wildlife interface (Ray, 2010). Human activities often conflict with needs of carnivores. The question of how to integrate land exploitation and carnivore conservation in human-dominated landscapes poses one of the major challenges in conservation. Mammalian carnivores are undoubtedly a challenging group of organisms for conservation biologists. Large carnivores often cause problems at the livestock-wildlife interface and small carnivores are potential reservoirs of emerging infectious diseases, such as coronavirus responsible for recent SARS outbreaks (Bell et al., 2004; McLean et al., 2005). However, small carnivores such as rodents play a crucial role in the functioning of the ecosystem, such as dispersers of seeds and controllers of pest species (Jordano et al., 2007; Roemer et al., 2009).

Although the major challenges in mitigating the imminent threats to biodiversity in Southeast Asia are primarily socio-economic in origin (Sodhi et al., 2004), modelling is an essential element of efforts to convert conservation in Southeast Asia into success (Fordham & Brook, 2010). Especially useful are models that capture the complexities and uncertainties underlying biological mechanisms that drive species distribution and abundance. Ideally, one would use models that integrate demography, the spatial structure of the landscape, and ecosystem processes, but they tend to be complex and require detailed data (Wiegand et al., 2004a; Kramer-Schadt et al., 2005). Therefore the first important step is to predict the potentially suitable area for the species and to understand the underlying environmental factors. This is the basic knowledge required for the effective management of natural resources for conservation.

Species distribution modelling (SDM) has become an important tool in conservation ecology that allows approaching the basic question about the potentially suitable areas for a species and the underlying environmental factors (Elith & Leathwick, 2009). This statistical technique relates species occurrences or abundance with environmental information and/or spatial characteristics of those locations (Elith & Leathwick, 2009; Franklin, 2009). Predictions of SDMs are useful in identifying the core area for the conservation of species and can be the first step in management applications, such as site selection in reserve design (Zielinski et al., 2006), forecasting the response of species to environmental change and climate change (Carroll, 2007), studying large scale biogeographical issues such as geographic range contraction and taxonomic boundaries (Gates & Donald, 2000, Donald & Greenwood, 2001), invasive species biology (Peterson, 2003; Herborg et al., 2007; Loo et al., 2007) and ecosystem studies (Ferrier et al., 2002; MacNally & Fleishman, 2004). Habitat maps derived from SDMs can also be used to identify conflict areas at the human-wildlife interface (Kanagaraj et al 2011a; De Angelo et al. 2013), to pin down areas of carnivore conservation concern, and to delineate and evaluate corridors in order to maintain connectivity between suitable habitats for long-term conservation of carnivore populations (Kanagaraj et al., 2011a).

This review presents an overview over the different techniques of species distribution modelling and data bases needed to answer applied questions in carnivore conservation in the tropics. This is a specially challenging task because of limited financial resources, climatic challenges for researchers as well as material and inaccessibility of study areas. Several studies provide information on general aspects of SDM. They include reviews on technical aspects and methodological advice (Guisan & Zimmermann, 2000; Stauffer, 2002; Guisan & Thuiller, 2005; Richards et al., 2007; Schröder, 2008), and historical and cross-disciplinary features including the review of Elith & Leathwick (2009). Franklin (2009) reviews and synthesises the vast literature on SDMs in her recent book, and Peterson et al. (2011) aim to offer a body of terminology and schemes by which to understand and discuss the complex relationships between ecological niches and geographic distributions of species. Here, we guide the ecologist through different methods which have become established approaches in the scientific literature and through resources on abiotic data (environmental layers) available freely for conducting such studies. We summarise the steps involved in predictive distribution modelling (Fig. 1), where the (carnivore) occurrence data come from different resources (such as museum records, voluntary surveys, systematic surveys, etc.). Finally, we explore the applications of such predictions in carnivore conservation.

I: SPECIES OCCURRENCE DATA

Although species distribution modelling algorithms currently use four different types of data, presence-only, presence-absence, presence-pseudoabsence, and presence-background (see sub-section Modelling algorithms), the types of species occurrence data required as input data in species distribution modelling are usually presence-only or presence-absence data. Documentation of presence or absence of a species at a survey site is often complicated because two groups of factors have to be taken into account: biological factors and factors related with the detectability of the species. Thus, to obtain species occurrence data of good quality one should consider these factors when planning the survey (Peterson et al., 2011). Different modelling approaches have been developed to deal with presence-only and presence-absence data. Presence-only data report known occurrences (presence) of species at a given location, but do not provide information about absences. Presence-only data may stem from different sources including direct sightings in transects, sign surveys, non-systematic surveys, incidental direct sightings, and museum specimens.

The most reliable and accurate presence-only data sets are provided by direct sightings in transect counts that may use spotlights in night transect, trapping data, camera traps, and radio telemetry data (e.g. Durant et al., 2010; Pettorelli et al., 2010; Kanagaraj et al., 2011a). However, the effort of covering vast areas with such intensive techniques is large. This renders direct sighting methods ineffective for wide-ranging carnivores. Alternative methods include non-invasive sign survey methods which do not rely on capturing or direct observation of wide-ranging carnivores (Long et al., 2008). Sign surveys are similar to spotlighting and audio playbacks in terms of detection efficiency, precision, effort, and cost in landscape-scale surveys (Thorn et al., 2010). Sign survey data include the locations of indirect evidences such as tracks, faecal samples, depredation evidences, and scraps. Sign surveys are usually conducted by surveying along features that are likely to conserve carnivore sign such as dirt roads, dry water courses, and animal trails. They may use systematic sampling schemes (e.g., Smith et al., 1999; Thorn et al., 2010; Jhala et al., 2011; Kanagaraj et al., 2011a) or non-systematic surveys related to monitoring programs based on the collaboration of a network of volunteers and researchers (e.g. De Angelo et al., 2011).

Although novel quantitative methods have been developed to identify tracks of different carnivore species (Smith et al., 1999; Jhala et al., 2010; De Angelo et al., 2010), tracks of many carnivore species can often not be distinguished in the tropics even by highly experienced researchers. Mathai et al. (2010) observed that out of 14 small carnivore species recorded sign surveys were found useful for only three species (Malay Civet, Sun Bear, and otters) in a Southeast Asian forests. In contrast to regions outside tropical rainforests, where carnivore diversity is lower and/or substrates are more suitable for tracks (a leaf layer covering the ground), reliable identification of data based on tracks is only possible for species with diagnostic tracks such as the largest carnivores (e.g., tigers, bears). Similar difficulties arise in the tropics for the use of faecal samples as presence information because species identification from scats is difficult and supplementary evidences in the form of associated tracks and scraps are seldom available (e.g., Smith et al., 1999). Fast degrading DNA in tropical environments also complicates the successful application of molecular techniques (Goossens & Salgado-Lynn, 2013) even if they are developed specifically for different species (Fernandez et al., 2006; Haag et al., 2009).

Incidental direct sightings (e.g., De Angelo et al., 2011) or records of museum specimens, which are now widely available through networking of museum collections (Graham et al., 2004), are often a much more reliable source. However, because they are usually not collected in a systematic manner these data sets are typically biased towards certain locations where sightings are easy (e.g., roads) or places favoured by specimen hunters (Reddy & Davalos, 2003; Vaughan & Ormerod, 2003; Phillips et al., 2006). As we will see, non-systematically selected data must cover the environmental space sufficiently well (i.e., cover the environmental conditions where the species occurs and not occurs in the geographical study area), otherwise they may only reflect the species detectability (Phillips et al., 2009).

Additionally, this type of data may include observer error because people with different levels of expertise (i.e., faculty, students, collection managers, amateur collectors, not equipped with GPS) may be involved in collecting and identifying specimens and the trading port rather than the actual location where the species was found is given as location. Another potential problem is that the historic presence records extracted from museum collections often show poor temporal correspondence with environmental variables like current land-cover classification (Anderson &

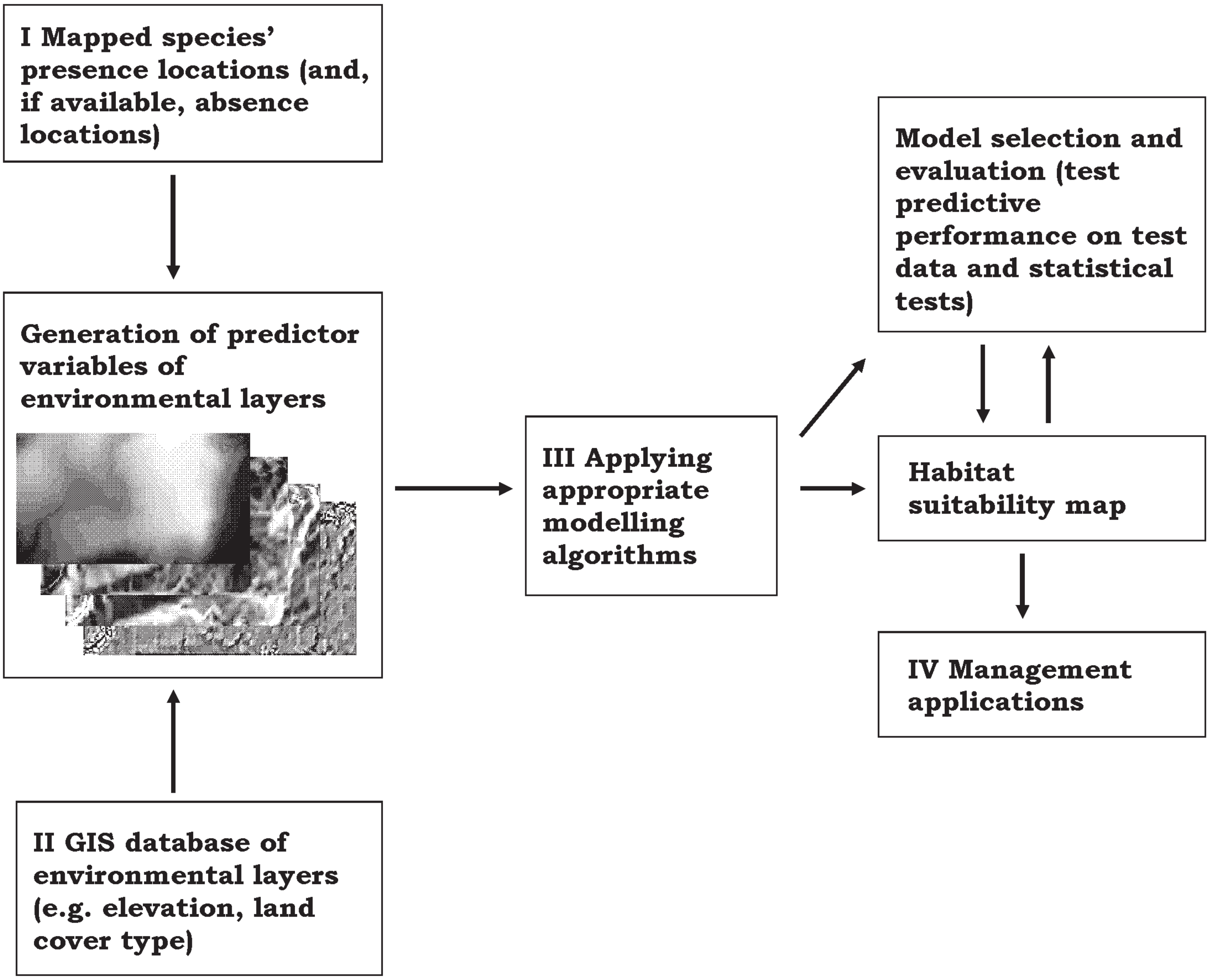

Fig. 1. From observation to conservation: Steps involved in species distribution modelling.

Martinez-Meyer, 2004; Gaubert et al., 2006). However, given all these potential pitfalls that may affect the accuracy of species distribution models, use of such data is often justified by the lack of more systematic survey data and widespread demand for mapped predictions (Elith & Leathwick, 2009). Because of their relatively low costs, presence-only data remain the major source of occurrence data for a species with large area requirements such as many carnivore species (Krishtalka & Humphrey, 2000).

Presence-absence data comprise additional information on reliable absence locations. This is difficult because a site may be used but not noticed. Therefore, the effort to collect presence-absence data is usually larger than collecting presence only data. It often involves several repeated censuses at the same locations and may require, additional to the SDM, calculation of the detection probability of the species in order to avoid the management consequences of false negative observation rates in presence/absence surveys (Wintle et al., 2004). Presence-absence data are therefore usually collected using a form of stratified random sampling (e.g., McAlpine et al., 2006; Rhodes et al., 2006) or follow a systematic sampling scheme (e.g., Fernandez et al., 2006; Gormley et al., 2011). Sites, usually in the form of equally sized grid cells or administrative units (e.g., Jhala et al., 2011), are selected from the study area and the presence or absence of the target species is then determined using the surveys. Field survey methods may include sign surveys as explained in presence-only data collection and camera traps. However, we would like to make the point that for almost none of the tropical carnivore species we can conclude on true absence due to the difficulties mentioned above.

II: ENVIRONMENTAL DATA

This section discusses the types of environmental data that are suitable for species distribution modelling and reviews data sources (Tables 1, 2). The most common environmental data that are used as predictor variables in statistical SDMs are related to land cover types, topography, and climate variables. However, remote sensing data that are not related to land cover classification are increasingly used for SDM.

Environmental variables may comprise either continuous data (data that can take any value within a certain range, such as elevation or slope) or categorical data (data that are split into discrete categories, such as land cover types). Because one of the aims of SDMs is to project the model as map over the entire study area and because several SDM methods require "background data", the values of an exploratory variable should be available for all grid cells in the entire study area. If this is not the case one may create a continuous surface using interpolation methods such as kriging (e.g., kriging interpolation using Geostatistical or Spatial Analyst tool in ArcGIS) or smoothing (e.g., spline and radial basis function smoothing methods in the R mgcv, gstat and geoR libraries; e.g., Horning et al., 2010).

Land cover variables. — Remote sensing (satellite) images have often been used indirectly through land cover classification for modelling species distributions (e.g., Schadt et al., 2002a; Pearson et al., 2004; see Table 1 for available sources of remote sensing data). Land cover classification can be derived from satellite images by applying unsupervised or supervised classification methods or a hybrid method which combines both (Richards, 1993; Bouman & Shapiro, 1994; Ehsani & Quiel, 2010; see supplementary material on classification steps). However, some studies directly used seasonal NDVI (see below) composite images and clustered NDVI data derived from time-series NOAA AVHRR imagery as surrogates for land cover maps (Egbert et al., 2002). For example, Vaniscotte et al. (2009) and Lahoz-Monfort et al. (2010) used several spectral bands provided by satellite images as predictor variables in SDMs, and Wiegand et al. (2008) used the seasonal pattern of NDVI as an indicator for brown bear habitat quality. Egbert et al. (2002) found that direct NDVI data performed as well as or better than topographic land cover data. However, when climate data were added to the model, land cover data performed slightly better.

Land cover types are categorical variables which cannot be used directly in several modelling algorithms such as BIOCLIM, DOMAIN, ecological niche factor analysis (ENFA), and Mahalanobis (see below). Hence, it is useful to transform them into a set of quantitative neighbourhood variables that yield the proportion of a given land cover type within distance *r* (e.g., De Angelo et al., 2011; Kanagaraj et al., 2011a; see below). Based on land cover one can also calculate several fragmentation metrics such as the number of forest patches, mean patch size, the Euclidean nearest neighbour distance, forest patch density or largest patch index, using software such as FRAGSTATS (Jaeger, 2000; McGarigal et al., 2002).

Topographic and other variables. — A digital elevation model (DEM), which can be obtained from the SRTM program (see Table 2), is often processed in a GIS software to generate a number of topography related variables such as elevation, slope, aspect, surface area, surface ratio index, topographic wetness index, vertical distance from the channel network or hydrological information such as watersheds and water flow direction (e.g., Jenness, 2004; Hengl et al., 2009; Vaniscotte et al., 2009; De Angelo et al., 2011; Kanagaraj et al., 2011a,b). However, since elevation itself can be a proxy for climatic conditions, it should rather be exchanged by climatic predictors in models that use both elevation and climate variables (see also the section on multicollinearity of predictors "Problems encountered: spatial autocorrelation and multicollinearity").

Vegetation metrics from multi-spectral satellite imagery, such as the normalised difference vegetation index (NDVI) (Tucker, 1979) and tasseled cap transformation (TCT) metrics (known as greenness, wetness, and brightness), have been employed in previous carnivore species–environment

Table 1. Available satellite imagery. This list does not claim completeness.

Available satellite imagery[*§]	**Description (resolution/ no. of bands available)**	**Pros**	**Cons**	**Websource**
Landsat	MSS multi-spectral (B: 4, R: 60 m). TM multi-spectral (B: 6, R: 30 m). TM thermal (B: 1, R: 120 m). ETM+ multi-spectral (B: 6, R: 30 m). ETM+ thermal (B: 1, R: 60 m).	Free. Multi-temporal, multi-spectral, and multi-resolution range of imagery at global level since 1972. Mosaics of images also available. Appropriate for land cover analysis.	More suitable for homogeneous landscapes (Koutsias & Karteris, 2003). Classification accuracy may diminish with highly heterogeneous landscapes such as eastern Mediterranean regions (Benedetti et al., 1994). Recent Landsat7 images are not suitable if study area is large (Trigg et al., 2006, Lahoz-Monfort, 2010)	Global Land Cover Facility: http://glcf.umiacs.umd.edu/data/landsat/
ASTER	VNIR (B: 3, R: 15 m) SWIR (B: 6, R: 30 m) TIR (B: 5, R: 90 m)	Free. Multi-temporal, multi-spectral, and multi-resolution range of imagery at global level since 2000. Appropriate for land cover analysis. VNIR is very useful for homogeneous and heterogeneous landscapes (Benedetti et al., 1994, Yüksel et al., 2008).	Visible near-infrared and shortwave infrared bands with two different resolutions. Combining all three sensors (VNIR, SWIR, and TIR) usually increases classification accuracy (Bagan et al., 2008).	Global Land Cover Facility: http://glcf.umiacs.umd.edu/data/aster/
MODIS	MODIS (B: 36, R: 200–250 m)	36 bands with a swath width of 2,330 km.	Low resolution: ranges from 250 m (two visible bands) to 500 m (five visible to shortwave infrared bands) and 1,000 m (29 visible, near infrared, shortwave infrared and mid-infrared bands).	Global Land Cover Facility: http://glcf.umd.edu/data/modis/index.shtml and http://modis.gsfc.nasa.gov/ (Parkinson & Greenstone, 2000)
IKONOS	Multi-spectral (B: 4, R: 4 m)	Finer spatial resolution	Data from commercial sector and costly. Limited in both spatial and temporal coverage and spectral coverage is limited to the visible and near infrared wavelengths.	available from Global Land Cover Facility: http://glcf.umd.edu/data/ikonos/ Dial et al., 2003
SPOT	Multi-spectral (B: 4, R: 2.5–20 m)	Finer spatial resolution	Data from commercial sector and costly. Limited in both spatial and temporal coverage and spectral coverage is limited to the visible and near infrared wavelengths.	http://www.astrium-geo.com/en/143-spot-satellite-imagery Martin et al., 1988
QuickBird	Multi-spectral (B: 4, R: 2.44–2.88 m)	Finer spatial resolution	Data from commercial sector and costly. Limited in both spatial and temporal coverage and spectral coverage is limited to the visible and near infrared wavelengths.	available from Global Land Cover Facility: http://glcf.umiacs.umd.edu/data/quickbird/
Rapid Eye	Multi-spectral (B: 5, R: 5 m)	Finer spatial resolution	Data from commercial sector and costly. No long-term data: available since 2008. Limited in temporal coverage and spectral coverage is limited to the visible and near infrared wavelengths.	http://www.rapideye.com/

[*] there are other resources through which classified land cover data can be obtained (e.g., Global Land Cover Facility, GlobCover project), often with low spatial resolution. See the following links for the lists of available resources: http://landcover.usgs.gov/landcoverdata.php and http://gif.berkeley.edu/resources/data_subject.html.

[§] also see Appendix 4 in Horning et al. (2010) for the relative cost information on the price for purchasing the imagery from commercial companies and the archives containing free remotely sensed data.

Table 2. Available global environmental data. This list does not claim completeness.

Data Type[*]	**Description (resolution)**	**Websource**
Elevation	Gap-filled 90 m, SRTM Digital elevation Model (DEM)	http://srtm.csi.cgiar.org/
NDVI	(i) 15-day, resolution 8 km (Tucker et al., 2005)	Global Inventory Modelling and Mapping Studies: http://glcf.umd.edu/data/gimms/
	(ii) 16-day MODIS dataset, resolution 250 m	Global Land Cover Facility: http://glcf.umd.edu/data/ndvi/
Stable Isotopes (Oxygen, Hydrogen)	Grid with resolution 10'–20'	http://wateriso.eas.purdue.edu/waterisotopes/index.html
WorldClim	Grid with resolution 30''–10', climate Data (temp, precipit, bioclim, altitude)	http://www.worldclim.org/download
World Database on Protected Areas WDPA	(i) World Database on Protected Area	http://www.wdpa.org/Default.aspx
	(ii) World map of intact forest landscapes at scale 1:1,000,000 (Potapov et al., 2008)	http://www.intactforests.org/
	(iii) World Wilderness Areas at scale 1:1,000,000 (McCloskey & Spalding, 1989)	http://geodata.grid.unep.ch/
Meteorological	(i) SEVIRI 15-minutes images at 1 km resolution from Meteosat Second Generation (MSG) satellites (Meteosat-8 onwards)	http://www.eumetsat.int/Home/index.htm
	(ii) MODIS/Terra Land Surface Temperature at 0.05-degree resolution (Wan et al., 2004).	https://lpdaac.usgs.gov/products/modis_products_table/mod11c3
	(iii) Japan Aerospace Exploration Agency (precipitation products (Kubota et al., 2007)	http://sharaku.eorc.jaxa.jp/GSMaP_crest/
Country-level data	Variable grid resolutions for administrative boundaries, roads, railroads, altitude, land cover, population density. Available at scales 1:1,000,000 and 1:250,000 (selected locations).	National Geospatial-Intelligence Agency (NGA): formerly known as Digital Chart of the World (DCW): http://geoengine.nima.mil/geospatial/SW_TOOLS/NIMAMUSE/webinter/rast_roam.html. Global Administrative Areas (GADM): http://www.gadm.org/ Global data sources: http://www.diva-gis.org/Data SRES 0.25-degree gridded global population data (Bengtsson et al., 2006): http://www.ciesin.columbia.edu/datasets/downscaled/ Global population density (Socioeconomic Data and Application Center SEDAC) at 1 km from 1990–2015 (maps for 2010 and 2015 are projected densities): http://sedac.ciesin.columbia.edu/gpw/ Global water resources at 30-arcsec (Global Lakes and Wetlands Database GLWD; Lehner & Doll, 2004): http://www.worldwildlife.org/science/data/item1877.html World river basins shape files (International Water Management Institute IWMI): http://waterdata.iwmi.org/

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*A list of available global GIS data (geology, soil types) is available at the EDEN project website: http://www.edenextdata.com/ and a list of resources to obtain various data sources (e.g., satellite imagery, biological data, climate, demography, land cover) can be found in the following link: http://gif.berkeley.edu/resources/data_subject.html.

modelling studies (Mace et al., 1999; Carroll et al., 2001; Alexander et al., 2006; Wiegand et al., 2008; Vaniscotte et al., 2009). The NDVI is the most commonly used and remote sensed variable in SDMs which is available for many years for most areas. It is based on the normalised ratio of the reflectance in the two spectral bands, near infrared and visible red, and quantifies the difference between photosynthetic activity related absorption in the visible range and reflectance in the near-infrared which is related to electro-magnetic emission by plants. NDVI is therefore correlated with vegetation biomass and has been used for quantifying productivity and above-ground biomass of ecosystems that influence species living in seasonal environments, local abundance of individuals and species distribution (Brown, 1988; Oindo & Skidmore, 2002; Seto et al., 2004; Wiegand et al., 2008; Vaniscotte et al., 2009).

An integrated normalised vegetation index (INDVI) can be calculated as an index of vegetation productivity from the NDVI, if the field survey has been conducted for several months or seasons (e.g., Pettorelli et al., 2006; Singh & Milner-Gulland, 2011). However, an enhanced vegetation index (EVI) can also be computed from the satellite imagery as the NDVI suffers from saturation when vegetative biomass is high and sensitive to the canopy background in open forested areas (Huette et al., 2002; Vaniscotte et al., 2009).

Bioclimatic variables (e.g., variables related to temperature and precipitation) can be derived from the WorldClim database (Hijmans et al., 2005). Global climate models have been used to generate scenarios of future climates and to simulate climatic conditions since the end of the last glacial period. Bioclimatic models are used to predict geographic ranges of organisms as a function of climate, and are widely used to forecast range shifts of organisms due to climate change, predict the eventual ranges of invasive species, or to infer paleoclimate from data on species occurrences (see Jeschke & Strayer, 2008 for an extensive review).

The environmental variables discussed so far were mostly related with factors characterising the natural environment. However, for carnivores, human induced mortality is an important factor which does often not correlate with features of the natural environment (Woodroffe & Ginsberg, 1998; Naves et al., 2003) and may therefore create attractive sinks (Delibes et al., 2001). Therefore, it is important to use environmental variables associated with human activities that have direct impact on carnivore distribution, abundance, and survival, such as intensities of hunting/poaching, livestock grazing and food, fodder, and fuel wood collections. In absence of such measures, proxy variables that quantify the potential human disturbance such as human population density and presence of roads can be used in the analysis. Disturbance variables such as digital vector layers of transportation and population densities or other thematic layers such as drainage systems and boundaries can be obtained with the scale of 1:1,000,000 from the Global Map Data project and Digital Chart of the World Data Server (Table 2). Two different measures can be calculated from these vector layers using a GIS or modelling software (e.g., "Spatial Analyst" in ArcGIS and "Circular Analyst" in open source Biomapper): 1) variables calculating the straight line distance to the closest target location (e.g., town, road, river) in the target layer; and 2) variables calculating the frequency of cells (grids) occupied by the target locations in a circle of radius (see section Neighbourhood variables) around the focal cell in the target layer.

Neighbourhood variables. — The grain of environmental variables is often small and is not necessarily related to the spatial scales at which the target (carnivore) species perceives the landscape and at which resources need to be available (Schadt et al., 2002b; Naves et al., 2003; Wiegand et al., 2008; Kanagaraj et al., 2011a). Hence, it is often useful to transform the original categorical land cover (or other environmental) variables into a set of neighbourhood variables. A neighbourhood variable is the mean value of the target variable within a specified neighbourhood radius around the target cell. Because the critical scale at which the species perceives its environment is often not known a priori, variables need to be constructed for several neighbourhood radii. They should cover spatial scales larger than the home range size of the target species (Schadt et al., 2002b; Naves et al., 2003; Wiegand et al., 2008; De Angelo et al., 2011; Kanagaraj et al., 2011a).

III: STEPS INVOLVED IN SDM

Species and environmental data used for modelling are usually stored in a Geographic Information System (GIS). Species data, i.e., sites where a species has been observed (or not observed), are usually stored as point localities (termed point vector data). Environmental variables are stored either as point vector data (e.g., percentages of trees or grass cover measured at sites where the species has been observed), as polygon layer defining an area (termed polygon vector data; e.g., areas with different soil types) or as a grid of cells (termed raster data; e.g., elevation or land cover types derived from remote sensing). For use in a species distribution model, it is common to reformat all environmental data to a raster grid.

The cells containing the species data and the environmental data are used to build the SDM. After the statistical model is constructed, it is evaluated using independent species data, cross-validation or other evaluation measures (reviewed in Franklin, 2009 and Elith & Leathwick, 2009). Then the occurrence of species in the entire study area is predicted with the mathematical formula given by the statistical model using the environmental variables identified by the final model and mapped by returning probability values of occurrence or habitat suitability for each raster cell (Fig. 1).

Modelling algorithms. — A number of alternative modelling algorithms have been developed to classify the probability of species' presence (and absence; or abundance) as a function of a set of environmental variables. The quality of species distribution models depends on the quality, grain and extent of the data (e.g., Trivedi et al., 2008; von dem Bussche et al., 2008), and on the effectiveness of the statistical model. The differences between model algorithms in dealing with several technical issues should be considered when selecting a method to apply. Major issues are:

1. The ability of different algorithms to deal with the different species data types
2. The ability of different algorithm to deal with categorical environmental variables (i.e., ENFA does not work with categorical variables)
3. Complex non-linear responses of species in multi-dimensional environmental space
4. Presence of spatial and temporal autocorrelation (Legendre, 1993; Barry & Elith, 2006; Dormann et al., 2007)
5. Non-equilibrium distribution of species (e.g., population extension or reduction)
6. Non-stationarity, i.e., the variation in modelled relationships over space and/or time (Osborne et al., 2007), as the model assumes that the effects of environmental variables are fixed and universal (e.g., Hothorn et al., 2011)

In the following we will discuss how the different algorithms of SDM deal with these issues.

Presence-only methods. — There are several approaches that use presence-only data for species distribution modelling (see Table 3 for the list and abbreviations). Models used to fit presence-only data predict the relative likelihood of species presence at a site, or the relative habitat suitability, but not the actual probability of species presence which can only be estimated by presence-absence methods (Elith & Leathwick, 2009; Franklin, 2009). The presence-only methods BIOCLIM, DOMAIN, LIVES, and Mahalanobis, use only presence records, and all other methods require presence and some form of absence from a background (Table 3). They either compare use with availability or are based on "pseudo-absences" to apply methods of presence-absence modelling. In short, we can distinguish three types of presence-only methods:

1. **Methods that rely solely on presence (occurrence) data (e.g. BIOCLIM, DOMAIN and LIVES)**: Envelope techniques (e.g., BIOCLIM, DOMAIN, LIVES, and Mahalanobis) fit a minimal envelope in a multidimensional space to presence-only data and do therefore not require background data.

2. **Methods that require presence and a background sample of absence data (e.g., ENFA or Maxent)**: In most techniques, the recursive selection of an absence sample from the background is automatically performed in the modelling software (e.g. Maxent, GARP, and Biomapper (ENFA); see Table 3 for references where these methods have been applied in carnivore habitat modelling studies).

3. **Methods that require presence data and pseudo-absences from the study area**: Pseudo-absences can be generated in several ways—They can be selected: A) at random from the study area (e.g., Stockwell & Peters, 1999; Hirzel et al., 2002; Rosalino et al., 2010); B) in two steps, first generating an SDM with a group discriminative technique and random pseudo-absences, and then obtaining pseudo-absences only from the areas predicted to have higher suitability values (Zaniewski et al., 2002); C) based on a weighting criterion (e.g., Engler et al., 2004; Chefaoui & Lobo, 2007, 2008; Acevedo & Cassinello, 2009; Kanagaraj et al., 2011a); and D) using distribution data from species—called auxiliary species—with similar environmental requirements to the species being studied (Lütolf et al., 2006). Another effective way to generate the pseudo-absences is based on a strategy called target-group absences (Mateo et al., 2010a). Important differences between the pseudo-absence approach and the background approach are that the pseudo-absence methods do not include occurrence localities within the set of pseudo-absences and pseudo-absences can be selected in a GIS and the number and the location criteria can be controlled by the researcher. In principle, any presence-absence method can be implemented using pseudo-absences (e.g., ANN, BIOMOD, BRT, DCM, GLM, GAM, and MARS; see Table 3).

Regarding their performance, a study by Elith et al. (2006) identified new tools such as MARS and Maxent to be better suited than the well-established and more widely used modelling methods such as DOMAIN, GARP, and BIOCLIM. Among the presence-only and presence-absence methods, Maxent has become a popular method that has performed generally well (Elith et al., 2006; Philips et al., 2006, 2009; Guisan et al., 2007; Hernandez et al., 2008), especially when only a small sample of observations is available (Hernandez et al., 2006; Pearson et al., 2007; Wisz et al., 2008; Franklin, 2009). Also, the Maxent model algorithm considers linear, non-linear, and interaction effects (Phillips et al., 2006). A recent study by Hoffman et al. (2010) showed that there was little difference in the performance of presence-absence models (GAM, GLM or logistic regression) compared to the presence-only models, and that relatively accurate models can be generated using Maxent and/or discrete choice models (DCM). They noted that DCMs are conceptually similar to other resource selection functions (RSFs) such as logistic regression where data is collected from sites where the species is present and absent (Manly et al., 2002; Keating & Cherry, 2004), however, unlike logistic regression in RSFs, absence sites in DCMs are selected at random and confined to a "choice set", which can be controlled by the researcher. Often, these presence-only methods have been implemented in user-friendly software that is free and easy to obtain (Table 3).

Presence-absence methods. — Presence/absence data can be used to predict the actual probability of species occurrence. Example methods include regression methods such as GLM, GAM, BRT, and MARS, and DT and ANN (also the approaches mentioned in type 3 presence-only methods; Table 3; see Franklin (2009) for more details). Generalised linear models (GLMs) and generalised additive models

Table 3. Approaches for modelling species resource selection, habitat suitability and distribution. Information compiled mostly from Franklin (2009) and Elith & Leathwick (2009).

Species data and Model	Method	Pros	Cons	Software	Key reference	Application in (carnivore) research
Presence-only						
BIOCLIM	envelope model		Performs poorer than statistical models and underestimates species presence.	DIVA-GIS, BIOCLIM ArcView extension	Busby, 1991	
DOMAIN	Gower metric; multivariate distance		Underestimates distribution in novel conditions.	DIVA-GIS	Carpenter et al., 1993	
LIVES	multivariate distance				See Elith et al., 2006	
Mahalanobis	Mahalanobis distance based on the correlations of the predictors			R mahal() in the dismo package	Mahalanobis, 1936	Corsi et al., 1999
Presence-only ('background' environment)						
ENFA	ecological niche factor analysis		Overestimates current distributions compared to statistical methods.	BIOMAPPER	Hirzel et al., 2002	Pettorelli et al., 2009, 2010; Durant et al., 2010; Basille et al., 2008; Unger et al., 2008; Huck et al., 2010; De Angelo et al., 2011; Kanagaraj et al., 2011a
Maxent	maximum entropy	Often performs better than other methods. Performs well in data-poor situations.		MaxEnt	Philips et al., 2006	Wilting et al., 2010; Rosalino et al., 2010; Papes & Gaubert, 2007; Jennings & Veron 2011
GARP	genetic algorithm	Advantage over other methods (GLM, classification tress) when presence records are very few.	Overall poor performance in comparison with other methods. Overestimates current distribution and underestimates in novel conditions.	Desktop GARP and OpenModeller (GARP 3.0)	Stockwell, 1999	Papes & Gaubert, 2007
DCM	discrete choice models	New approach in ecology and little information exists on its potential for predicting species distributions.	Although most applications are based on telemetry data, it can also be used in presence data	R clogit() in the survival library	Cooper & Millspaugh, 1999	Thomas et al., 2006; Güthlin et al.,2011

Table 3. Cont’d.

Species data and Model	Method	Pros	Cons	Software	Key reference	Application in (carnivore) research
Presence-absence*						
GLM	generalised linear model	Effective global modeling method, performs well with adequate data. Non-linear response of species can be handled by fitting linear, quadratic and/or cubic terms. Model results can be transferred to different regions and environments.		R base package	McCullagh & Nelder, 1989	Naves et al., 2003; McAlpine et al., 2006; Klar et al., 2008; Conde et al., 2010; Barbosa et al., 2010; Kanagaraj et al., 2011a
GAM	generalised additive model	Performs better than GLM. Handle complex non-linear response of species		R gam and mgcv packages	Hastie & Tibshirani, 1990	Pearce et al., 2001
GLMM	generalised linear mixed-effect models	Deals with autocorrelation in the data.	Models are analytically complex that may inhibit convergence.	various R packages, e.g. lme4 or nlme	McCulloch & Searle, 2001	Gillies et al., 2006; Rhodes et al., 2009; Klar et al., 2008; Kneib et al., 2009
GEE	generalised estimating equations	Deals with autocorrelation. Robust to misspecification of the correlation structure	Sensitive to the choice of the link function	Procs GENMOD in SAS; R package geepack	Hardin & Hilbe, 2003	
CAR, SAR	conditional autoregressive models, spatial autoregressive models	Deals with spatial autocorrelation. SAR tends to perform better than non-spatial models, but limited to spatial density of data available for calibration.	Autocovariate may mask importance of environmental predictors.	R spdep package, WinBUGS.	Lichstein et al., 2002	
MARS	multivariate adaptive regression splines	Performs slightly better than GLM. Computationally faster than GAMs for complex data.	Fitting to categorical response requires special software. Model reliability and stability decrease with sample size.	R mda package	Friedman, 1991; Hastie et al., 2001; Leathwick et al., 2006; Elith & Leathwick, 2007; Mateo et al., 2010b	
ANN	artificial neural network	Good performance when used by skilled practitioners.	Performance sometimes worse than other statistical methods.	SPECIES	Pearson et al., 2002	

Table 3. Cont'd.

Species data and Model	**Method**	**Pros**	**Cons**	**Software**	**Key reference**	**Application in (carnivore) research**
CT; CRT	decision trees; classification and regression trees	Deals with complex non-linear response of species.	Perform poorly compared to other methods and tend to overpredict the area of occupancy, especially when the species has low prevalence.	R tree and rpart packages	Venables & Ripley, 2002; Meynard & Quinn, 2007	
BRT, RF	boosted regression trees, random forests	Good predictive performance given adequate sample size.			De'ath et al., 2007; Elith et al., 2008	
Boosting methods	model based boosting	Handle nonlinearity, interaction, autocorrelation, nonstationarity.		R mboost	Hothorn et al., 2011	
Ensemble forecasting	Ensemble forecasting	Treatment of methodological uncertainties in models, project species distributions into different environmental conditions and dispersal functions.		R BIOMOD	See Araújo & New, 2007 for a review; Thuiller et al., 2009.	Thuiller et al., 2006

* in principle, any presence-absence method can be implemented using pseudo-absences, i.e., an artificially selected set of absence points

(GAMs) have been used extensively in species distribution modelling, including carnivore habitat modelling studies (e.g., Mladenoff et al., 1995; Palma et al., 1999; Schadt et al., 2002b; Woolf et al., 2002; Naves et al., 2003; Hoving et al., 2004; Muntifering et al., 2006; Varela et al., 2009; Conde et al., 2010; Rosalino et al., 2010; Zielinski et al., 2010; Kanagaraj et al., 2011a). They are the preferred tool because of their strong statistical foundation and ability to realistically model ecological relationships and produce robust models (Austin, 2002), and they performed better than classification trees and GARP (Meynard & Quinn, 2007). GLMs fit parametric terms, usually some combination of linear, quadratic, and/or cubic terms, whereas GAMs use non-parametric, data-defined smoothers to fit non-linear functions and are more capable of modelling complex ecological response shapes than GLMs (Yee & Mitchell, 1991; Elith et al., 2006).

Models such as autoregressive models (AR), generalised linear mixed-effect models (GLMM; Rhodes et al., 2009; Klar et al., 2008), generalised estimating equations (GEE), and spatial filtering can handle spatially autocorrelated species data (see Table 6.2 in Franklin, 2009 for details). However, a new modelling framework described by Hothorn et al. (2011) handles non-linearity, interaction, spatiotemporal autocorrelations, and non-stationarity in a single non-parametric modelling framework (model-based boosting). Presence-absence and abundance data can be used in this framework.

When telemetry data is available, one can estimate resource selection functions (RSFs), which compare used (telemetry locations) with available habitat (Manly et al., 2002). RSF models can also be developed for sign survey data when the sampling protocol represents a true presence-absence design (see Alexander et al., 2006; Carroll & Miquelle, 2006). These RSF models have been used in several carnivore habitat modelling studies (e.g., Apps et al., 2004; Carroll & Miquelle, 2006; Klar et al., 2008; Rozylowicz et al., 2010).

Occupancy modelling. — Since the utility of predictive distribution models for designing reliable conservation planning depends on our capacity to obtain the best quality data possible for developing habitat models, it is also particularly important to explicitly account for imperfect detectability for studies of rare and elusive species (Thompson, 2004). The detection-nondetection data with repeated independent survey data are suitable for occupancy estimation and modelling (MacKenzie & Royle, 2005), however, detection probability can be estimated directly from single surveys of multiple trail segments following newly developed sign survey protocols (Thorn, 2009; Hines et al., 2010). The likelihood-based occupancy modelling (MacKenzie et al., 2002; Mackenzie & Bailey, 2004; MacKenzie et al., 2006) permits the simultaneous estimation of site occupancy and detectability and allows to produce predictive probability of occurrence models from detection-nondetection data of wide-ranging carnivores (e.g., Gardner et al., 2010; Long et al., 2011; Sollmann et al., 2011; Sunarto et al., 2012).

Ensemble forecasting. — According to Araújo & New (2007), a forecast ensemble can be defined as “multiple simulations (copies) across more than one set of initial conditions (IC), model classes (MC), parameters (MP), and boundary conditions (BC)”. Although this method has been widely used in a variety of other fields of research such as economics, meteorology, climatology, etc., it has only been recently applied in ecological studies for bioclimatic modelling of species distributions (see Araújo & New, 2007 and references therein). Though several SDM modelling techniques such as ANNs, GARP, MAXENT, RFs, etc., incorporate the notion of this method (see Table 1 in Araújo & New, 2007), these techniques do not consider all possible combinations of IC, MC, MP, and BC, providing an unclear picture of the potential model uncertainties (Araújo & New, 2007). Thuiller et al. (2009) developed a software platform called ‘BIOMOD’ for ensemble forecasting methods that enables the treatment of a range of methodological uncertainties in models and allows users to test several modelling techniques, project species distributions into different climate or land use change scenarios and dispersal functions.

Problems encountered: Spatial autocorrelation and multicollinearity. — Spatial autocorrelation describes the phenomenon that species occurrences that are close in space are more similar to each other than the occurrences that are further away from each other. This lack of independence in the data can lead to pseudo-replications that will give variables a higher significance. Serial autocorrelation, especially in the GPS telemetry data, can lead to the inaccurate estimation of RSFs (Koper & Manseau, 2009). These problems may be solved by achieving independence in the data set by destructive sampling (Way et al., 2004), but it may require dropping as many as 95% of data collected (Saher, 2005; Koper & Manseau, 2009). One way to assess the extent of spatial autocorrelation in the presence/absence data is to look at correlograms of the data and of the residuals (Cliff & Ord, 1981; Bjornstad & Falck, 2001; Dormann et al., 2007). A spline correlogram of the raw (presence/absence) data and the residuals of the regression model can be produced to investigate the spatial autocorrelation (e.g., Rhodes et al., 2009; R package ‘ncf’). Dormann et al. (2007) distinguish four approaches to address spatial autocorrelation in linear models: autocovariate models, spatial eigenvector mapping, generalised least squares, and generalised estimation equations. The modelling framework described by Hothorn et al. (2010) handles spatial and temporal autocorrelation in presence-absence and abundance data sets.

Spatial autocorrelation in the presence (presence-only) localities can also be minimised through the use of a constrained random split of sampled locations forcing all pairs of points below a threshold distance to split dichotomously into the training and the test sets (Parolo et al., 2008). Another option is to overlay a grid with a cell size equal to the home-range of the target (carnivore) species and randomly select a single point from each cell that contains more than one record (Sattler et al., 2007; De Angelo et al., 2011; Kanagaraj et al., 2011a). Alternatively, the background area can be also manipulated (e.g., Kramer-Schadt et al., 2013).

An important issue to be considered before fitting regression models is to check whether there is high collinearity between the explanatory variables (Graham, 2003). The problem with collinearity is that if one variable depends on the others, an ecological interpretation impact of a given variable on habitat suitability is not possible. Collinearity can be identified by looking at the pairwise Spearman rank correlation coefficient between explanatory variables. As a rule of thumb, correlation coefficients between pairs of variables with magnitude of $|r| > 0.7$ indicate high collinearity (Dormann et al., 2012). Another way to check the collinearity is to calculate the variance inflation factors (VIFs) for each variable. A cut-off value of 5 or 3 can be used to remove collinear variables (e.g., Zuur et al., 2009, chapter 16, R package 'AED'). For more available methods we recommend readers to consult Dormann et al. (2012) who tested several available collinearity diagnostics methods and evaluated their performance based on a simulation study.

Problems encountered: Complex non-linear response and interactions. — Environmental variables that may act nonlinearly can be identified by plotting the explanatory variable against the response. Non-linearity of the continuous predictor variable can be included in the model by squaring it or using its n^{th} polynomial. This is the simplest and generally sufficient way to include non-linear effects in the model (Dormann, 2011). Another way to avoid this problem is to use smoothing models such as GAM (Zuur et al., 2009). However, the influence of explanatory variables on species occurrence can also be non-additive and can be estimated by random forests (Cutler et al., 2007) or boosted regression trees (Moisen et al., 2006; De'ath, 2007; Elith et al., 2008; Zurell et al., 2009; Hothorn et al., 2011).

Another potential problem in this context can be caused by interaction effects of explanatory variables. An interaction effect occurs if the effect of one variable depends on the level of the other variable. Thus, including only the main effect of the variable (i.e., the effect of each variable, independent of the other variables) in the model may lead to misinterpretation if interaction effects are present.

Problems encountered: Non-equilibrium distribution of species. — SDMs are fundamentally static in nature and usually require the assumption that the species is in equilibrium with its environment. That means that the species is present at locations that show a good suitability and the species is absent at locations that show a low suitability. However, this assumption is often not met. For example, many endangered species are showing range reduction due to increasing human disturbance. In this case one may adapt the data scheme and use only absence locations which are close enough to the known species presences assuming that the species could potentially use this site. This allows then for identifying potential habitat which is currently outside the dispersal range of the species. However, if these areas would be included as unsuitable (because they were unused) a severe bias may be the result.

Ironically, climate change is one of the most important motivations for the booming use of SDMs. However, if the environment changes, a species is likely not to be in equilibrium with its environment and the prediction accuracy of the species distribution will severely be affected (Zurell et al., 2009; Peterson et al., 2011). The spatial and temporal variability in the environment resulted from changing climate must be accounted for in SDMs (Zurell et al., 2009). To correctly predict and understand range shifts of species the dynamic nature of populations, also dispersal at the leading edge and extinction or persistence at the trailing edge of the range shift should be incorporated into the SDMs (Zurell et al., 2009).

Model selection and validation. — In the multiple regression context model subset selection in species distribution modelling has two distinct purposes: 1) to find the single best 'predictive' model; and 2) explanation of causal relationships between the dependent variable and the independent variables using an explanatory approach (Mac Nally, 2000). In the first approach a quantitative model is desired for 'prediction'. In the second case, however, no quantitative model is desired, but 'further studies and experiments may be suggested for testing the causal nature of relationships' (Mac Nally, 2000). The predictive model can be used to make predictions of the current and future distribution of species based on measurements of a few explanatory variables. An appropriate selection criterion (e.g., Akaike information criterion [AIC] or Bayesian information criterion [BIC]) can be used to find the single best 'predictive' model. The explanatory approach can be used to test predictions of models, i.e., testing whether the outcomes of the explanatory approach are in agreement with the 'predictive' approach, and to develop new insights and design new research (Mac Nally, 2000). A suitable method for the explanatory approach to explore potentially causal/explanatory relationships between the dependent variable and the independent variables is hierarchical partitioning (Mac Nally, 2000).

Regression methods provide sophisticated tools of model selection that allow the researcher to identify the hypothesis and the single best 'predictive' model that receives most support from the data, given a predefined array of competing hypotheses about the environmental variables that influence habitat suitability (Burnham & Anderson, 1998; Johnson & Omland, 2004). Using the accumulated knowledge of ecology of the target species provides a basis for guided a priori selection of explanatory variables that may influence species occurrence (e.g., Fernandez et al., 2003; Fernandez et al., 2006; Klar et al., 2008; Kanagaraj et al., 2011a). Information-theoretic methods can then be used for model selection where model fit is assessed using an appropriate criterion (e.g., AIC or BIC) that balances fit against model complexity (i.e., number of parameters). The most parsimonious model is usually selected based on lowest AIC value (Burnham & Anderson, 1998). Regularisation methods for logistic regression, such as lasso and ridge, have also been proven as useful and risk-averse model strategies especially at small sample sizes (Reineking & Schröder, 2006).

Model diagnostics is an important step to check the quality of the model. It is important to investigate the model residuals to be confident that model assumptions are valid (e.g., plotting the residuals against fitted values to verify homogeneity, making a histogram of the residuals for normality and residuals against each explanatory variable to check independence; Zuur et al., 2009). Additionally, model residuals should be tested for spatial autocorrelation. Several methods are available to correct spatial autocorrelation in the occurrence data (see Dormann et al., 2007).

Performance of the fitted model can be divided into calibration and discrimination (Pearce & Ferrier, 2000) and quantified by deriving several statistical measures by comparing the model predictions with field data. Both performance criterions should be used to evaluate the performance of the fitted model (Reineking & Schröder, 2006), as they measure different aspects of model performance (Harrell, 2001). Calibration can be quantified using a calibration curve (e.g.,Reineking & Schröder, 2006) and by calculating the explained deviance (e.g., Zuur et al., 2009). The threshold independent measure AUC (area under curve) is the most commonly used measure that could be used to evaluate model discrimination for presence-absence data (Fielding & Bell, 1997) whereas k-fold cross validation. can be used for presence-available models (Boyce et al., 2002). The AUC-value, estimated by calculating the area under a receiver operating characteristic (ROC) curve, is 0.5 in the random model case and 1 if the classification is perfect. There are other performance measures such as classification error and kappa, which are based on binary predictions. For this purpose, the probability predictions from the fitted model are converted into presences and absences using an appropriate threshold value (Liu et al., 2005). A confusion matrix can then be used to calculate the measures such as commission and omission error, kappa, etc.

IV: APPLICATION OF SDMS IN CARNIVORE CONSERVATION PLANNING

Predictions obtained from SDMs can be used in a range of conservation and management applications. First, in a static manner, single species distribution or habitat suitability maps can be used to evaluate the currently available area for the species under study. This allows addressing basic questions such as if the area is large enough to sustain a population, are the best areas those which may bear the largest conflicts with human use, or which areas may be suitable for restoration? Additionally, the predicted habitat maps can be used to assess functional landscape connectivity for inter-patch dispersal and to identify barriers to species movement at regional scales (e.g., Beier et al., 2006; Kanagaraj et al., 2011a). In this context, the least-cost modelling approach (reviewed in Sawyer et al., 2011) has been widely used for designing wildlife corridors. Least-cost path models use a GIS raster and assign weights (or landscape resistance values) to landscape elements such as certain land cover types or roads that describe the cost of moving through this element. The least-cost algorithm then searches the path with the lowest cost. Instead of assigning weights to landscape elements one can also use directly habitat suitability maps (Clevenger et al., 2002; Chetkiewicz & Boyce, 2009; Huck et al., 2010). The weighted input GIS maps can be generated based on techniques that include expert-based models (Schadt et al., 2002a; Singleton et al., 2002; Wikramanayake et al., 2004; Johnson & Gillingham, 2005; Beier et al., 2006; Beier et al., 2009), compositional and Euclidean and Mahalanobis distance analyses (Clevenger et al., 2002; Kautz et al., 2006), RSFs (Chetkiewicz et al., 2006; Chetkiewicz & Boyce, 2009), weights-of-evidence (Kindall & Van Manen, 2007) and profile methods such as ENFA (Huck et al., 2010). It results in connections between delineated areas that contain the least amount of barriers or unfavourable conditions and are therefore assumed to represent the most promising wildlife corridors (Sawyer et al., 2011).

Distribution or habitat suitability maps can also be used to identify conflict areas at the human-wildlife interface or to pin down areas of carnivore conservation concern. Predicted habitat suitability values have been used in reserve selection (e.g., Margules & Nicholls, 1987; Williams & Araujo, 2002; Zielinski et al., 2006). Algorithms such as MARXAN can be used to identify priority habitat areas for individual species, and for combined species groups, and to compare these areas with existing reserves in order to identify habitats that do not align with existing reserves (Zielinski et al., 2006).

In biodiversity research, habitat suitability models developed for individual species can be used to assess intra-guild competition and reveal differences in habitat use patterns within the carnivore community (e.g., Alexander et al., 2006; May et al., 2008; Durant et al., 2010; De Angelo et al., 2011). They can be used to calculate the degree of overlap among species and patch sizes in order to identify the necessary scales for regional zoning for conservation and management implications (May et al., 2008; De Angelo et al., 2011). For example, BIOMAPPER software tools can be used for direct species comparison (e.g., Durant et al., 2010; Pettorelli et al., 2010) or to understand how ecologically similar species respond to anthropogenic transformations of the landscape (De Angelo et al., 2011) and to estimate traditional niche breadth (Levins' standardised index) and overlap indices (Pianka's overlap index and Lloyd's asymmetric overlap index) by applying a discriminant analysis (Hirzel et al., 2008; Qi et al., 2009; Simard et al., 2009; De Angelo et al., 2011). Environmental favourability functions derived from habitat suitability models (Real et al., 2006) enable direct model comparison and combination when more than one species is involved (e.g., Estrada et al., 2008; Real et al., 2008; Real et al., 2009), for example, directly comparing the degree of favourability for a rare predator and a more common prey (Real et al., 2009).

When different factors determine carnivore mortality (often human disturbances) and reproduction (often natural habitat factors; Woodroffe & Ginsberg 1998; Naves et al., 2003), a two-dimensional habitat model can be developed where one axis describes suitability for reproduction and the second axis survival. Ideally, each axis would be constructed from data about reproduction and mortality (e.g., Nielsen et al., 2006; Falcucci et al., 2009). However, since such information is often not available, Naves et al. (2003) proposed to use species presences-absence data, but with different hypotheses on the environmental variables where the reproduction model would be based on variables related to food resources and cover, and the survival model would be based on variables related to human disturbances. This allows a more sophisticated look at habitat suitability than possible with traditional one-dimensional approaches that rank habitat suitability from unsuitable matrix to poor and to good. A two dimensional habitat model can categorise a landscape into demographically motivated categories that leads to the identification of critical areas for management such as attractive sinks (i.e., good natural suitability but high levels of human disturbance; Naves et al., 2003; Kanagaraj et al., 2011a; De Angelo et al., 2013) and refuge areas (i.e., poor natural suitability but low levels of human disturbance).

When the inclusion of land cover and other human disturbance is not possible (e.g., because of temporal differences in the occurrence data and landscape features), predictions can be overlaid with current habitat quality and disturbance status (e.g., current land use, location of protected areas, and human population density) to estimate the conservation status of the species (e.g., Papes & Gaubert, 2007) or to assess habitat loss (Lopez-Arevalo et al., 2011). For the flat-headed cat in Borneo, Wilting et al. (2010) showed the discrepancy between potentially suitable habitat and habitat loss due to palm oil plantations and concluded that connectivity maybe only possible via river beds; thus a conservation goal resulting from this modelling exercise would be restoring riparian vegetation.

Second, in a dynamic manner habitat suitability maps can be used as the spatial basis for simulation modelling assessing habitat connectivity and population viability, e.g., for reintroduced or expanding carnivore populations in human-dominated landscapes (Wiegand et al., 2004a,b; Kramer-Schadt et al., 2005; Imron et al., 2010; Marucco & McIntire 2010). Species distribution maps can also be included in land use development simulation scenarios that include the economic aspect. To link biodiversity to monetary values is a crucial aspect in tropical biodiversity conservation. In this context, Koh & Ghazoul (2010) developed spatial palm oil expansion models focussing either on agricultural expansion, forest protection, or carbon conservation in Indonesia. For this, they included species biodiversity maps to assess the degree of biodiversity loss due to each palm oil expansion scenario. We conclude that SDMs are an important and multidimensional prerequisite in carnivore conservation.

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SUPPLEMENTARY MATERIAL – CLASSIFICATION OF REMOTE SENSING DATA

In classification, the satellite image has been processed to put each pixel into a category by segmenting each pixel separately or by segmenting the image into regions. The result of this classification is a vegetation map, land use map, or other map grouping related features. In unsupervised classification, the classification is performed using an algorithm, e.g., the ISODATA (Iterative Self-Organising Data Analysis Technique) clustering method, on satellite images that groups similar pixels into spectral classes. The number of spectral classes, which is decided by the researcher, is usually more than the desired number of categories (e.g., land cover types). In the next step, these spectral classes are assigned to one of the land cover types based on the ground-truthing points collected from the field (e.g., Wikramanayeke et al., 2004; Kanagaraj et al., 2011a).

Ground-truthing can be conducted in the sites selected by a stratified random sampling procedure recording the land use and structural vegetation parameters. These points can be divided in two parts: training sites and test sites. The land cover type for an unsupervised spectral class may be decided by visual interpretation of training ground-truthing points or the results of unsupervised classification can be used in the supervised classification method to determine land cover types (Richards, 1993). In the supervised classification method, the computer uses an algorithm (e.g., sequential maximum a posteriori, parallelepiped, minimum distance, maximum likelihood, Mahalanobis distance, etc.) to automatically classify the satellite image into desired number of land cover classes using the training data set (e.g., Izquierdo et al., 2008; Yüksel et al., 2008; De Angelo, 2011). In addition to (vegetation) ground-truthing points, additional ancillary data (e.g., aerial photos or previous land cover maps and vector overlays such roads, rivers and populated places), if available, can be incorporated in a way subjected to selected classification method to improve the classification (Gao et al., 2006). For example, using an expert classification model which incorporates ancillary geo-referenced data (land use data, spatial texture and digital elevation model) the initial supervised classification is reclassified to provide high classification accuracy (Stefanov & Netzband, 2005; Yüksel et al., 2008; Kahya et al., 2010).

The band combination for image classification can best be selected using a quantitative method such as optimum index factor (OIF; Chavez, 1984). Using first and second ranks of the OIF calculation with inclusion of thermal band (e.g., band 6 in Landsat imagery) along with reflective (spectral) bands in data set may provide the best bands combination for classifications (Ehsani & Quiel, 2010). Other methods include first applying the principal component analysis to the bands in the imagery and then, implementing a supervised maximum likelihood classification approach on the principal components for classification (Gomez et al., 2005). Wavelet fusion concept has proved to be a highly efficient method to deal with data with different spatial resolutions (e.g., ASTER images with three different spatial resolutions) to convert the bands to the same spatial resolution before performing the land cover classification (Ranchin & Wald, 2000; Bagan et al., 2008). These classifications are usually accomplished with the remote sensing software (e.g., ERDAS Imagine, RSI ENVI, PCI Geomatics, MultiSpec, ArcGIS extension: Image Analysis, open source GRASS GIS). Finally, the accuracy (overall accuracy, omission (i.e., producer's accuracy) and commission (i.e., user's accuracy) error, kappa index, e.g., Kappa Tool extension in ArcView 3.x, using confusion matrix analysis) of these classified land cover types can be estimated using the test points collected from filed or referenced topographic map (e.g., Jensen, 1996; Yüksel et al., 2008; Ehsani & Quiel, 2010; Kahya et al., 2010).