

Ecological Niche modeling, concept, approaches and applications.

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Abstract:

Ecological Niche Modeling (ENM) serves as an alternative and effective tool for predicting suitable habitats for species with encouraging conservation implications. They are extremely useful in modelling species richness patterns, predicting future distributions, predicting the extent of species invasions and addressing ecological and evolutionary questions. Recently numerous modeling approaches have been successfully applied to predict species distributions especially for species having scarce presence. Here we focus on the conceptual and theoretical foundations on which ENM approach is based. We evaluated various approaches and methods that are being used to model species distributions. We present an overview of two important parameters viz. spatial scale of environmental data and choice of environmental variables both of which have a significant influence on model quality and prediction of suitable habitats. A brief review of the significance of ecological niche modeling is also presented.

Key words: Niche Modelling, environmental variables, data, spatial scale, prediction, Biodiversity, Invasion, conservation.

Overview

Ecological Niche Modeling (ENM), also popularly known as species distribution modeling, is a recent tool which uses algorithms to relate known occurrences of a species across landscapes to digital raster GIS coverages summarizing environmental variation across landscapes to develop a quantitative picture of the ecological distribution of the species. They help in gaining ecological and evolutionary insights into species geographic distributions. Presently there are a wide range of environmental niche models for studying species distributions such as Bioclim (Busby, 1991), Domain (Carpenter *et al.*, 1993), linear, multivariate and logistic regressions (Mladenoff *et al.*, 1995; Felicísimo *et al.*, 2002; Fonseca *et al.*, 2002), generalized linear modelling and generalized additive modelling (Frescino *et al.*, 2001; Guisan *et al.*, 2002), discriminant analysis (Manel *et al.*, 1999), classification and regression tree analysis (Death and Fabricius, 2000; Kelly, 2002),

genetic algorithms (Stockwell and Peters, 1999), artificial neural networks (Manel *et al.*, 1999; Moisen and Frescino, 2002), and support vector machines (Guo *et al.*, 2005). Ecological niche models find immense applications in conservation, modelling species richness patterns, predicting future distributions, predicting the extent of species invasions, addressing ecological and evolutionary questions. However ENMs have faced a good amount of criticism recently. ENMs are seriously flawed as these approaches do not consider biotic interactions and species dispersal patterns. None the less ENMs serve as an important tool in conservation and planning management strategies. However, these models need to be used carefully when dealing with conservation issues. The present review of literature provides an overview of distribution modelling and various modelling techniques used and their applications in ecology and biogeography.

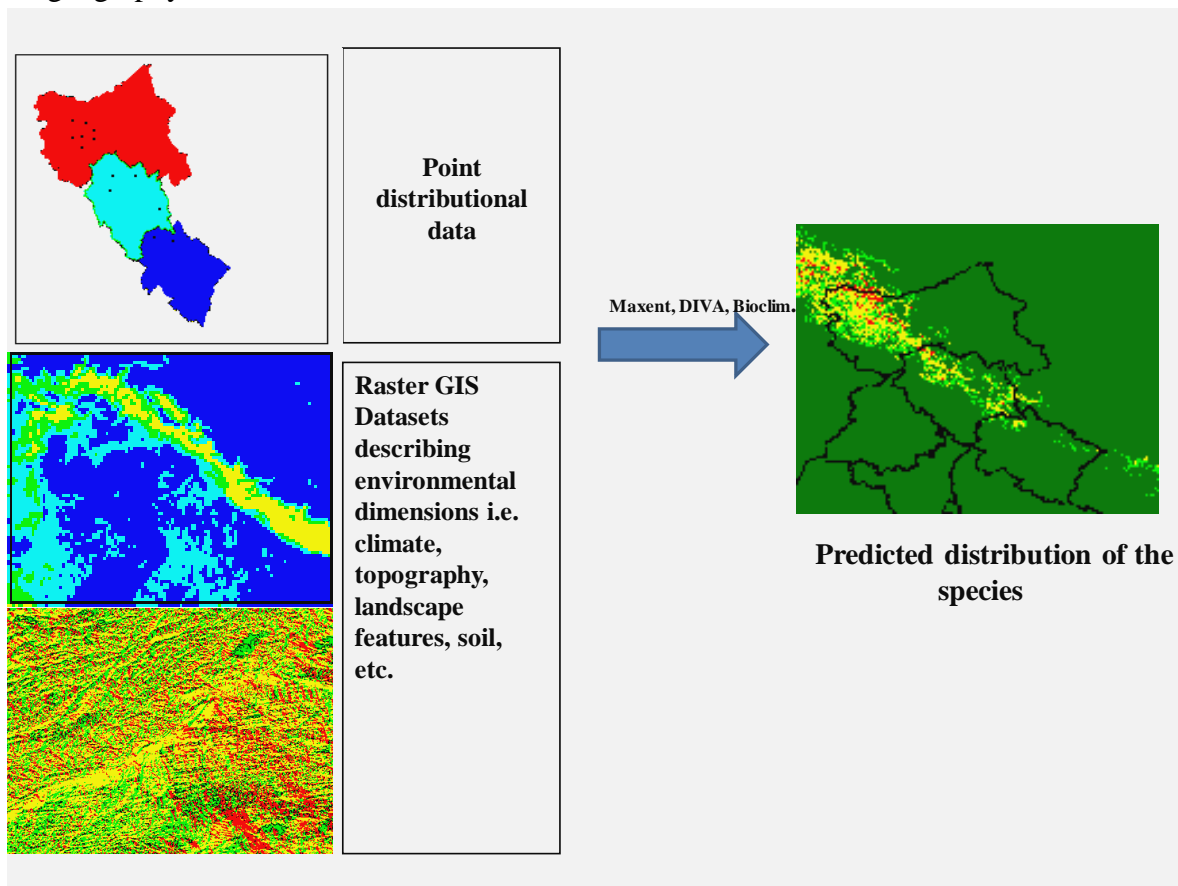


Fig. 1: Outline of Ecological Niche Modelling procedure

Ecological Niche

The concept of niche was first proposed by Grinnell (1917) in his classical paper ‘The niche relationships of the California Thrasher’, as the sum of the ecological conditions that allows a species to persist and produce offspring. It is widely accepted that the real founder of the niche concept was Grinnell, who in a series of papers, discussed the niches of a variety of species, including their abiotic requirements, habitat, food, and natural enemy relationships (Grinnell,

1917, 1924; Grinnell and Swarth, 1913). Grinnell used the concept to map all the necessary conditions for a species' existence, including physiological tolerances, morphological limitations, feeding habits, and interactions with other members of the community. The second concept about niche was proposed by Elton (1927). As per Elton niche is defined as the functional role which a species have in its ecosystem. However, the revolutionary concept about the niche was proposed by Hutchinson. Hutchinson stated, "The term niche (in Gause's sense, rather than Elton's) defined as the sum of all the environmental factors acting on the organism; the niche thus defined is a region of an n dimensional hyper-space." Hutchinson differentiated between the fundamental niche, which represents a possibility range, and the actual occupied part of niche, what he called as realized niche. Since an organism is prevented from occupying the fundamental niche by various biotic interactions so, the realized niche is smaller as compared to fundamental niche (Giller, 1984).

Ecological niche modeling

For conservation and management of biodiversity detailed knowledge about the geographical distribution of species is crucial. However for most taxa detailed species distribution data is sparse and to acquire such data is labour intensive (Prendergast *et al.*, 1999; Bowker, 2000; Ottaviani *et al.*, 2004, Williams *et al.*, 2009; Newbold, 2010, Niamir *et al.*, 2011). Thus, ecologists have developed various predictive models as a means for estimating patterns of species distribution and informing conservation strategies. These distribution models are proving to be an important tool in biogeography, evolution, ecology, conservation, invasive-species management and for the purposes of informing IUCN Red List assessments (Fleishman *et al.*, 2001; Peterson and Vieglais, 2001; Boone and Krohn, 2002; Fertig and Reiners, 2002; Scott *et al.*, 2002, Gaubert, 2006, Sergio *et al.*, 2007, Buisson *et al.*, 2010, Cardoso *et al.*, 2011, Jiménez-Alfaro *et al.*, 2012, Pena *et al.*, 2014;) These approaches combine species occurrence data with ecological/environmental variables (temperature, precipitation, elevation, geology, and vegetation) to create a model representing species distributions (Elith and Leathwick, 2009) (Fig.1.) Species distribution data are obtained from museums or herbarium specimens as georeferenced coordinates and are now increasingly getting available due to various efforts to digitize historical distribution records obtained from national and local natural history collections (Booth *et al.*, 1999; Funk *et al.*, 1999; Soberón, 1999; Ponder *et al.*, 2001; Stockwell and Peterson, 2002; Constable *et al.*, 2010; GBIF, 2013). Species distribution data are now increasingly getting available due to various efforts to digitize historical distribution records obtained from national and local natural history collections (Constable *et al.*, 2010; GBIF, 2013).The use of species distribution models has increased rapidly in the last two decades and recent years have seen the development of several new modelling techniques (Stockwell and Noble, 1992; Phillips *et al.*, 2006, Peterson *et al.*, 2011). While distribution models have been applied primarily to terrestrial species, there have also been several attempts to model marine species as well (Wiley *et al.*, 2003; Hawkes *et al.*, 2007). Several authors have argued that distribution models capture the realized niche, even if they only use abiotic variables in the

models, because data on species occurrence used to build models describe actual (realized) distributions (Guisan and Zimmermann, 2000; Austin, 2002; Pearson and Dawson, 2003; Araújo and Guisan, 2006). On the other hand, Soberón and Peterson (2005) argue that, unless variables describing biotic interactions or dispersal limitation are included as explanatory variables, distribution models generally capture the fundamental niche. An exception to this rule occurs when biotic variables co-vary with abiotic variables, in which case the model may more closely approximate the realized distribution (Soberón and Peterson, 2005).

Modelling approaches

A large number of methods for modelling are in vogue (Guisan and Zimmermann 2000; *Scott et al.*, 2002; Guisan and Thuiller, 2005; Hegel *et al.*, 2010; Grenouillet *et al.*, 2011) (Table 1) and evaluating the relative performance of different methods remains a continuous challenge in ecology and conservation biology (Loiselle *et al.*, 2003; Thuiller, 2003; Ottavianiet *al.*, 2004; Vaughan and Ormerod, 2005; Elith *et al.*, 2006; Pearson *et al.*, 2006, Elith and Graham, 2009). In general, the various methods used in species distribution modelling can be classified in two categories, one set of methods require species presence and absence data for model construction and other set of methods rely on presence only data for making predictions. Presence-only data differ from presence–absence data in that they indicate locations where the target organism was observed to occur, but cannot be used to define locations where the organism does not occur. Predictions based on presence-absence or abundance data are more robust because it gives valuable information about surveyed locations (Phillips *et al.*, 2009) and at the same time absence records convey valuable information regarding a habitat that is unsuitable or habitat that is suitable but is unoccupied, perhaps because of inaccessibility. This idea is commonly linked to the concept of modelling potential distributions (Jimenez-Valverde *et al.*, 2008). However, absence data are also sometimes viewed as misleading because the species or environment is not at equilibrium (e.g., invasions, climate change) or the species not easily detected. Data from various sources like herbaria, museums have immensely contributed to presence-only models of species distribution for plant and animal species (Ponder *et al.* 2001; Williams *et al.* 2002; Constable *et al.*, 2010; GBIF, 2013). Presence-only information is also much more available and requires much less collection effort than presence–absence information.

Table 2: Various types of environmental data used in species distribution models and their web source (Source: Barik *et al.* 2012).

Environmental variables	<u>Web address</u>
Climatic variables (including precipitation and temperature)	http://www.worldclim.org/ http://www.cru.uea.ac.uk/ http://gisweb.ciat.cgiar.org/GCMPPage/download_sres.html http://pmip.lsce.ipsl.fr/http://www.ncdc.noaa.gov/paleo/

Vegetation type, tree cover	http://edcdaac.usgs.gov/glcc/glcc_version1.html#Global http://glcf.umiacs.umd.edu/data http://edcimswww.cr.usgs.gov/pub/imswelcome
Physiographic/topographic/bathymetric data (elevation, slope, aspect)	http://edc.usgs.gov/products/elevation.html http://www2.jpl.nasa.gov/srtm/dataproduct.htm http://www.worldwildlife.org/freshwater/hydrosheds.cfm http://ibis.grdl.noaa.gov/cgi-bin/bathy/bathD.pl
Marine Data	http://www.nodc.noaa.gov/OC5/indprod.html http://www.cpc.noaa.gov/products/predictions/30day/SSTs/sst_clim.html
Hydrology (drainage basin, flow accumulation, flow direction)	http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html
Landuse, Landcover	http://glcf.umiacs.umd.edu/data/ http://edcimswww.cr.usgs.gov/pub/imswelcome http://glovis.usgs.gov/ http://www.landsat.org/ortho/default.html http://www-gvm.jrc.it/glc2000/
Soils (Soil type, texture, Water holding capacity, pH)	http://www.fao.org/AG/agl/agll/prtsoil.stm http://www.daac.ornl.gov/SOILS/soils_collections.html
Socio-economic data (Anthropogenic biomes, Gridded population of the world, Human footprint, Net primary productivity)	http://sedac.ciesin.columbia.edu/data.html

Climate envelopes

Climate envelope models are a type of species distribution models that predict suitable environments for a species based on climatic variables. These models define climate envelopes for a species by comparing species known occurrences with climatic conditions prevailing at the occurrence site. Climate envelopes use only records of species presence, and thus may be useful when information about species absence is not available (Elith *et al.*, 2006). The most commonly used climate envelope model is BIOCLIM (Busby, 1986; Nix, 1986). It was first used to model plant species distribution in Australia, using one-by-one degree latitude–longitude grid cells. In its simplest form it produces a binary prediction of presence and absence, but it can also produce a prediction of relative environmental suitability by using different proportions of the species occurrence data to define the climate envelope. In some studies, BIOCLIM has been reported to model the distributions of species reasonably well (Penman *et al.*, 2005; Finch *et al.*, 2006; Richardson *et al.*, 2006). However, in comparisons of several techniques, BIOCLIM has

emerged amongst the worst-performing (Elith, 2002; Ferrier *et al.*, 2002; Loiselle *et al.*, 2003; Elith *et al.*, 2006; Tsoar *et al.*, 2007). It has a tendency to over-predict observed distributions (Elith 2002), particularly for more widespread species (Finch *et al.*, 2006). Most examples of BIOCLIM's poor performance have come from studies focusing on small areas. BIOCLIM may be useful for modelling the broad environmental limits to distributions over very large study areas. DOMAIN (Carpenter *et al.*, 1993) is a better performing technique as compared to BIOCLIM and has been shown to overcome some of the problems of over-prediction associated with BIOCLIM (Carpenter *et al.*, 1993). In comparison of modelling techniques its performance has been generally intermediate (Tsoar *et al.*, 2007; Wisz *et al.*, 2008) to poor (Elith *et al.*, 2006), although relatively better than other techniques with very small number of presence records (Wisz *et al.*, 2008).

Logistic regression

Logistic regression modeling techniques model species distributions as a binomial response against climate predictors. Among various logistic regression modeling techniques 'General Linear Models' (GLMs) have been used widely to predict the distribution of species because the model outputs are easy to interpret and also the software is available freely (Wintle *et al.*, 2005). GLMs have generally performed very well in comparisons of different modelling techniques (Hirzel *et al.*, 2001; Loiselle *et al.*, 2003; Elith *et al.*, 2006; Meynard and Quinn, 2007; Wisz *et al.*, 2008), although relatively poorly with very small sample sizes (Pearce and Ferrier, 2000). The second category of logistic regression modelling techniques is 'Generalized Additive Models' (GAMs). GAMs have also performed very well in published studies, and often somewhat better than GLMs (Pearce and Ferrier, 2000; Ferrier *et al.*, 2002; Moisen and Frescino, 2002; Zaniwski *et al.*, 2002; Elith *et al.*, 2006; Wisz *et al.*, 2008), although they are even more sensitive to small sample sizes (Wisz *et al.*, 2008). As with GLMs, the software is freely available and relatively easy to use, but the output is not easy to interpret (Wintle *et al.*, 2005).

Maximum Entropy Method (Maxent)

Phillips *et al.* (2006) introduced the use of the maximum entropy method (MaxEnt) for modelling species geographic distributions with presence-only data. MaxEnt is a general-purpose machine learning method with a simple and precise mathematical formulation. It has many important advantages over other methods of modeling species distributions (Elith *et al.*, 2011). Maxent uses principle of maximum entropy (Jaynes, 1957) to estimate the distribution of a species. Maximum-entropy is quite useful for modelling species geographic distributions, a critical problem in conservation biology and is currently one of the most popular methods used in species distribution modelling (Elith *et al.*, 2006, Pearson *et al.*, 2007; Monterroso *et al.*, 2009; Williams *et al.*, 2009; Torres *et al.*, 2010). The models can be easily interpreted by experts, a property of great practical importance (Phillips *et al.*, 2004). Other advantages of Maxent include. (i) it works on presence only data and does not require data on species absence (Phillips

et al. 2006; Elith *et al.*, 2006; Pearson *et al.*, 2007; Papes and Gaubert, 2007, Wisz *et al.*, 2008, Rebelo and Jones, 2010; Elith *et al.*, 2011). (ii) the predictive power of maxent has been proven to outperform other modelling methods (Elith *et al.*, 2006; Hernandez *et al.*, 2006; Pearson *et al.*, 2007, Wisz *et al.*, 2008; Williams *et al.*, 2009; Braunisch *et al.*, 2011). (iii) it can utilize both continuous and categorical data, and can incorporate interactions between different variables. (iv) It has a precise mathematical definition, hence easy for analysis (v) over-fitting can be avoided by using regularization.

Genetic Algorithm for Rule-set Prediction (GARP)

Genetic Algorithm for Rule-set Prediction is another machine-learning modelling technique that has seen widespread use. GARP develops a set of if-then statements which decide whether the species will be present or absent as per the environmental conditions of the given grid (Stockwell and Noble, 1992). It is a presence only model, however there is a provision to include absences by sampling a set of pseudo absences from the pixels where the species has not been recorded. Many studies have shown that GARP models species distribution accurately (Peterson and Cohoon, 1999; Peterson *et al.*, 2002; Loiselle *et al.*, 2003; Peterson and Kluza, 2003; Peterson and Robins, 2003., Raxworthy *et al.*, 2003; Papes and Gaubert, 2007). However in comparison to other several modelling techniques, GARP has been reported to perform relatively poorly (Elith *et al.*, 2006; Pearson *et al.*, 2007) and has a tendency to over predict the distributions (Peterson and Robbins 2003). On the other hand GARP has been shown to be effective in modelling species with small sample sizes (Solano and Fera, 2007; Wisz *et al.*, 2008).

Table 1 Published predictive SDM packages, reference paper, related modelling methods, and web links.

Modeling Tool	Reference	Methods used	Web address
BIOCLIM	Busby (1991)	CE	http://www.arcscripsts.esri.com
ANUCLIM	Busby (1991)	CE	http://www.cres.anu.edu.au/~anuclim .
BAYES	Aspinall (1992)	BA	Arc View extension available at the discretion of the author
BIOMAPPER	Hirzel et al. (2002)	ENFA	http://www.unil.ch/biomapper
BIOMOD	Thuiller (2003)	GLM,GAM,CART, ANN	At the discretion of the author
DIVA	Hijmans et al. (2001)	CE	http://www.diva-gis.org
DOMAIN	Carpenter et al. (1993)	CE	http://www.cifor.cgiar.org/docs/ref/research_tools/domain/index.htm
ECOSPAT		GLM, GAM	http://www.ecospat.unil.ch ; at the discretion of the author
GARP	Stockwell and Peters (1999)	GLM, ANN, GA, CE,	http://www.lifemapper.org/desktopgarp
GDM	Femier et al. (2002)	GDM	At the discretion of the author
GRASP	Lehmann et al. (2002)	GLM, GAM	http://www.cscf.ch/grasp
MAXENT	Phillips et al. (2005)	ME	At the discretion of the author
SPECIES	Pearson et al. (2002)	ANN	At the discretion of the author
Disperse	Carey (1996)	CE	At the discretion of the author
Shift	Iverson et al. (1999)	CART	At the discretion of the author

Variable choice.

The distribution of a species is determined by a number of factors and selection of an appropriate variable is important to get accurate predictions (Parolo *et al.*, 2008; Peterson and Nakazawa, 2008). Using too many explanatory variables in distribution models will cause overfitting and too less variables can lead to under prediction of species distributions (Chatfield, 1995; Elith *et al.*, 2006; Wisz and Guisan, 2009). The choice of environmental variables for modelling is often driven by the availability of variables in a format suitable for modelling. As a result, many distribution-modelling exercises have considered only variables describing the abiotic environment, such as climate, edaphic factors and topography, or non-specific biotic variables, such as land cover, habitat and plant productivity (Elith *et al.*, 2006) (Table 2). Many of the variables that can be obtained as maps covering entire study areas are those that have only an indirect effect on species (Austin, 2007). Very few studies have made a priori hypotheses regarding the determinants of species distributions, and then used these variables to model distributions. However, the aim is often to model the distributions of many species simultaneously. In this case, choosing directly relevant variables for each species in turn would probably be too time-consuming. Climate and habitat variables have repeatedly been shown to be very good correlates of species distributions (Guisan and Hofer, 2003; Araújo *et al.*, 2005; Wintle *et al.*, 2005; Elith *et al.*, 2006; Guisan *et al.*, 2006; Anderson *et al.*, 2012) and many have been hypothesized to have direct effects on species occurrence (Turner *et al.* 1987; Hawkins *et al.*, 2003). Therefore, it will often be desirable to build models using these readily-available rather than developing a series of variables for each species.

Spatial scale

Habitat assessment for rare and endemic species at multiple scales is an important component of conservation planning. The prior knowledge and understanding of the theory and processes which drive the observed distributional patterns of rare and endemic plant species is crucial, so that appropriate modelling based on appropriate scale can be employed (Guisan *et al.*, 2005). Since the factors which influence the distribution of species and biodiversity patterns are highly dependent on spatial scale, with factors operating at a finer scale being subordinated to factors operating at a larger scale (Milbau *et al.*, 2008). Hence, the use of data at appropriate scale for those variables which are crucial for species distribution would be cost effective for planning conservation strategies. The most appropriate scale and factors for species distribution modelling occur in hierarchic manner from global to local scales; at global scale climate appears to be the dominant factor determining species distribution, while at regional to local scales topography and land use are more important (Figure 2) (Pearson and Dawson, 2003; Guisan *et al.*, 2005). However, the biotic interactions and other micro climatic factors finally shape the species distribution at the finest scales (Willis and Whittaker, 2002, Pearson and Dawson, 2003). Although climatic factors can be useful both at global and local scales, the distribution of rare and endemic plant species are often associated with specific vegetation types, including land-cover data and hence these factors can significantly enhance the predictive potential of models to

predict the species suitable areas (Pearson *et al.*, 2004; Gogol-Prokurat, 2011; Vicente *et al.*, 2011). Thus, despite large-scale factors being generally dominant, small-scale factors are more important to make precise and accurate predictions on small spatial scale (Milbau *et al.*, 2008). These models can improve spatial allocation of conservation efforts and resources, and facilitate strategic planning to minimize impacts on rare plant resources and potential land use conflicts (Wu *et al.*, 2000). As an example fine scale environmental variables at local scale can result in smaller total areas of habitat predicted as suitable for rare species, thus making the use of predictions for conservation planning more meaningful (Gogol-Prokurat, 2011).

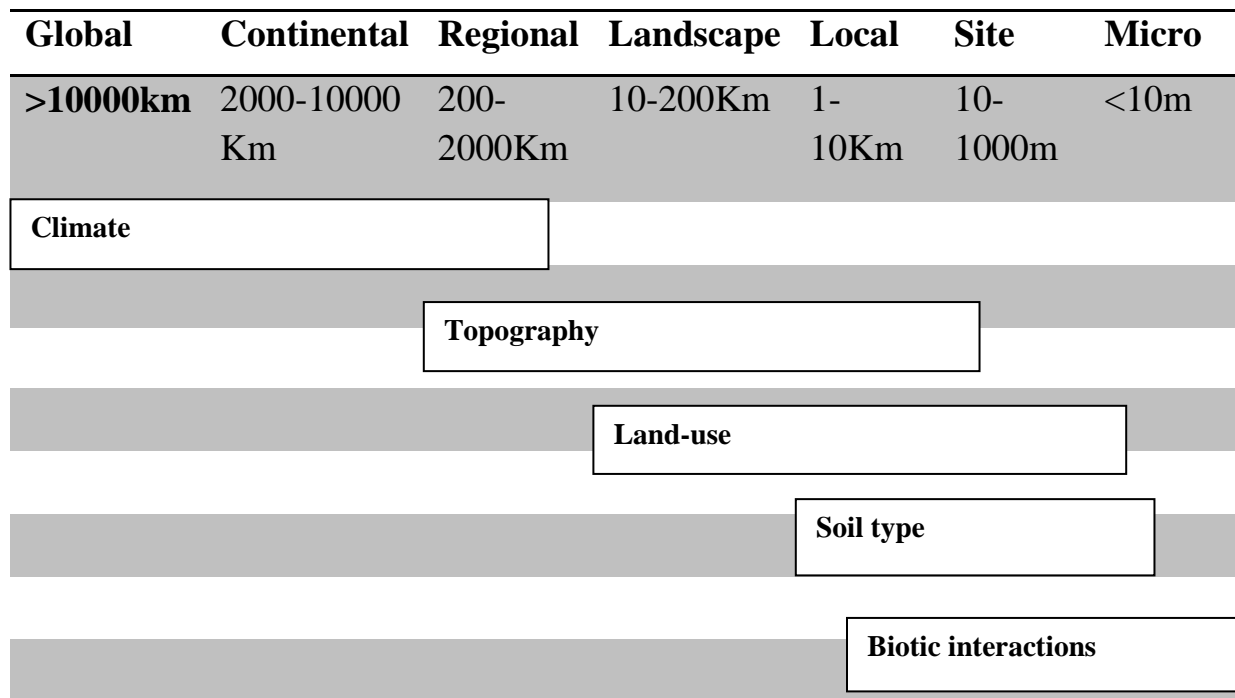


Fig.2: Hierarchical modelling framework proposed by Pearson and Dawson, (2003).

Applications of species distribution models

Species distribution models find immense applications in the field’s ecology and conservation biology (Table 3), some of the applications are:

a) **Conservation of species**

Species distribution models have been widely and successfully used in many conservation biology studies mainly focusing on conservation issues (Brotons *et al.*, 2004; Niamir *et al.*, 2011; Jiménez-Alfaro *et al.*, 2012, Pena *et al.*, 2014). Species distribution models are widely used in making decisions regarding the conservation of particular, often threatened, species and guiding surveys for species (Cano Carmona *et al.*, 2019). For example, Walther *et al.* (2007) modelled the poorly-known wintering distribution of the threatened aquatic warbler (*Acrocephalu*

spaludicola) in sub-Saharan Africa, proposing that the model be used to direct surveys in order to increase knowledge about the specie's distribution. Likewise, Guisan *et al.* (2006) used distribution models for alpine sea holly (*Eryngium alpinum*) in Switzerland to guide field surveys, leading to the detection of seven new populations. Raxworthy *et al.* (2003) discovered seven new species of chameleon in Madagascar on the basis of their distribution models. Data from the new surveys can be used to build more accurate distribution models, which can in turn be used to direct further surveys, and so on (Guisan *et al.*, 2006). Models can also be used to identify potential areas for species reintroductions (Rodríguez *et al.*, 2007). For example, one study (Klar *et al.*, 2008) modelled the distribution of European wild cats (*Felis silvestris*) in Germany. It was suggested that a suitable, but unoccupied, area could be used for reintroductions of the species (Klar *et al.*, 2008). Similarly, Adhikari *et al.* (2012) modelled the suitable habitats for reintroduction of *Illex khasiana* a critically endangered species of eastern Himalayan region and identified the suitable habitats where the species can be reintroduced. Species distribution models have been recently used to frame the reserve designs and protected areas and ultimately identifying priority areas for conservation (Margules *et al.*, 2002). Species distribution models can also be used to infer the causes for species decline. For example, Southgate *et al.* (2007) developed distribution models for the bilby (*Macrotis lagotis*) in Australia to assess different hypotheses for its decline. Nogués-Bravo *et al.* (2008) used distribution models to investigate the extent to which the extinction of the woolly mammoth (*Mammuthus primigenius*) was caused by environmental change or by an increase in human hunting pressure, concluding that both factors may have played a role.

a) **Predicting future distributions of species**

Species distribution models can be used to predict how the distributions of species will change in the future as a result of climate and human induced land-use changes (Bellard, 2012; Watson, 2013; Gritti *et al.*, 2013; Watson *et al.*, 2014; Lourenço-de-Moraes *et al.*, 2019)). A distribution model is built for the current time, using species occurrence and climate data. This model is then updated to reflect predicted changes in the climate or land use in the future. Many workers have used distribution models in this way, mostly at regional or global scales (Huntley, 1995; Saetersdal *et al.*, 1998; Iverson *et al.*, 1999; Bakkenes *et al.*, 2002; Berry *et al.*, 2002; Peterson, 2003; Miles *et al.*, 2004; Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Levinsky *et al.*, 2007; Hole *et al.*, 2009; Randin *et al.*, 2009, Bellard *et al.*, 2012) but sometimes at more local scales (Peterson *et al.*, 2001; Peterson *et al.*, 2002). Most have considered only changes in the climate, but land-use changes also known to have important effects on the distributions of species (Thuiller, 2007), and very few have considered these.

b) **Predicting the extent of species invasions**

One of the important applications of Species distribution models is prediction of suitable habitats for species invasion at regional (Mercado-Silva *et al.*, 2006; Muñoz and Real, 2006, Uma Shanker *et al.*, 2013; Kannan *et al.*, 2013) and global scales (Thuiller *et al.*, 2005; Bradley *et al.*,

2010; Gallien, 2012). Such projections can be used, for example, to predict where invasive species will be able to establish and survive outside their native ranges. A number of studies have used distribution models in this way, often finding that invasions are predicted very successfully (Peterson and Vieglais, 2001; Peterson and Robins, 2003; Thuiller *et al.*, 2005; Herborg *et al.*, 2007). On the other hand, in some cases the distributions of species in their invaded ranges are predicted very poorly by distribution models based on data from their native ranges (Randin *et al.*, 2006; Broennimann *et al.*, 2007). Model failure may be caused by differences in the fundamental or realized niches in the invaded range (Broennimann *et al.*, 2007; Steiner *et al.*, 2008). Differences in realized niches may result from species not yet having reached equilibrium with climate in the new range owing to dispersal limitation, from the species not having been in equilibrium with climate in its native range, or from changes in interactions among species (Thuiller *et al.*, 2005; Steiner *et al.*, 2008). In species invasions, suitability of climate is only one of several factors that determine invasion success. Propagule pressure, characteristics of the invading species, species composition of the invaded area and human influence can also be important (Thuiller *et al.*, 2005; Thuiller *et al.*, 2006; Ficetola *et al.*, 2007; Ficetola *et al.*, 2009).

c) Addressing ecological and evolutionary questions

Species distribution models can also be used to tackle more fundamental ecological or evolutionary issues (Zimmermann *et al.*, 2010; Guisan *et al.*, 2006, 2007; Franklin, 2010; Alvarado-Serrano and Knowles, 2014). For example, they have been used to assess the extent to which climate drives distribution patterns compared to other factors, such as interactions among species (Araújo and Luoto, 2007), dispersal limitation (Svenning *et al.*, 2008) or habitat. Other studies have used distribution models to test whether niches are evolutionarily conserved by comparing modelled niches among closely-related species (Peterson *et al.*, 1999).

Conclusions: Ecological niche modeling is now increasingly being used for addressing various ecological issues like invasion of species, effects of climate change on species distributions and conservation of species. Different methods have been used in past and many are in practice currently. Our review gives a comprehensive outlook of the methods and applications of Ecological niche models used in ecology. This review will serve as a basic information source for those intended to undertake deep research studies in the field of Ecological niche modeling. The scale at which a species is modeled and the set of variables which are used to determine the geographic distribution of a species are of paramount importance. These two issues determine to a greater extent the success and accuracy of models, as choosing irrelevant environmental predictors and inappropriate scale will lead to erroneous and inaccurate predictions. These two parameters have been broadly reviewed in present manuscript. In the end we present a lucid description about applications of Ecological niche models to highlight the vast areas where Niche modeling could be used in ecology.

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