



Shapes and functions of species–area curves: a review of possible models

Even Tjørve* *Lillehammer College, 2626 Lillehammer, Norway*

Abstract

Aim This paper reviews possible candidate models that may be used in theoretical modelling and empirical studies of species–area relationships (SARs). The SAR is an important and well-proven tool in ecology. The power and the exponential functions are by far the models that are best known and most frequently applied to species–area data, but they might not be the most appropriate. Recent work indicates that the shape of species–area curves in arithmetic space is often not convex but sigmoid and also has an upper asymptote.

Methods Characteristics of six convex and eight sigmoid models are discussed and interpretations of different parameters summarized. The convex models include the power, exponential, Monod, negative exponential, asymptotic regression and rational functions, and the sigmoid models include the logistic, Gompertz, extreme value, Morgan–Mercer–Flodin, Hill, Michaelis–Menten, Lomolino and Chapman–Richards functions plus the cumulative Weibull and beta-P distributions.

Conclusions There are two main types of species–area curves: sample curves that are inherently convex and isolate curves, which are sigmoid. Both types may have an upper asymptote. A few have attempted to fit convex asymptotic and/or sigmoid models to species–area data instead of the power or exponential models. Some of these or other models reviewed in this paper should be useful, especially if species–area models are to be based more on biological processes and patterns in nature than mere curve fitting. The negative exponential function is an example of a convex model and the cumulative Weibull distribution an example of a sigmoid model that should prove useful. A location parameter may be added to these two and some of the other models to simulate absolute minimum area requirements.

Keywords

Species–area curves, Monod, negative exponential, asymptotic regression, logistic, Gompertz, Morgan–Mercer–Flodin, Chapman–Richards, extreme value, rational function, Weibull distribution, beta-P distribution.

INTRODUCTION

The species–area relationship (SAR) is one of the most important tools available in the study of species diversity, conservation biology and landscape ecology (see e.g. Schoener, 1976; Lomolino, 1989, 2000a; Palmer & White, 1994; Rosenzweig, 1995). It is one of the oldest and most well-proven patterns in ecology. The shapes of species–area curves have been discussed extensively, sometimes even fiercely, for most of the last century (e.g. Arrhenius, 1921; Gleason, 1922, 1925; Connor & McCoy, 1979; Sugihara, 1981; Connor

et al., 1983; Lomolino, 2000a, 2002; Williamson *et al.*, 2001).

As the shape of the curve has been extensively debated over the years, the best known and most commonly applied curves are the two convex upward shaped curves: the exponential curve (Gleason, 1922, 1925; Fisher *et al.*, 1943) and the power curve (Arrhenius, 1921; Preston, 1962a,b), whereof the power (log–log) model is the most frequently encountered in recent literature. Both curves are convex but not asymptotic. The power function goes through the origin of axes, but the exponential function does not. They are usually transformed into log–log and log–linear space, respectively.

They are perhaps the most cited functions, but by no means the only plausible models (Connor & McCoy, 1979).

*Correspondence: Even Tjørve, Lillehammer College, 2626 Lillehammer, Norway. E-mail: even.tjorve@hil.no

It is argued that we may be using the wrong model, or at least an overly simplistic one (Lomolino, 2000a). Several authors (e.g. Williamson, 1981; Legendre & He, 1996; Rosenzweig & Ziv, 1999) have argued that the power model is best suited for, i.e. will produce straight lines in log-log space for, intermediate and larger sampling areas, and the exponential model is best and will produce straight lines in log-linear space for smaller sampling areas. It is probable that the success of the power model and the exponential model is due to the fact that they are used for data within a restricted scale, and these curves are most useful at these scales. They might not be fitted successfully to data from very small or very large areas.

It is important to note that the species-area curve was originally intended to describe the increase in species number found as the size of the sampling area increases. These sample areas (census-patches) are pieces of some large unbounded universe. When MacArthur & Wilson (1967) presented their theory of island biogeography, they treated the species-area curve as the result of bounded areas, or islands. Within the tradition of landscape ecology, nature consists of mosaics of isolates that can be treated more or less as islands. Species-area curves from sample areas, from isolates and from large continuous areas should differ in shape and other properties (Tjørve & Turner, unpubl. data.).

In the discussions of the shape of species-area curves, one should therefore bear in mind that historically the aim has been to fit empirical data (i.e. observed patterns). The Preston and the Arrhenius functions were chosen out of convenience and not from biological causes. As fitted curves they lack biological explanatory power. Only later have SARs become part of theories of species diversity (e.g. Preston, 1962a,b; MacArthur & Wilson, 1967; May, 1975).

The shapes of species-area curves

Why is it so important to know the shape of the species-area curve? Based on the curve shape, one may estimate total species diversity or species pools from counted numbers of samples or isolates, or estimate species extinction as a result of habitat loss and fragmentation. We also need to discuss the shape of species-area curves to be able to address more complex models or theories of SARs within landscape patterns and at different scales.

Both the power and the exponential functions have convex upward shapes and lack upper asymptotes. These models are usually indiscriminately used on isolate (island and habitat-patch) data, without considering other possible models. Several authors have tried to find alternatives to the power function. A few have advocated convex upward models that have an asymptote (Holdridge *et al.*, 1971; Miller & Wiegert, 1989). Lately, an increasing number of authors have argued that some SARs are perhaps best represented by functions that are sigmoid in arithmetic space (e.g. Williams, 1995, 1996; Legendre & He, 1996; Lomolino, 2000a,b, 2001). There are also a number of recent studies where sigmoid models have been fitted to empirical data (see Williams, 1995; Flather, 1996; Burbidge *et al.*,

1997; Lomolino, 2000a; Veech, 2000; Belant & Van Stapen, 2002).

Many have fitted data that show sigmoid shapes in log-linear space or discussed sigmoid shapes in log-linear space (e.g. Archibald, 1949; Vestal, 1949; Hopkins, 1955; Coleman *et al.*, 1982; Palmer & White, 1994; He *et al.*, 1996; Legendre & He, 1996; Plotkin *et al.*, 2000). Unfortunately, a sigmoid shape in log-linear space does not imply a sigmoid shape in arithmetic space (and vice versa). Neither are sigmoid shapes in log-log space always sigmoid also in arithmetic space. Sigmoid species-area curves in log-log space are rarely found in the literature. Some have appeared in some modelling papers (e.g. Durrett & Levin, 1996; Leitner & Rosenzweig, 1997; Ney-Nifle & Mangel, 1999). The sigmoid log-log space curves (covering many orders of magnitude of area) found in Preston (1960) and Williams (1964) go from decreasing slope to increasing slope, contrary to the models discussed here.

Thus, discussions of biological explanations for sigmoid SARs (in arithmetic space) do not necessarily apply to and cannot be supported by sigmoid shapes in log-linear or log-log space. This has led to some confusion in the literature, as one often does not discern between different types of space. One always needs to be careful and aware of what type of space is used, when discussing the possibility of sigmoid species-area curves. I believe biological explanations and patterns that shape species-area curves are best discussed in arithmetic space.

Two kinds of small-scale species-area curves, the sample curve and the isolate curve, have been distinguished (Preston, 1962a; Tjørve & Turner, in prep.). The sample curve is the result of species diversity of census patches (sample) of different sizes within an expanse of habitat with boundaries defined by the survey design, and is expected to be convex upward. The isolate curve is the result of species diversity within different sizes of habitat patches or islands (isolates) of the same type. One key distinction among functions may be their ability to fit data compiled from samples vs. data compiled from isolates, which should produce quantitatively different SARs (Rosenzweig, 1995; Tjørve & Turner, in prep.). The sample curve is expected to be convex upward and the isolate curve sigmoid. The failure to distinguish between these two patterns has produced considerable confusion in the literature.

There is a need to discuss the biological causes of SARs further and to evaluate possible species-area models that may coincide better with the way biological processes generate SARs. One should *a priori* be able to predict biological patterns in nature as the shapes of species-area curves. Failure to implicate these biological patterns while continuing to just indulge in mere curve fitting will hamper future understanding of these systems.

Aims

This paper reviews functions that in the literature have been fitted to species-area or species-accumulation data in the past. These functions will be evaluated and classified by

curve shape, number of parameters and how parameters affect shape. Looking at both asymptotic convex upward shaped models and sigmoid models, model characteristics are systemized and discussed with respect to their behaviour in arithmetic space. Six convex and eight sigmoid models are reviewed. Other important characteristics are asymptotes, inflection-points, symmetry and zero values. The relationship between different models is also discussed, with some models treated just as reductions of more complex models.

Sigmoid curve models should be expected to fit isolate (habitat-patch or island) data, and convex models should fit sample area (census patch) data. Convex shapes should also fit isolate type data where no data are present from the lower convex downward (j-shaped) part of the curve. Therefore strictly concave upward models can also be used successfully if only data from medium and large sized habitats or islands are included. One way to circumvent this problem has been by using different power line segments for different ranges, as is often performed to deal with the small island or minimum area effect. The minimum area effect is here defined as the effect of species minimum area requirements on species–area curves. That species have minimum area requirements is well known, but these have not been estimated empirically for most species (Gurd *et al.*, 2001).

The different models (Tables 1 and 3) are reviewed to see how their parameters behave (Tables 2 and 4). The behaviour of these parameters may provide an indication of which function type will give us a curve that coincides with biological explanations, arguments as the existence of

species pools and the minimum area effect. The nomenclature of these models is standardized so that x represents the independent variable (in this case area) and the parameters (constants) are named consecutively from 'a' to 'd', as no model has more than four parameters.

POSSIBLE CONVEX MODELS

Neither of the two most commonly used models, the *power* and the *exponential* models, have an upper asymptote. This means that the total number of species (i.e. the species pool) is infinite. As long as one does not need an upper asymptote or the lower j-shaped part of the curve (i.e. sigmoid shape), these are proven models that perform well. If one wants convex upward shaped SAR-models, then there are several possible functions (Table 1). All of the models except for the power and the exponential have upper asymptotes. The asymptote of a fitted curve may serve as an estimate of the species pool or the total number of species.

The *Monod function* (Monod, 1950) is also called the two-parameter hyperbola. It is one of several versatile models. The curve has an upper asymptote, but does not always go through the origin of axes. The first parameter represents the upper asymptote, while the other parameter affects curve shape (Table 2). The curve always goes through a point in space given by $x = 0, f(x) = a - b$. Flather (1996) reported that the Monod function did not perform well with his bird census data. Clench (1979) and de Caprariis *et al.* (1976) successfully used the Monod model to produce

Table 1 Convex curve models that have been proposed for the species–area relationship (SAR). The models have been used with different nomenclature, but here they are converted to the standard used by Flather (1996). In this case the independent variable (x) is area and the dependent $f(x)$ is number of species

Curve name	Model	Parameters (asymptote)	Source
Power	ax^b	2 (no)	Arrhenius (1921), Preston (1962a,b)
Exponential	$a + b \log(x)$	2 (no)	Gleason (1922, 1925), Fisher <i>et al.</i> (1943)
Monod	$a/(b + x)$	2 (yes)	Monod (1950), de Caprariis <i>et al.</i> (1976), Clench (1979)
Negative exponential	$a(1 - \exp(-bx))$	2 (yes)	Holdridge <i>et al.</i> (1971), Miller & Wiegert (1989), Ratkowsky (1990)
Asymptotic regression	$a - bc^{-x}$	3 (yes)	Ratkowsky (1983)
Rational function	$(a + bx)/(1 + cx)$	3 (yes)	Ratkowsky (1990)

Table 2 Function of the different parameters in the convex curve models. Parameters with an asterisk alter curve shape on both sides of a rotation point ($x = 1$ and $y = a$, for Monod curve $x = 0, f(x) = a - b$)

Curve name	First parameter	Second parameter	Third parameter	Curve through origin of axis
Power	Curve shape	Shape*		Yes
Exponential	Curve shape	Shape*		No
Monod	Upper asymptote	Shape*		Depends on parameters
Negative exponential	Upper asymptote	Shape		Yes
Asymptotic regression	Upper asymptote + y-axis intersection	Shape + y-axis intersection	Shape*	Depends on parameters
Rational function	Shape + y-axis intersection	Curve shape + upper asymptote	Shape + upper asymptote	Depends on parameters

species–accumulation curves from samples of number of individuals or some measure of effort.

The *negative exponential function* (Ratkowsky, 1990) is a very simple two-parameter model (Table 1) that always passes through the origin. It produces an ordinary convex upward curve with an upper asymptote. It is, contrary to the power and exponential functions, convex upward in space for all positive values of both parameters. More than 30 years ago Holdridge *et al.* (1971) used this function to fit tree species data from sample plots in Costa Rica. Miller & Wiegert (1989) fitted the negative exponential function to cumulative plots of number of rare plant species to area, and reported a close agreement between the model curve and the data. Flather (1996), on the other hand, reported that the model performed poorly relative to all other candidate models he tested. The negative exponential function should also be useful on species–accumulation data (Sorberon & Llorente, 1993; Colwell & Coddington, 1994).

The *asymptotic regression* (Ratkowsky, 1983) has an upper asymptote but does not always go through the origin of axes. The three-parameter model is not as easy to handle as the Monod and the negative exponential functions. This is because two of the parameters in the asymptotic regression affect more than one curve trait at the same time (shape, upper asymptote and y -axis intersection). Flather (1996) tested the asymptotic regression but found it did not perform well on his bird survey data.

The *rational function* (Ratkowsky, 1990) also has an upper asymptote but does not always go through the origin. This three-parameter function is perhaps also more difficult to handle than the other convex upward models. This is again because each parameter in the model affects more than one curve trait at the same time (shape, upper asymptote and y -axis intersection). It is only convex with positive values of x and $f(x)$ only for some values of the two parameters. Flather (1996) also tested the rational function and reported that of the convex upward models it fit his data best, better than the power and the exponential functions, which performed second and third best of the models he tested (see Table 5).

POSSIBLE SIGMOID MODELS

A number of sigmoid mathematical functions have recently been suggested as alternatives to the power and exponential functions (Williams, 1995, 1996; Flather, 1996; Legendre & He, 1996; Lomolino, 2000a). Of the several functions proposed to describe sigmoid growth rates in biology, eight different candidate sigmoid functions are shown in Table 3. The functions treated here are perhaps the most relevant, but other functions (e.g. Ratkowsky, 1983, 1990), may also be used to describe SARs. All sigmoid functions reviewed have upper asymptotes. A basic distinction between different types of sigmoid functions is that some are symmetrical on each side of the inflection point, whereas others are not.

By adding parameters, one may get increased possibilities to manipulate curve shape, inflection point, axis intersection and asymptotes. The effect caused by manipulation of the different parameters is shown in Table 4. The upper asymptote is given by a parameter value that constitutes the total species pool. The value for the upper asymptote can of course be set to one if one wants the model to describe the cumulative expected probability of occurrence of a given species with increasing area (species incidence curve) (see e.g. Schoener & Adler, 1991; Williams, 1995; Ney-Nifle & Mangel, 1999; Nupp & Swihart, 2000; Bartha & Ittzes, 2001).

The *logistic function* (Ratkowsky, 1990) is the only function considered here that is symmetrical about the inflection point. This property makes the function less flexible than other sigmoid models, which may limit its ability to fit data well. But the logistic function is still one of the most useful models for fitting sigmoid responses (Ratkowsky, 1990). The logistic function as presented here has three parameters (Table 3). The first represents the upper asymptote. The two other parameters alter the curve shape. The curve has a lower asymptote of zero, and the intersection with the y -axis depends on all three parameters. Thus it never goes through the origin, which should not be a major problem when fitted to empirical data, but may pose problems if used in a model type approach. Natuhara & Imai

Table 3 Candidate sigmoid models for the species–area relationship (SAR). All have an upper asymptote. The independent variable (x) is in this case area, and the dependent $f(x)$ is number of species. For models where $f(x) = 0$ when $x = -\infty$, an inflection point occurs on the y -axis

Curve name	Model	Parameter (when $y = 0$)	Source
Logistic function	$a/(1 + \exp(-bx + c))$	3 ($x = -\infty$)	Ratkowsky (1990)
Gompertz model	$a \exp(-\exp(-bx + c))$	3 ($x = -\infty$)	Ratkowsky (1990)
Extreme value function	$a(1 - \exp(-\exp(bx + c)))$	3 ($x = -\infty$)	Williams (1995, 1996), Burbidge <i>et al.</i> (1997)
Morgan–Mercer–Flodin (Hill-function)	$a x^c / (b + x^c)$	3 ($x = 0$)	Morgan <i>et al.</i> (1975)
Lomolino function	$a / (1 + (b \log(c/x))^c)$	3 ($x = 0$)	Lomolino (2000a)
Chapman–Richards	$a(1 - \exp(-bx))^c$	3 ($x = 0$)	Ratkowsky (1990)
Cumulative Weibull distribution	$a(1 - \exp(-bx^c))$	3 ($x = 0$ and $c = 0$)	Weibull (1951), Reid (1978), Yang <i>et al.</i> (1978), Brown & Mayer (1988), Rørslett (1991), Flather (1996)
Cumulative beta-P distribution	$a(1 - (1 + (x/c)^d)^{-b})$	4 ($x = 0$)	Mielke & Johnson (1974)

Table 4 Function of the different parameters in the sigmoid curve models

Name curve	First parameter	Second parameter	Third parameter	Fourth parameter
Logistic function	Upper asymptote + y-axis intersection	Shape + y-axis intersection	Shape + y-axis intersection	
Gompertz model	Upper asymptote + y-axis intersection	Shape + y-axis intersection	Shape + y-axis intersection	
Extreme value function	Upper asymptote + y-axis intersection	Shape + y-axis intersection	Shape + y-axis intersection	
Morgan–Mercer–Flodin	Upper asymptote	Shape	Shape	
Lomolino function	Upper asymptote	Shape	Shape	
Chapman–Richards	Upper asymptote	Shape	Shape	
Cumulative Weibull distribution	Upper asymptote	Shape	Shape	
Cumulative beta-P distribution	Upper asymptote	Shape	Shape	Shape

(1999) compared the logistic curve with the power and the exponential functions and reported that bird data from urban wood remnants were better fitted by the power function. The logistic function is seldom fitted to species–area plots, but is in common use for multiple regressions where the explanatory power of several parameters in addition to area is assessed (e.g. Schoener & Adler, 1991; Morrison, 1997; Miller & Cale, 2000). Where area or other parameters are evaluated to explain species number, some papers may also present graphs or results where the logistic function is fitted to show species incidence (single-species probability–area) curves (e.g. Schoener & Adler, 1991; Nupp & Swihart, 2000). Some confusion results when the term ‘logistic curve’ is used interchangeably with ‘sigmoid’. In fact, the logistic function is only one of many models producing sigmoid curves.

The *Gompertz model* (Ratkowsky, 1990) is related to and behaves somewhat similar to the logistic function. It is also presented with three parameters but it is not symmetrical about the inflection point. It has a lower asymptote of zero and all three parameters affect the intersection with the y-axis.

The *extreme value function* (Williams, 1995, 1996) also has three parameters and behaves quite similarly to the logistic and Gompertz models. The extreme value function has one parameter that gives the upper asymptote and two that affect shape. It also has a lower asymptote of zero and thus never goes through the origin.

Williams (1995) used Coleman’s (1981) model and showed that if individuals are randomly distributed over area, then the cumulative extreme value function is an appropriate model for the species incidence curve. He showed the appropriate log-transformation that linearizes the extreme value function. He claimed that this function is superior to the logistic function and that the parameters have biologically meaningful interpretations. Williams also demonstrated that it is an appropriate model even when the assumption of random distribution is severely violated. The extreme value function has later been fitted to empirical species–area data by several authors (Burbidge *et al.*, 1997; Veech, 2000; Belant & Van Stappen, 2002; Matter *et al.*, 2002) (see Table 5).

The *Morgan–Mercer–Flodin function* (Morgan *et al.*, 1975), with three parameters, has an upper asymptote and

Table 5 Some papers where species–area functions other than power and exponential are fitted

Author	Model fitted	Type of areas	Taxonomic group
Holdridge <i>et al.</i> (1971)	Negative exponential	Sample	Trees
Miller & Wiegert (1989)	Negative exponential	Hypothetical sample	Plants
Rørslett (1991)	Weibull distribution	Isolate	Plants
Williams (1995)	Extreme value function	Isolate	Birds, mammals
Legendre & He (1996)	Hill-function	Sample	Trees, birds
Flather (1996)	Monod, negative exponential, asymptotic regression, rational function, Chapman–Richards, Weibull distribution and cumulative beta-P distribution	Sample	Birds
Burbidge <i>et al.</i> (1997)	Extreme value function	Isolate	Mammals
Natuhara & Imai (1999)	Logistic	Isolate	Birds
Veech (2000)	Extreme value function	Sample	Many
Belant & Van Stappen (2002)	Extreme value function	Isolate	Mammals
Matter <i>et al.</i> (2002)	Extreme value function	Isolate	Birds, mammals

goes through the origin of axes. The Morgan–Mercer–Flodin model can be reduced to the familiar Hill (Hill, 1913) and the Michaelis–Menten (Michaelis & Menten, 1913 functions, or to the simplified Hill-function used by Legendre & He (1996). It is also possible to add more parameters to the Morgan–Mercer–Flodin, e.g. to change the y-axis intersection.

The *Chapman–Richard function* (Ratkowsky, 1990) is a modification of the negative exponential function used by Miller & Wiegert (1989). It is yet another three-parameter model that behaves similarly to the Morgan–Mercer–Flodin, has an upper asymptote and goes through the origin. Flather (1996) also tested this model on his bird survey data and found that it performed well.

The *Lomolino function* (Lomolino, 2000a) differs from the Morgan–Mercer–Flodin and the Chapman–Richard functions in that the second parameter (b) changes the inflection point. Lomolino called his function a Hill function, but it is not. He only used it on a hypothetical data set.

The cumulative *Weibull distribution* (Weibull, 1951) is here shown with three parameters. It also has an upper asymptote and goes through the origin of axes. The Weibull is probably the most versatile sigmoid model presented here. It is flexible enough to accommodate most biological growth curves (see e.g. Reid, 1978; Yang *et al.*, 1978), and it has also been shown to fit empirical species–area data well (Flather, 1996). Flather (1996) reported that the Weibull fitted his data better than the other models. He compared nine candidate models (see Table 5), both sigmoid and non-sigmoid models, by fitting them to data of bird species numbers in different regions of North America. Rørslett (1991) found the Weibull useful for multiple regressions on plant diversity data from lakes.

The cumulative *beta-P distribution* behaves similarly to the Weibull distribution, but has four parameters instead of three. The beta-P distribution also possesses very desirable computational properties (Mielke & Johnson, 1974), as it is very flexible and has a great ability to fit data sets closely. The only investigator who tried to fit this model to species–area plots was Flather (1996). It performed well, but not as well as the cumulative Weibull distribution. The Weibull is probably just as flexible as the beta-P distribution and may be preferable because it has one less parameter than the beta-P.

WHICH MODEL TO CHOOSE?

The power function and the exponential function dominate the literature, but there are, as we see, a handful of papers where other species–area models are fitted to empirical data (Table 5). Sigmoid models have been fitted to both sample area data and isolate type data. However, the better fit of sigmoid curves, such as the Weibull distribution, does not necessarily prove sigmoid relationships. The better fit may be just the result of the flexibility of the model.

The sigmoid species–area models could nevertheless be more appropriate for isolates. But one should bear in mind that convex models may be sufficient, e.g. at scales above a possible inflection point or if the inflection point is so close

to the lower end of the curve that the convex downward part of the curve becomes very small compared with the rest of the curve. This should be the case if the minimum area requirements of the organisms studied are very small compared with the scale in question.

Convex or sigmoid models?

It is important to distinguish between sample areas (census patches) on one hand and isolates (habitat patches or islands) on the other. One should not expect the same species–area models to be the best for both sample area data sets and isolate data sets, or across scales of communities, habitats, regions or provinces. If one takes known biological patterns, as the effect of minimum area requirements and species pools, into consideration, then the theoretically correct choice for sample curves seems to be a convex upward model with an upper asymptote, and for isolates a sigmoid model with an upper asymptote. These expected shapes do not conflict with the fact that one may find other shapes that fit a given set of data better.

If one wants a function just for theoretical models, then one should look for the simplest possible model that will fit the biological arguments for the shape of the curve. If one can only argue that the curve should be convex upward, then the traditional power function or the exponential function will do. But if an upper asymptote is inferred, then the negative exponential function would be the simplest model to conform to that condition. Such a convex asymptotic model allows one to estimate species pools from sample areas (Colwell & Coddington, 1994). Convex asymptotic function should also be useful for upper parts of isolate curves. For modelling purposes the negative exponential is recommended for isolate data as a result of its simplicity and ease of handling. However it may not fit empirical data as well as the asymptotic regression or the rational function with three parameters.

For isolates, the Weibull distribution should be a very versatile and desirable model. It can be used in a simple form with only two parameters ($a(1 - \exp(-x^b))$) for modelling situations, and with three parameters (Table 3) it easily fits most empirical data sets requiring a sigmoid shape. If one wants a curve that is symmetrical on each side of the inflection point, then the logistic function is a possibility. If manipulation of inflection points is important, then the Lomolino function may also be considered. The extreme value function should also be considered as a possible sigmoid model.

Adding a location parameter

The first three sigmoid functions, the logistic, the Gompertz and the extreme value function, have the x-axis as a lower asymptote, so one cannot manipulate the curve to start on the x-axis. The other five models can be shifted to the right by adding a location parameter to the x-value. This could simulate an absolute minimum area, for example for any species or particular species group. If a location parameter

(c) is added to the negative exponential model, it would be expressed as

$$a(1 - \exp(-b(x - c))) \quad (1)$$

and by adding the location parameter (d) the Weibull distribution would become

$$a(1 - \exp(-b(x - d)^c)) \quad (2)$$

These two models should be both relatively simple and flexible candidates for asymptotical, convex shaped species–area curves and sigmoid curves, respectively. Figure 1A shows the negative exponential model with and without a location parameter ($c = 3$), and Fig. 1B shows the cumulative Weibull distribution with and without a location parameter ($d = 3$).

The start point at the x -axis for this Weibull distribution (2) is actually a curve minimum. In order for the model to make sense as a species–area curve, one must disregard values of $x < d$. This parameter (d) locates where the minimum of the curve touches the x -axis. The negative exponential and the Weibull models are closely related, as the Weibull can easily be reduced to the negative exponential. In conclusion, models that allow a start-point at the x -axis should be particularly desirable when absolute minimums are needed.

CONCLUDING REMARKS

Several authors have discussed alternative species–area models, but most only discussed one or a few function types. Flather (1996) is the exception, as his paper reviewed nine candidate models and tested their fit to empirical data. The overwhelming majority of authors only tried to fit either the power function or the exponential function to their data. Different possible models have been reviewed in this paper. The behaviour of model parameters and implications for theoretical discussions or mathematical modeling of more complex SARs was also discussed.

Biology suggests that the SARs represent convex curves in some cases and sigmoid curves in other cases. On the other hand, the choice of model has in the past been based on what has fit the data and less on what should be expected from a biological understanding of the system under study. This highlights shortcomings in our understanding of biological processes and the manner in which these generate SARs. The selection of species–area models should be based on the recognition of biology rather than statistics, by incorporating biological patterns found in nature into our models. Examples of factors that may affect curve shape are species minimum area or resource requirements, competition, predation and species pools. Basic curve fitting will not further our biological understanding. The basis for the two most used models, the power and the exponential functions, is phenomenological, not biological. If we see the need to include biological interpretations into our models, several of the other models reviewed in this paper should be useful or appropriate alternatives both in theoretical modeling and in fitting empirical data.

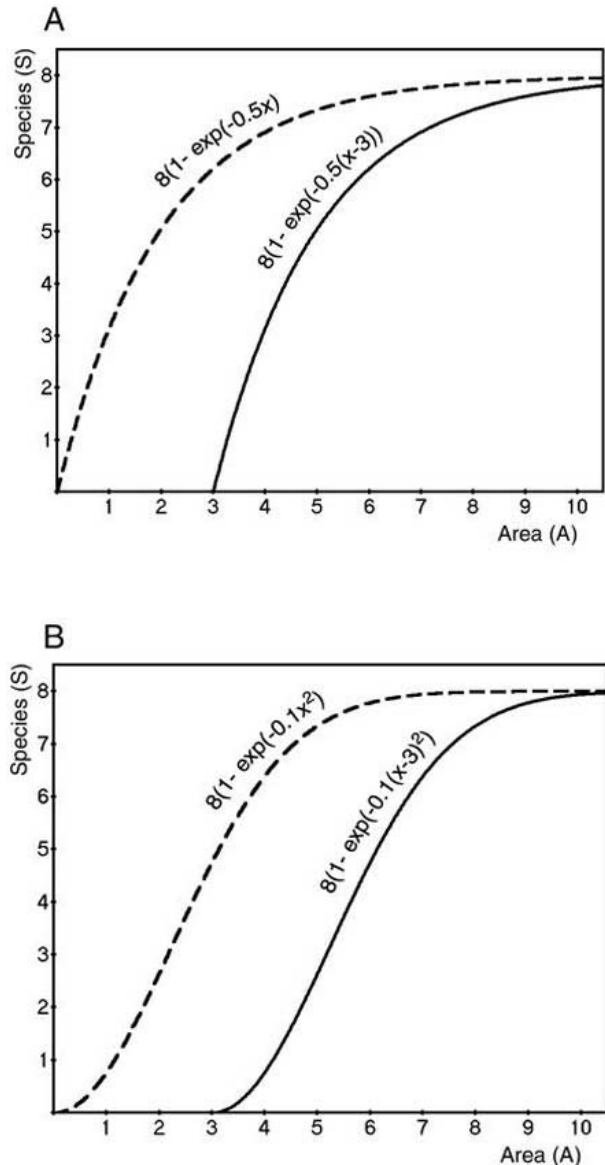


Figure 1 (A) Negative exponential function. The dashed line shows the function without and the unbroken line with a location parameter. The curves are $8(1 - \exp(-0.5x))$ and $8(1 - \exp(-0.5(x - 3)))$, respectively. (B) Weibull distribution. The dashed line shows the function without and the unbroken line with a location parameter. The curves are $8(1 - \exp(-0.1x^2))$ and $8(1 - \exp(-0.1(x - 3)^2))$, respectively. For the last curve, values of $x < 3$ are not shown.

REFERENCES

- Archibald, E.E.A. (1949) The specific character of plant communities, I. Herbaceous communities. *Journal of Ecology*, **37**, 260–273.
- Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.

- Bartha, S. & Ittzes, P. (2001) Local richness–species pool ratio: a consequence of the species–area relationship. *Folia Geobotanica*, **36**, 9–23.
- Belant, J.L. & Van Stappen, J.F. (2002) Island biogeography of mammals in Apostle Islands National Lakeshore, USA. *Natural Areas Journal*, **22**, 180–185.
- Brown, R.F. & Mayer, D.G. (1988) Representing cumulative germination. 2. The use of the Weibull function and other empirically derived curves. *Annals of Botany*, **61**, 127–138.
- Burbidge, A.A., Williams, M.R. & Abbot, I. (1997) Mammals of Australian islands: factors influencing species richness. *Journal of Biogeography*, **24**, 703–715.
- de Caprariis, P., Lindemann, R.H. & Collins, C.M. (1976) A method for determining optimum sample size in species diversity studies. *Mathematical Geology*, **8**, 575–581.
- Clench, H.K. (1979) How to make regional lists of butterflies: some thoughts. *Journal of the Lepidopterists' Society*, **33**, 216–231.
- Coleman, B. (1981) On random placement and species–area relationships. *Mathematical Biosciences*, **54**, 191–215.
- Coleman, B.D., Mares, M.A., Willig, M.R. & Hsieh, Y.-H. (1982) Randomness, area and species richness. *Ecology*, **64**, 1121–1133.
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. B*, **345**, 101–118.
- Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species–area relationship. *American Naturalist*, **113**, 791–833.
- Connor, E.F., McCoy, E.D. & Cosby, B.J. (1983) Model discrimination and expected slope values in species–area studies. *American Naturalist*, **122**, 789–796.
- Durrett, R. & Levin, S. (1996) Spatial models for species–area curves. *Journal of Theoretical Biology*, **179**, 119–127.
- Fisher, R.A., Corbet, A.S. & Williams, C.B. (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology*, **12**, 42–58.
- Flather, C.H. (1996) Fitting species–accumulation functions and assessing regional land use impacts on avian diversity. *Journal of Biogeography*, **23**, 155–168.
- Gleason, H.A. (1922) On the relation between species and area. *Ecology*, **3**, 158–162.
- Gleason, H.A. (1925) Species and area. *Ecology*, **6**, 66–74.
- Gurd, D.B., Nudds, T.D. & Rivard, D.H. (2001) Conservation of mammals in eastern North American wildlife reserves: how small is too small? *Conservation Biology*, **15**, 1355–1363.
- He, F., Legendre, P. & LaFrankie, V. (1996) Spatial patterns of diversity in a tropical rain forest of Malaysia. *Journal of Biogeography*, **23**, 57–74.
- Hill, A.V. (1913) The combinations of haemoglobin with oxygen and with carbon monoxide. I. *Biochemical Journal*, **7**, 471–480.
- Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T. & Tosi, J.A. (1971) *Forest environments in tropical life zones*. Pergamon Press, Oxford.
- Hopkins, B. (1955) The species–area relations of plant communities. *Journal of Ecology*, **43**, 409–426.
- Legendre, P. & He, F. (1996) On species–area relations. *American Naturalist*, **148**, 719–737.
- Leitner, W.A. & Rosenzweig, M.L. (1997) Nested species–area curves and stochastic sampling: a new theory. *Oikos*, **79**, 503–512.
- Lomolino, M.V. (1989) Interpretations and comparisons of constants in the species–area relationships: an additional caution. *American Naturalist*, **133**, 277–280.
- Lomolino, M.V. (2000a) Ecology's most general, yet protean pattern: the species–area relationship. *Journal of Biogeography*, **27**, 17–26.
- Lomolino, M.V. (2000b) A species-based theory of insular zoogeography. *Global Ecology and Biogeography Letters*, **9**, 39–58.
- Lomolino, M.V. (2001) The species–area relationship: new challenges for an old pattern. *Progress in Physical Geography*, **25**, 1–21.
- Lomolino, M.V. (2002) '... there are areas too small, and areas too large to show clear diversity patterns...' R. H. MacArthur (1972: 191). *Journal of Biogeography*, **29**, 555–557.
- MacArthur, R. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Matter, S.F., Hanski, I. & Gyllenberg, M. (2002) A test of a metapopulation model of the species–area relationship. *Journal of Biogeography*, **29**, 977–983.
- May, R.M. (1975) Patterns of species abundance and diversity. *Ecology and evolution of communities* (eds M.L. Cody and J.M. Diamond), pp. 81–120. Belknap Harvard University, Cambridge.
- Michaelis, L. & Menten, M.L. (1913) Die Kinetik der Invertinwirkung. *Biochemische Zeitschrift*, **49**, 333–369.
- Mielke, P.W.J. & Johnson, E.S. (1974) Some generalized distributions of the second kind having desirable application features in hydrology and meteorology. *Water Resources Research*, **10**, 223–226.
- Miller, J.R. & Cale, P. (2000) Behavioral mechanisms and habitat use by birds in a fragmented agricultural landscape. *Ecological Applications*, **10**, 1732–1748.
- Miller, R.I. & Wiegert, R.G. (1989) Documenting completeness, species–area relations, and the species–abundance distribution of a regional flora. *Ecology*, **70**, 16–22.
- Monod, J. (1950) La technique de culture continue, théorie et applications. *Annales de l'Institut Pasteur*, **79**, 390–410.
- Morgan, P.H., Mercer, L.P. & Flodin N.W. (1975) General model for nutritional responses of higher organisms. *Proceedings of the National Academy of Science, USA*, **72**, 4327–4331.
- Morrison, L.W. (1997) The insular biogeography of small Bahamian cays. *Journal of Ecology*, **85**, 441–454.
- Natuhara, Y. & Imai, C. (1999) Prediction of species richness of breeding birds by landscape-level factors of urban wood in Osaka Prefecture, Japan. *Biodiversity and Conservation*, **8**, 239–253.
- Ney-Nifle, M. & Mangel, M. (1999) Species–area curves based on geographic range and occupancy. *Journal of Theoretical Biology*, **196**, 327–342.
- Nupp, T.E. & Swihart, R.K. (2000) Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy*, **81**, 512–526.
- Palmer, M.W. & White, P.S. (1994) Scale dependence and the species–area relationship. *American Naturalist*, **144**, 717–740.
- Plotkin, J.B., Potts, M.D., Leslie, N., Manokaran, N., LaFrankie, J. & Ashton, P.S. (2000) Species–area curves, spatial

- aggregation, and habitat specialization in tropical forests. *Journal of Theoretical Biology*, **207**, 81–99.
- Preston, F.W. (1960) Time and space and the variation of species. *Ecology*, **41**, 611–627.
- Preston, F.W. (1962a) The canonical distribution of commonness and rarity: Part II. *Ecology*, **43**, 410–432.
- Preston, F.W. (1962b) The canonical distribution of commonness and rarity: Part I. *Ecology*, **43**, 185–215.
- Rørslett, B. (1991) Principal determinants of aquatic macrophyte richness in northern European lakes. *Aquatic Botany*, **39**, 173–193.
- Ratkowsky, D.A. (1983) *Nonlinear regression modelling: a unified approach*. Marcel Dekker, New York.
- Ratkowsky, D.A. (1990) *Handbook of nonlinear regression models*. Marcel Dekker, New York.
- Reid, D. (1978) The effects of frequency of defoliation on the yield response of a perennial ryegrass sward to a wide range of nitrogen application rates. *Journal of Agricultural Science*, **90**, 447–457.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Rosenzweig, M.L. & Ziv, Y. (1999) The echo pattern of species diversity: pattern and processes. *Ecography*, **22**, 614–628.
- Schoener, T.W. (1976) The species–area relations within archipelagoes: models and evidence from island land birds. *Proceedings of the XVI International Ornithological Congress*, pp. 629–642.
- Schoener, T.W. & Adler, G.H. (1991) Greater resolving of distributional complementarities by controlling for habitat affinities: a study with bahamian lizards and birds. *American Naturalist*, **137**, 669–692.
- Sorberon, J.M. & Llorente, J.B. (1993) The use of species accumulation functions for the prediction of species richness. *Conservation Biology*, **7**, 480–488.
- Sugihara, G. (1981) $S = CAz$, $z = 1/4$: a reply to Connor and McCoy. *American Naturalist*, **117**, 790–793.
- Veech, J.A. (2000) Choice of species–area function affects identification of hotspots. *Conservation Biology*, **14**, 140–147.
- Vestal, A.G. (1949) Minimum areas for different vegetation: their determination from species–area curves. *University of Illinois Biological Monographs*, **20**, 1–70.
- Weibull, W. (1951) A statistical distribution function of wide applicability. *Journal of Applied Mathematics*, **18**, 293–296.
- Williams, C.B. (1964) *Patterns in the balance of nature*. Academic Press, London.
- Williams, M.R. (1995) An extreme-value function model of the species incidence and species–area relations. *Ecology*, **76**, 2607–2616.
- Williams, M.R. (1996) Species–area curves: the need to include zeroes. *Global Ecology and Biogeography Letters*, **5**, 91–93.
- Williamson, M. (1981) *Island populations*. Oxford University Press, Oxford.
- Williamson, M., Gaston, K.J. & Lonsdale, W.M. (2001) The species–area relationship does not have an asymptote! *Journal of Biogeography*, **28**, 827–830.
- Yang, R.C., Kozak, A. & Smith, J.H.G. (1978) The potential of Weibull-type functions as flexible growth curves. *Canadian Journal of Forest Research*, **8**, 424–431.

BIOSKETCH

Even Tjørve is Associate Professor at Lillehammer University College. His research interests are in biogeography, landscape ecology and macroecology with emphasis on the effect of spatial patterns on species diversity and abundance. Other interests include bird migration and landscape history. He is currently working with theoretical models on species diversity in multi-habitat environments, based on species–area curves. He is also currently involved in the writing of the Norwegian Bird Banding Atlas (*Norsk ringmerkingsatlas*), which will be published in two volumes.