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BIODIVERSITY REVIEW

BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MAXENT studies

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ABSTRACT

Aim Interest in species distribution models (SDMs) and related niche studies has increased dramatically in recent years, with several books and reviews being prepared since 2000. The earliest SDM studies are dealt with only briefly even in the books. Consequently, many researchers are unaware of when the first SDM software package (BIOCLIM) was developed and how a broad range of applications using the package was explored within the first 8 years following its release. The purpose of this study is to clarify these early developments and initial applications, as well as to highlight BIOCLIM's continuing relevance to current studies.

Location Mainly Australia and New Zealand, but also some global applications.

Methods We outline the development of the BIOCLIM package, early applications (1984–1991) and its current relevance.

Results BIOCLIM was the first SDM package to be widely used. Early applications explored many of the possible uses of SDMs in conservation biogeography, such as quantifying the environmental niche of species, identifying areas where a species might be invasive, assisting conservation planning and assessing the likely impacts of climate change on species distributions.

Main conclusions Understanding this pioneering work is worthwhile as BIOCLIM was for many years one of the leading SDM packages and remains widely used. Climate interpolation methods developed for BIOCLIM were used to create the WorldClim database, the most common source of climate data for SDM studies, and BIOCLIM variables are used in about 76% of recent published MAXENT analyses of terrestrial ecosystems. Also, some of the BIOCLIM studies from the late 1980s, such as measuring niche (both realized and fundamental) and assessing possible impacts of climate change, are still highly relevant to key conservation biogeography issues.

Keywords
Biogeography, bioclimate envelope, biological conservation, climate change, climate interpolation, ecological niche, ecological modelling.

INTRODUCTION

The idea that variations in climate exert a strong influence on plant distribution dates back in the literature to around the 5th century BCE (Woodward, 1987). However, the development in the mid-1980s of reliable methods for estimating mean climatic conditions for any location allowed analyses of plant and animal species distributions to be placed on an explicit and quantitative basis for the first time. Various names have been given to these studies including bioclimatic envelope, species niche and habitat suitability modelling, but here we use the term ‘species distribution modelling’ (SDM)

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(Franklin, 2009). Generally, SDM software packages take in geocoded information on species distributions, relate these to environmental space and map likely species distributions, under current or possible future conditions, in geographic space (see figure 1.1 in Franklin, 2009 for an illustration of this generic correlative SDM process). There has been a rapid increase in species distribution and ecological niche modelling in recent years (see books by Franklin, 2009 and Peterson *et al.*, 2011 as well as reviews by Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Elith & Leathwick, 2009).

The purpose of this study is to describe some of the features and limitations of the first SDM package known as BIOCLIM and its associated climatic interpolation relationships. The study outlines some of its early applications from its appearance in 1984 to 1991 when alternative methods began to appear (e.g. Walker & Cocks, 1991) and describes its continuing relevance to SDM studies. BIOCLIM was the first package to implement the process outlined in figure 1.1 in Franklin (2009). It simply relates the bioclimatic envelope for a species to the range (or percentile range) of a number of bioclimatic variables (initially 12 in the first version), such as annual mean temperature and annual mean precipitation (see any of the papers listed in the 'early applications' section below for more details of the method). BIOCLIM has been one of the most widely used SDM packages and was recognized as one of only three 'well-established modelling methods' by Elith *et al.* (2006).

BIOCLIM: BACKGROUND AND DEVELOPMENT

Pre-BIOCLIM

Important conceptual elements underpinning the development of BIOCLIM can be traced back to Evelyn Hutchinson's formalization of the niche concept as a series of independent environmental variables with simple ranges of suitable conditions defining an 'n-dimensional hyperspace' within which the species can survive and reproduce (Hutchinson, 1957).

Some reviewers of SDMs, such as Guisan & Zimmermann (2000), mention a relationship between early species distribution models and the work of Box (1981). This related the environmental requirements of about 90 plant life-forms (such as a tropical rain forest trees group) to eight ecoclimatic factors. It then predicted where the life-forms were likely to occur for 1225 locations (mostly in a 10° grid) across the world. There are some conceptual similarities to SDMs, such as BIOCLIM, in the development of bioclimatic envelopes. However, there are considerable differences as the programmes developed by Box (1981) did not involve the use of individual species data, did not support climate interpolation estimates for distributional data, and mapping was based on spatially coarse climate data.

Guisan & Thuiller (2005) suggest that 'the earliest species distribution modelling attempt found so far in the literature seems to be the niche-based spatial predictions of crop species by Henry Nix and collaborators (Nix *et al.*, 1977)'. In fact, this study is related to mechanistic-based approaches to modelling species distributions rather than the correlative approaches usually associated with SDMs. It assessed the potential for growing exotic legumes, particularly Pigeon Pea (*Cajanus cajan* (L.) Millsp.) in Australia. The study used the Fitzpatrick & Nix (1970) GROWEST model, which takes in weekly climate data for a selected site. A growth index is calculated based on multiplying together temperature, light and moisture indices. The temperature and light indices are related to simple functions, while the moisture index is derived from a water balance calculation. The GROWEST model was modified by Sutherst & Maywald (1985) to create the CLIMEX model. This calculates an ecoclimatic index not only based on the core weekly calculations of the GROWEST growth index (GI), but also including a yearly stress factor multiplicatively derived from four modifiers to allow for hot stress and cold stress as well as dry stress and wet stress. CLIMEX is commercially available and has become widely used for assessing species distributions, particularly potential distributions of pests, diseases and invasive species. For a comparison between mechanistic models, such as CLIMEX, and correlative SDM approaches, see Booth & Williams (2012).

Climate interpolation

Before considering the BIOCLIM package, it is worth outlining the advances in climate interpolation that made SDMs possible. Building on the work of Wahba & Wendelberger (1980), Hutchinson developed improved versions of thin-plate spline interpolation methods (see, e.g. Hutchinson & Bischof, 1983; Hutchinson *et al.*, 1984). A key aspect in the accuracy of these surfaces was the incorporation of an appropriately scaled dependence on land elevation, as later demonstrated by Hutchinson (1995). To facilitate the development of BIOCLIM, Hutchinson developed Australia-wide monthly mean maximum and minimum temperature surfaces fitted to measured data for 901 meteorological stations. Validation tests indicated that the mean true error, averaged over all the data points, used was <0.5 °C for every month of the year for both maximum and minimum temperatures. Monthly mean precipitation data were analysed for about 11,000 meteorological stations. With the exception of some months at the beginning and end of the wet season in northern Australia, all mean precipitation errors were <10 mm or <10% of the monthly mean, whichever was smaller. These continent-wide interpolation analyses were summarized in Hutchinson (1991).

The programmes developed by Hutchinson have been widely used to develop climate interpolation relationships for other parts of the world. See, for example, papers describing the development of relationships for China and Southeast Asia (Zuo *et al.*, 1996), Indonesia (Jovanovic & Booth, 1996a) and the Philippines (Jovanovic & Booth, 1996b). The programmes continue to be widely used internationally [see, e.g. recent work for Canada (Hopkinson *et al.*, 2012)]. Perhaps most significantly for those interested in SDMs, the interpolation programmes, now known as the ANUSPLIN package (for current version see Hutchinson, 2011), were used to develop the WorldClim database (Hijmans *et al.*, 2005), which is a very commonly used source of data (>2700 citations) for ecological studies including SDMs.

BIOCLIM

The BIOCLIM package was conceived by Henry Nix, who also led the development of the package, so the key reference to cite in relation to BIOCLIM is Nix (1986). The basic concept involved the mobilization of site and specimen data through the estimation of climatic data, and building primary climate datasets to support the development of BIOCLIM began in the mid-1960s. Dissatisfaction with then available procedures for bioclimatic analysis led to the appointment of Michael Hutchinson and the improvement in climatic interpolation methods. The ability to generate maps of estimated species distributions was just part of the BIOCLIM concept. The incorporation of exploratory data analysis tools in the package was also important, and these allowed users to identify important variables, as well as extreme outlier values that need checking.

The BIOCLIM package, complete with operating manual, became accessible to users throughout Australia on CSIRONET in January 1984. Thanks to differences in publishing schedules, two papers describing the use of the package became available before the Nix (1986) publication (Booth, 1985; Prendergast & Hattersley, 1985), but they both acknowledged the origins of the package. They are available from the Web of Knowledge™ and provide descriptions of the use of the package, including the list of 12 bioclimatic factors used in the first version of the package. The bioclimatic factors were selected on the basis of a process-based understanding of the climatic constraints on plant growth, building on the understanding provided by preceding mechanistic-based studies. As the Nix (1986) paper is not available via electronic sources, a short description of the paper follows.

Nix (1986) identified a number of strengths and limitations of BIOCLIM, most of which are applicable to SDMs in general:

1. Error associated with estimation of primary climate attributes at a point – This outlines the reliability of the climate interpolation relationships mentioned here in the previous section.

2. Relevance of the bioclimatic indices – BIOCLIM initially accesses 36 primary climate attributes (12 monthly mean values for precipitation as well as maximum and minimum temperatures) from which 12 bioclimatic indices are calculated. The possibility of including additional factors is raised and indeed the number of factors increased in later years to 35, including some factors involving complex interactions associated with water balance calculations (see, e.g. Xu & Hutchinson, 2011, 2013).

3. Derivation of the bioclimatic envelope – The ranking of factors is described, and the use of percentiles to indicate core and marginal conditions is outlined.

4. Accuracy and level of resolution of the grid used for predicting potential distribution – The bioclimatic profiles are matched against a grid of points to identify locations with potentially suitable climatic environments. The 0.5° grid for Australia used represented a massive increase in resolution over the 10° global grid used by Box (1981). However, Nix (1986) recommended that even greater resolution than 0.5° would be desirable for mountainous and complex terrain (see, e.g. the 0.025° digital elevation model developed by Hutchinson & Dowling, 1991).

5. Versatility of graphic display and plotting procedures – Maps could be generated at any scale and for a wide range of projections using the MAPROJ package (Hutchinson, 1981).

6. Taxonomic uncertainty – The value of bioclimatic profiling is very much dependent on the taxonomic integrity of the target taxa.

7. Accuracy of identification and labelling – Herbarium specimens or any other sources from which locations are derived may be mislabelled or misidentified. BIOCLIM proved to be useful in identifying potential anomalies and subspecies (see, e.g. Fischer *et al.*, 2001).

8. Accuracy of geocoding – This was a significant problem when locations had to be estimated from maps and hand entered into databases. It is still a potential source of error where old records are used, but with the advent of global positioning systems (GPS), it should no longer be a significant problem for recently collected data.

9. Adequacy of point sampling within total distribution – There is considerable sampling bias as many collections are made close to large centres of population or along roads.

10. Checking of anomalous data points – BIOCLIM generated cumulative frequency curves for each of the 12 bioclimatic factors, which assisted the identification of anomalous outliers.

Following this consideration of strengths and limitations, Nix (1986) described the bioclimatic analysis of 73 species of elapid snakes. BIOCLIM-generated maps are provided indicating climatically suitable locations across Australia for the 73 species, and their bioclimatic profiles are included in appendix 3 of the report.

Busby (1991a) provides a general overview of BIOCLIM. By 1991, a version 2.0 of BIOCLIM was available across Australia on the PAXUS COMNET computing network, and 16 bioclimatic factors were used. Busby (1991a) concludes that BIOCLIM had proved to be a highly flexible and powerful tool for evaluating distributions on a variety of spatial, and even temporal, scales. The Busby (1991b) article is just a brief one and a half-page summary. A summary is available on the Web of Knowledge™, but neither the Busby (1991a) nor Busby (1991b) paper are available electronically, hence the need for the review presented here.

EARLY APPLICATIONS OF BIOCLIM

Between BIOCLIM coming online in January 1984 and 1991, a number of applications were published. We review the applications here using the types of possible use in ecology and conservation biology identified in table 1 of Guisan & Thuiller (2005) and highlighting features that may be of interest to current users of SDMs. As Guisan & Thuiller (2005) were concentrating on 'recent advances in this field', they provided examples for the categories in their table using mainly examples from the previous 5 years. Here, we show how most of these categories were first investigated in BIOCLIM studies published before 1991. Guisan & Thuiller (2005) identified two types of applications for which published examples could not be found, so these are not included here. These two potential applications were 'Building bio- or ecographic regions' and 'Improving the calculation of ecological distance between patches in landscape meta-population dynamic and gene flow models'.

Quantifying the environmental niche of species

Nix (1986): As mentioned earlier, this report published bioclimatic profiles and BIOCLIM-generated distribution maps for 73 species of elapid snakes.

Busby (1986): Records of 333 occurrences of *Nothofagus cunninghamii* (Hook.) Oerst. in Tasmania and Victoria were analysed, and a map of bioclimatically suitable and marginal locations was produced. Suitable locations were identified beyond its present range, and it is possible that it occurred within the predicted range prior to the last ice age.

Read & Hope (1989): Estimates of mean minimum temperature of the coldest month made using BIOCLIM were related to foliar frost resistance in some tropical and extratropical *Nothofagus* species.

Testing biogeographical, ecological and evolutionary hypotheses

Prendergast & Hattersley (1985): An SDM analysis was used to complement a cytological analysis of various grasses in the *Neurachneae* tribe. Species distributions, habitats and chromosome counts were discussed in relation to past and present climates as well as evolutionary history.

Markgraf *et al.* (1986): Bioclimatic analysis was used to assess individual vegetation- and pollen- sample sites from more than 300 sites to help evaluate pollen records and palaeoclimates in south-western Tasmania during the last 13,000 years. Pollen assemblage characteristics were related to current climate conditions.

Hill *et al.* (1988) and Read & Busby (1990): BIOCLIM was used along with laboratory measurements of net photosynthesis in relation to temperature to assist, respectively, with the interpretation of evolutionary history of Australian temperate rain forest trees from the Tertiary to the present and the biogeography of Tasmanian temperate rain forest trees.

Kohlmann *et al.* (1988): SDM analysis was used to explore distributional limits of four chromosomal taxa of *Caledia captiva* (F.) (Australian grasshopper). At least one of the boundaries appeared to be relatively recent in origin (2000–6000 years).

Kershaw & Nix (1988): Vegetation plot data and modern pollen spectra from north-east Queensland rain forest were examined bioclimatically prior to analysis of fossil pollen assemblages from Lake Euramoo. The method showed great promise particularly for areas dominated by floristically diverse vegetation.

Assessing species invasion and proliferation

Booth (1985): BIOCLIM was used to analyse 84 locations representing the distribution of *Eucalyptus citriodora* Hook. (now *Corymbia citriodora* (Hook.) K.D. Hill & L.A.S. Johnson) in Australia, and the bioclimatic profile was used to identify potential locations for introducing the species in Africa.

Panetta & Dodd (1987): Skeleton weed (*Chondrilla juncea* L.) became a serious weed of cereal crops after its introduction in south-eastern Australia in 1910. Bioclimatic techniques were used to analyse conditions at 71 locations in eastern Australia and 22 locations in Western Australia. It was concluded that practically the entire Western Australian wheatbelt was vulnerable to invasion by the weed.

Podger *et al.* (1990): Bioclimatic conditions at more than 1000 locations were assessed to estimate areas of Tasmania likely to be vulnerable to the soil borne mould *Phytophthora cinnamomi* Rands.

Assessing the impact of climate, land use and other environmental changes on species distributions

Busby (1988): SDM analysis was used to examine possible impacts of climate change on alpine vegetation (represented by 121 generic sites), temperate rain forest [represented by 325 *Nothofagus cunninghamii* (Myrtle or Southern Beech) sites], *Potorous longipes* (the Long-footed Potoroo; 32 sites) and *Macropus antilopinus* (the Antilopine Wallaroo; 22 sites). The analyses indicated the potential for significant distributional changes, with severe reductions in some places.

Booth & McMurtrie (1988): The possible impacts of climate change on *Pinus radiata* plantations in Australia were assessed using BIOCLIM to estimate conditions at 71 major plantations representing about 90% of the total resource. An interesting feature of the analysis was the use of a detailed process-based model at two representative sites to assess the impacts of atmospheric changes (i.e. the effects of increased atmospheric carbon dioxide levels on water-use efficiency) as well as climatic changes. Assessing the impacts of atmospheric as well as climatic changes remains a major challenge for SDMs (Booth & Williams, 2012).

Booth *et al.* (1988): Bioclimatic analysis was used to analyse the realized niche of 13 commercially significant eucalypt species in Australia. Forestry trials are often located in conditions outside those of species' natural distributions, and foresters do everything practical to reduce negative impacts of other species on the trial species. So, results from trials outside Australia were used to provide some indication of the fundamental niche. Understanding the fundamental niche (sensu Hutchinson, 1957) is important for predicting how existing well-established native stands may cope with climate change (Booth & Williams, 2012).

In a thought experiment, Peterson *et al.* (2011) imagined that 'individuals of a species could be introduced in experimental settings suitably replicated, and protected from competitors, predators and diseases' to help estimate the 'abiotically suitable area' of the niche of particular species. Many forestry trials around the world have tested genetic material for particular species in this way. They use genetic material collected from specific locations (provenances) in natural stands, and so these results are potentially very relevant to ecological studies (Booth, 2013).

Booth & Jovanovic (1988): Climatic conditions within the natural distribution of *Acacia mearnsii* De Wild. (Black Wattle) in Australia were analysed using BIOCLIM and compared with conditions at more than 50 successful plantation sites outside Australia, some of which experienced mean annual temperatures more than 5 °C above those at the hottest sites in its natural distribution.

Suggesting unsurveyed sites of high potential of occurrence for rare species

Lindenmayer *et al.* (1991): Bioclimatic analysis was used to predict and define the potential limits of *Gymnobelideus leadbeateri* (McCoy; Leadbeater's possum), which is a rare species of arboreal mammal found in the Central Highlands of Victoria. The bioclimatic analyses were used as a basis for selecting survey sites outside the known distribution, although the species was not found in these surveys.

Supporting appropriate management plans for species recovery and mapping suitable sites for species reintroduction

Very little species recovery work was being carried out in the 1980–1991 period, so there are no good examples of very early BIOCLIM applications from within the review period. However, just 5 years later, the Action Plan for Australian Marsupials and Monotremes (Maxwell *et al.*, 1996) was recommending BIOCLIM analyses be carried out as part of several species recovery plans.

Supporting conservation planning and reserve selection

Gibson (1986): Huon pine [*Lagarostrobos franklinii* (Hook. F.) Quinn] is a conifer found in south-western Tasmania. Occurrence records from 107 locations were analysed using SDM techniques as a small part of developing a conservation and management plan. The species occupies habitats that are relatively mild and wet. A small shift to colder/drier conditions could result in extinction of the species, while a shift to warmer, wetter conditions could greatly increase its range.

Mackey *et al.* (1989): The representativeness of the Wet Tropics World Heritage property of north-east Queensland was assessed. As part of the analysis, bioclimatic methods were used to analyse the potential niche of two major structural classes of vegetation based on data from 291 sites. It was concluded that this provided useful insights into the types of rain forest that could be expected within different environmental groups.

Modelling species assemblages (biodiversity, composition) from individual species predictions

Nix & Switzer (1991): This book on rain forest animals found in Australia's wet tropics involved more than 30 contributors. It used BIOCLIM to analyse the distributions of 11 mammals, 13 birds, 13 reptiles, 20 frogs and three fishes. It includes a chapter on general biogeography, which also discusses palaeoclimatic information. Numerical taxonomic procedures were used to recognize species assemblages in terms of the similarities of their current bioclimatic profiles.

All the preceding authors found that the use of BIOCLIM provided useful new insights. For example, Markgraf *et al.* (1986) commented that the BIOCLIM method 'is not only more objective than other previously used methods, but also permits us to interpret which of the two parameters, precipitation or temperature, might have been primarily responsible for a given environmental shift', while Panetta & Mitchell (1991a) concluded that BIOCLIM 'can provide valuable new information to quarantine decision-makers'.

Busby (1991b) noted the only 'failure' of BIOCLIM of which he was aware within its first few years was an attempt to analyse the distribution of *Phascolarctos cinereus* Goldfuss (Koala) in western New South Wales. In this region, their distribution was linked to the distribution of *Eucalyptus camaldulensis* Dehnh. (River Red Gum) trees, which were restricted to watercourses and therefore not well associated with climate. Consequently, the BIOCLIM analysis predicted unrealistically large areas of suitable habitat for koalas over low-rainfall areas of western New South Wales.

By 1991, the use of BIOCLIM was becoming well established with eight references in ISI Web of Knowledge™ (e.g. Booth, 1991; Busby, 1991a; Lindenmayer *et al.*, 1991; Panetta & Mitchell, 1991a; Williams, 1991; Williams & Busby, 1991). The first SDM package was also beginning to spread to other countries with climate surfaces developed for New Zealand, BIOCLIM implemented and the distribution of *Agathis australis* (Kauri) analysed (Mitchell, 1991). The potential distribution of some weed species in New Zealand was also analysed using BIOCLIM (Panetta & Mitchell, 1991b).

Another significant step was the development of some modifications to the basic BIOCLIM approach in the form of the HABITAT package, which essentially trims the rectilinear climatic envelopes of BIOCLIM (Walker & Cocks, 1991). This began the very active field of SDM development using a variety of methods (see Franklin, 2009), which would result in papers such as the highly cited (>1500) Elith *et al.* (2006) paper, where 27 authors collaborated on the comparison of 16 different SDMs, including BIOCLIM, using data for 226 species. Although BIOCLIM had been widely and successfully used for more than 20 years, it appeared to perform poorly in relation to more recent methods. Following this comparison, MAXENT (Phillips *et al.*, 2006) has come to be one of the most widely used analysis methods in the SDM field. Although the use of BIOCLIM is in decline, more than 100 papers have cited the use of the package or BIOCLIM variables in the Web of Knowledge ™ since 2006. The widely used WorldClim database (Hijmans *et al.*, 2005) offers downloadable climatic data for 19 BIOCLIM variables, such as annual mean temperature and precipitation of the wettest month. BIOCLIM variables are also available and often used in MAXENT analyses of selected data from the more than 35 million species observation points available in the Atlas of Living Australia (see, e.g. Booth *et al.*, 2012). The Global Biodiversity Information Facility (GBIF) still cites Nix (1986) in the description of its 'envelope score' and uses a modified version of BIOCLIM (Pineiro *et al.*, 2007) to interrogate selections from its extensive database.

Article titles, abstracts and keywords do not always reflect the actual usage of BIOCLIM variables in particular studies. So, the 50 most recent papers citing MAXENT at the time of writing in the Web of Knowledge™ (starting from Liu *et al.*, 2013) were examined to see how frequently BIOCLIM variables were used in these analyses. Of the 50 papers, 42 papers were accessible and applied MAXENT to terrestrial biota. Four of these used monthly mean climate data and six small-scale studies only used landscape variables such as slope, aspect and distance to particular features such as water. The remaining 32 used BIOCLIM variables from WorldClim (Hijmans *et al.*, 2005), with 23 examples using the full 19 factors provided by WorldClim. So, if this small sample is indicative, not only do about 76% of terrestrial MAXENT analyses use BIOCLIM variables, but also the estimated climate values for these variables are derived from interpolation algorithms developed originally for BIOCLIM and used to create WorldClim.

CONCLUSIONS

The conceptual contribution of Hutchinson (1957) and Box (1981) to the development of SDMs in the pre-BIOCLIM period should be acknowledged. Similarly, the Nix *et al.* (1977) work provided some methodological underpinning for the development of mechanistic-based species distribution analysis (see Booth & Williams, 2012 for a comparison of correlative and mechanistic methods). However, like the Box (1981) study, the Nix *et al.* (1977) study used neither species distribution data nor interpolated climate, so we would not describe it as 'the earliest species distribution modelling attempt' as Guisan & Thuiller (2005) do.

It is true that relative to more recent models, such as MAXENT, BIOCLIM offers a simplistic approach to species distribution modelling. However, the use of simple ranges of environmental variables within an n-dimensional hyperspace was an approach that was closely related to current ecological theory (see particularly Hutchinson, 1957) when the system was developed. The chief limitation of the rectilinear approach is related to relationships between variables. For example, a species may require somewhat higher levels of precipitation to exist in the hotter environments within its distribution. One of the main reasons for increasing the number of variables used in analyses from 12 in the original version to 35 in the current version was to define the bioclimatic envelope more closely.

While BIOCLIM describes the n-dimensional hyperspace in terms of simple ranges, the MAXENT model develops a response curve for each environmental variable indicating which particular conditions within a range are most suitable (see Elith *et al.*, 2011 for more information). A detailed comparison of methods is beyond the scope of the present paper, but Peterson *et al.* (2011) wrote in relation to the comparison of methods of Elith *et al.* (2006) that 'since the evaluation data (used to compare SDMs) were drawn from the same geographic area as the calibration data, and were therefore spatially autocorrelated, models able to fit highly complex response curves could fit closely to calibration data and were thus more likely to yield particularly good statistics'.

The climate interpolation programmes developed by Hutchinson (see, Hutchinson, 2011 for the current version) were prepared to support the development of BIOCLIM. Their incorporation of elevation dependence had significant implications, for the accuracy of the interpolated surfaces and for its stimulus to the early development of digital elevation models and their many applications (Hutchinson & Dowling, 1991). They are one of the most important ways in which activities associated with the development of BIOCLIM continue to have relevance for current SDM researchers.

As Franklin (2009) recognized, the inclusion of climate interpolation relationships within BIOCLIM was one of its most important strengths. A user simply needed to prepare a file of species locations (latitude, longitude and elevation), and the whole SDM analysis process was completed within the one package. As Nix (1986) concluded, for the first time in biogeographical analysis of species, 'the methods are explicit, quantitative and specimen based'. Nix (1986) also identified significant weaknesses of the package, such as the reliance on climatic factors and the desirability of adding substrate factors, as well as information on the distribution of prey and predator species. Considerable progress has been made addressing these issues since BIOCLIM's introduction (see Franklin, 2009), but significant challenges remain particularly when environmental change is being considered.

The early applications of BIOCLIM in the 1984–1991 period provide examples for most of the eight possible uses of SDMs in ecology and conservation biology in table 1 of Guisan & Thuiller (2005). There was clearly a need for a review, such as that provided here, to show how early many of these topics were explored. Devising innovative applications and fresh insights in the SDM area of research (Richardson, 2012) requires an understanding of previous studies.

It is very challenging for those currently active in the SDM field to keep track of the rapidly expanding literature. However, useful approaches may be missed by failing to appreciate lessons learned in early work. For example, the use of results from analysis of forestry trials, as well as natural distributions, can provide useful insights into the fundamental and realized niche (Booth *et al.*, 1988). The use of simulation models in addition to SDMs can assist understanding how atmospheric as well as climate change will affect species distributions (Booth & McMurtrie, 1988).

The development of improved methods for climatic interpolation, which was part of the development of the BIOCLIM package, has made a far reaching and enduring contribution not just to SDM development but to ecological studies in general, particularly through the widespread use of WorldClim data. The creation of BIOCLIM as the first SDM was fundamental to the development of this area of ecological research. For more than 20 years, it was one of the most widely applied methods in the area and it continues to influence current SDM work. For example, bioclimatic variables developed for BIOCLIM have gone on to be widely used and continue to form the basis for many MAXENT analyses today.

Woodward (1987) wrote that 'in view of the importance of climate in controlling distribution of plants it is surprising that this area of subject is not a popular one in plant ecology'. With the arrival of SDM packages led by BIOCLIM and increasing concern about climate change, the study of climatic effects on both plant and animal distributions has become one of the most active areas of ecology.

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BIOSKETCH

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