

1 **TITLE PAGE.**

2

3 **Title.** Revisiting sigmoid functions in macro-ecology: mathematical definition and associated
4 ecological properties.

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16 **Abstract.**

17 Introduction: Defining mathematical terms and objects is a constant issue in ecology; often
18 definitions are absent, erroneous or imprecise.

19 Lack of a clear definition: Through a bibliographic review, we show that this problem appears in
20 macro-ecology (biogeography and community ecology) where the lack of definition for the
21 sigmoid class of functions results in difficulties of interpretation and communication.

22 Proposal of a clear definition: In order to solve this problem and to help harmonize papers that use
23 sigmoid functions in ecology, herein we propose a comprehensive definition of these mathematical
24 objects. In addition, to facilitate their use, we classified the functions often used in the ecological
25 literature, specifying the constraints on the parameters for the function to be defined and the curve
26 shape to be sigmoidal.

27 Ecological justifications: Finally, we interpreted the different properties of the functions induced
28 by the definition through ecological considerations in order to support and explain the interest of
29 such functions in macro-ecology.

30 **Keywords.** Biogeography; Nonlinear relationships; Curve shape; Species-area relationship;
31 Species-resource relationship

32

33 **MAIN TEXT.**

34

35 **1. Introduction**

36 Using well-defined and uniform terms is a key point in science. Yet, one of the main criticisms
37 that can be made in the science of ecology is the poor definition of terms and concepts or
38 inconstant use within its community (Herrando-Pérez, Brook, & Bradshaw, 2017; Pickett,
39 Kolasa, & Jones, 2007). Many concepts do not yet have a consensual definition, and
40 communication is therefore difficult. Furthermore, loosely defined concepts can cause not only
41 an unstable expression of a scientific concept, but can also result in inconsistencies within the
42 concept itself (e.g. Gosselin 2001). This is why many articles have tried to highlight this problem
43 and to establish precise definitions - i.e. “ecological niche” (Araújo & Guisan, 2006) or
44 “ecological function” (Jax, 2005). However, the problem is not restricted to ecological concepts;
45 it also concerns ecological domains (i.e. “ecological engineering”, cf. Gosselin, 2008) or certain
46 terms and concepts used in ecology and borrowed from other sciences. This is the case for
47 mathematical terms as, for example, the notions of extinction or demographic stochasticity
48 (clarified in Gosselin, 1997 or Lebreton, Gosselin, & Niel, 2007). Reflections on mathematical
49 definitions make it possible to conceptualize possibilities not yet foreseen (e.g. the importance of
50 dependence between individuals within demographic stochasticity or uncertainty in McCarthy,
51 Franklin, & Burgman, 1994). In the present paper, we deal with the term "sigmoid" and propose a
52 definition to overcome imprecision problems. Hereafter, we will call “sigmoid” the curve shape
53 that can be represented by different functions, and the “sigmoid class of functions”, the class that
54 contains these functions.

55 Ecologists often study relationships between two ecological variables (e.g. a biodiversity metric
56 as a function of an environmental variable/predictor). Although, the most often considered form
57 of these relationships is linear, nonlinear forms have also been used (power, exponential etc.),
58 including sigmoidal forms. In ecology, sigmoidal relationships are generally implicitly used in
59 binomial regressions. However, in the field of macro-ecology and, in particular, in the study of
60 species-area relationships (SARs), explicit sigmoidal forms occur fairly often. Indeed, a
61 sigmoidal shape is very likely to emerge when species richness is related to the area in which the
62 species were sampled (Preston, 1962). Many sigmoidal functions have been developed and used
63 in a SAR context; however, they can also be applied to the study of relationships between
64 biodiversity and a resource gradient other than available habitat area (species-resource
65 relationships, or SReRs). Furthermore, the sigmoidal form of a relationship may prove useful for
66 decision-making in forest or conservation management. Indeed, certain characteristics of the
67 curve can provide management targets like the inflection point or the upper asymptote (Ranius &
68 Jonsson, 2007).

69 In recent years, numerous articles have been published which review the use of nonlinear
70 functions, including sigmoids, in the field of biogeography and especially for SAR-type
71 relationships (Dengler, 2009; Tjørve, 2003, 2009; Williams, Lamont, & Henstridge, 2009).
72 Unfortunately, no clear definition of the term sigmoid was provided in these publications.

73 Despite the frequent use of sigmoidal functions, in most cases, there is no proper, accessible
74 definition of what exactly is meant by a “sigmoidal” shape. Classically defined as an S-shape, the
75 sigmoid may seem clear and that is the reason why it is so rarely defined. Yet, the precise
76 characteristics of these curves are not formalized or made explicit. This absence of a clear
77 definition results in a lack of harmonization between papers in ecology, and inconsistencies

78 between articles, or even within one and the same article can ensue. For example, although most
79 definitions include the presence of an upper asymptote (e.g. Tjørve, 2003; Veech, 2000),
80 Mashayekhi, MacPherson, & Gras (2014) define one of their functions (Persistence2) as
81 sigmoidal though it does not have an upper asymptote; this contradicts the general idea of a
82 sigmoid. There is therefore a need to more explicitly define the sigmoidal class of shapes.

83 Our first goal is to assess the use of the term sigmoid in biogeography studies and highlight the
84 lack of a clear definition. Then, we propose a definition of the term so that its use in the literature
85 is harmonized and no longer confusing. Finally, we justify the definition in relation with
86 ecological theory and we highlight the implications and advantages of this new definition. The
87 two underlying questions are: what characteristics should sigmoid curves exhibit? What functions
88 can be included in the sigmoid class?

89

90 **2. An obvious lack of a clear definition**

91 The word “sigmoid”, composed of “sigma” and “eidos” (*sigmoeidēs* in ancient Greek), means
92 something that has the form of the capital letter sigma (Σ). The term sigmoid is more generally
93 defined as an S-shaped curve. Yet these descriptions, in addition to being vague, are not accurate
94 since the form of an S (or a Σ) is impossible in mathematical curves described by functions. In
95 fact, if we apply an S form to mathematical curves, we notice that we obtain two or three values
96 of $f(x)$ for one x , which is impossible according to the very definition of a function. Moreover,
97 the representation of an S-shaped curve excludes forms that should logically be part of sigmoid
98 curves such as decreasing sigmoid curves.

99 Given this intrinsic difficulty with the notion of sigmoid, we investigated how authors in ecology
100 have used and define this term. We selected an ecological domain where sigmoid functions are
101 often explicitly used to describe relationships: biogeography with species-area relationships
102 (conventionally abbreviated as SARs) and species response to ecological gradients within
103 species-resource relationships (abbreviated here as SReRs).

104 In June 2017, we searched articles accessible via Scopus for a combination of keywords related
105 to sigmoid curves and to the above-mentioned domains of ecology. In some papers, the term
106 sigmoid is not mentioned even if sigmoidal functions are used. Our sigmoid keywords therefore
107 covered a wide range of meanings: we searched for “sigmoid” OR “nonlinear” OR “logistic”. We
108 combined these keywords with other keywords related to the targeted ecological aspect: “SAR”
109 OR “species-area” OR “species-resource” or “biogeography”.

110 Among the search results, we selected the papers where, according to the title and the abstract,
111 the authors either used sigmoid functions or were interested in a sigmoidal form of relationship.

112 The 36 selected papers (see Appendix S1 in Supporting Information for references) were sorted
113 according to the three possibilities: (i) papers that did not use a sigmoid family term; (ii) papers
114 that used a sigmoid family term but did not define it; and (iii) papers that either entirely or partly
115 defined the sigmoid.

116 As Table S1.1 (see Appendix S1 in Supporting Information) shows, sometimes authors use
117 sigmoidal function without ever specifically referring to the sigmoid family (13.9 %), but this
118 number may be underestimated due to the difficulty of finding such papers. Most of the time, the
119 authors use a word from the sigmoid family to define their functions (“sigmoid” or “sigmoidal”),
120 but they do not define what they mean by these terms (72.2 %). What is quite surprising is that

121 some authors create new sigmoid functions and state that their functions have a sigmoidal form,
122 but they never evoke the characteristics implied by this form and included in their function (e.g.
123 Kobayashi, 1976).

124 Finally, only a few authors take the time to define a sigmoid (13.9%), but typically the definition
125 is fragmented or the functions imprecisely characterized, thus giving the impression of an
126 incomplete definition. Sometimes definitions can even be confusing or contradictory.

127 Preston (1962) proposed a descriptive definition of the shape of the sigmoid curve, which gives
128 us an idea of the form but without specifying its properties: “it began at a low slope, steepened
129 considerably, and then became less steep”.

130 Tjørve (2003; 2009) does not give a complete definition of the sigmoid curve, but does mention
131 some of its characteristics when describing the functions he considers in his study. In Tjørve’s
132 papers (2003; 2009), the characteristics common to all sigmoid functions include: (i) the presence
133 of an upper asymptote; (ii) a lower j-shape (probably implying a lower asymptote); and (iii) the
134 presence of an inflection point. Tjørve (2003; 2009) also mentions two characteristics which vary
135 among different sigmoid functions: symmetry around the inflection point, which may or may not
136 exist; and the positions of the inflection point and of the asymptote.

137 Furthermore, in addition to being incomplete, these "definitions" may present other problems that
138 impede understanding. This is the case when mathematical terms characterizing a mathematical
139 object, here the sigmoid curve, are incorrectly used. For example, some authors erroneously
140 define their sigmoid functions as “convex” (e.g. Gentile & Argano, 2005; Tjørve, 2003, 2009).
141 Indeed, in mathematics, a curve/function is “convex” if, for any two points A and B of the curve,
142 the segment [AB] is entirely situated above the curve. Conversely, a concave function is the

143 opposite of a convex function (f is concave if and only if $-f$ is convex). A concave curve is
144 therefore a curve for which, for any two points A and B of the curve, the segment [AB] lies
145 entirely below the curve. Yet, some studies make no distinction between the two curves and use
146 “convex” for both convex and concave forms (Tjørve 2012), then distinguish them with the
147 mentions “downward” or “upward”. Usually, given the properties attributed to the curves defined
148 as convex, the term concave, rather than convex, is clearly the correct term. For example, what
149 Tjørve (2009) described as a "constantly decelerating" convex curve is actually concave, and
150 what he defined as a "J-shape" would correspond to the convex part of the sigmoid curve. This
151 error is common since convex and concave shapes are often respectively described as a hump and
152 a hollow (from the definition of a convex set), which can lead to confusion. Therefore, though the
153 study is very interesting, the discourse is blurred by terms that are confusing (as also pointed out
154 by Dengler, 2009). Consequently, we suggest using mathematical definitions and terms, so that
155 all researchers will refer to the same definition of sigmoid curves.

156 If one moves away from the literature in ecology, we find that few definitions are easily
157 accessible even in statistical literature. Hill and Lewicki (2006) propose one such definition in
158 their glossary: a sigmoid function is “an S-shape curve, with a near-linear central response and
159 saturating limits” (p724). This definition, which includes the notion of an S-shape discussed
160 above, make it possible to understand the general shape and to accept different forms, but they
161 are not necessarily very clear on which forms are included or excluded when we speak of a
162 sigmoid, and the properties of the functions are not precise. Menon, Mehrotra, Mohan, & Ranka
163 (1996) also start by defining the sigmoid curves as S-shaped; then the authors define two sub-
164 classes of sigmoids: (i) simple sigmoids are “odd, asymptotically bounded, completely monotone
165 functions in one variable”; and (ii) hyperbolic sigmoids are “a proper subset of simple sigmoids

166 and a natural generalization of the hyperbolic tangent”. Although detailed, notably when
167 characterizing certain functions, they seem to have forgotten to mention the monotonic character
168 that such a function should have. Moreover, the two defined classes do not integrate all the
169 possible sigmoidal forms; for example, “odd” excludes asymmetric curves and curves that do not
170 intersect the origin. Finally, concerning definitions easily accessible to the general public,
171 dictionaries are not of much better help since, for example, the French dictionary *Le Petit Robert*
172 defines a sigmoid as a "sinuous curve with two waves of growth separated by a point of
173 inflection" (translated from French), a very confusing definition (“Le Petit Robert : Sigmoide,”
174 2017).

175 To sum up, very few definitions of sigmoid functions are available in the ecological literature,
176 and they are usually vague, or based on only certain characteristics, or can even contain errors.
177 Therefore, it seems clear that the lack of a time-honored definition, or the use of unstable
178 definitions, can lead to difficulties in producing studies and articles. This is particularly true for
179 bibliographic research and for young researchers and students (PhD or Masters students) who are
180 still forging their knowledge (Herrando-Pérez et al., 2017). It can also sometimes distort
181 communication among collaborators. For example, within our own research group, differences of
182 wording regarding the properties of different curves have surfaced, with misunderstandings of
183 what is meant by “convex” and “concave”.

184

185 **3. Proposal of a clear definition**

186 Although the definition on Wikipedia is globally correct (“Wikipedia - Sigmoid function” n.d.),
187 this website cannot be used as a reference since the page can be modified at any time, making the
188 definition unstable. We have therefore decided to propose a definition, which is stable,

189 understandable for ecologists, and as complete as possible (including as many cases as possible)
190 in this paper. For this purpose, we first looked at the characteristics of the functions used in the
191 literature (cf. Table 1).

192 Ultimately, a sigmoid curve is a curve described by a real-valued, univariate function (a function
193 f of a unique real-valued variable x that takes real values $y=f(x)$), defined over the whole set of
194 real numbers, and which is continuous, infinitely differentiable, monotonic (always either
195 increases or decreases), has at least one inflection point and is bounded on the Y-axis. The term
196 “inflection point” refers to the point where the curve shifts in convexity: from convex to concave
197 or vice versa. The change in slope is continuous and should therefore be distinguished from the
198 term “breakpoint” used by ecologists, which, although we did not find a precise mathematical
199 definition, seems to refer to a non-continuous function (e.g. in change point models, Muggeo,
200 2003; Quandt, 1958).

201 Its inherent features imply that the sigmoid curve: (i) has an upper and a lower asymptote if (x)
202 varies over the set of real numbers; (ii) can increase (starting with the lower asymptote and
203 finishing with the upper asymptote, with a positive slope between them) or decrease (starting
204 with the upper asymptote and finishing with the lower asymptote, with a negative slope between
205 them, Fig. 1.b); and (iii) can be symmetrical or not around the inflection point or points (Fig. 1.c).

206 We extend the definition given above to two other cases where the explanatory variable (x) is
207 defined on the set of real positive numbers ($x \geq 0$) and: (i) $f(x)$ is a function of (x) over the entire
208 set of real numbers and has a sigmoid curve; or (ii) the above definition for the sigmoid curve
209 applies to $f(x)$ as a function of ($x \geq 0$) except for the requirement that $f(x)$ defined over the entire
210 set of real numbers. Indeed, in island biogeography, the function never occurs with negative x -
211 values (since area cannot be negative). In this case, the sigmoid curve has only one of the two

212 asymptotes. Even after extension, however, our definition does not include the case where x is
213 bounded on both sides and therefore possesses neither of the two asymptotes (see He &
214 Legendre, 2002). Note that $f(x)$ as a function of x can have a sigmoidal form without $f(x)$ as a
215 function of $\log(x)$ or $f(\exp(x))$ as a function of x being true, and vice versa.

216 The class of sigmoid functions includes the functions which, for the given parameters, meet the
217 above definition. The same function may or may not belong to the sigmoid class depending on
218 the value of its parameters. To return to a previous example, the Chapman-Richards function
219 belongs to the sigmoid class if $c > 1$. For other values of c , the function does not belong to the
220 sigmoid class.

221 The sigmoid class can be divided into two sub-classes: (i) simple sigmoids, containing the
222 functions that give curve shapes with a single inflection point, and (ii) multiple sigmoids
223 containing functions that give curve shapes with several inflection points (i.e. a double sigmoid
224 could fit the phenomenon described in Figure 6 in Lomolino, 2000). There must always be an
225 odd number of inflection points in order to keep the two asymptotes on the Y-axis.

226 Based on the definition of the sigmoid class that we propose above, we inventoried the classical
227 SAR or SReR functions selected from the review we conducted that belong to the simple sigmoid
228 class, at least for some parameter values (cf. Table 1). We also described their characteristics,
229 placing special emphasis on the constraints imposed on the parameter values or explanatory
230 variable to ensure that the function is mathematically defined, is suitable in macro-ecology and
231 does indeed have a sigmoidal form. We also provide the coordinates of the inflexion point, so
232 that readers can distinguish between functions that are sigmoidal only when the whole set of real
233 values for the explanatory variable is considered (i.e. functions with a negative abscissa value of
234 the inflexion point) and those that are sigmoidal even when the abscissa values are positive.

235

236 Another class of functions that is close to the sigmoid class is the class of inverse sigmoid
237 functions. These are bounded on the X-axis and do not have an asymptote over the Y-axis (Fig.
238 1.d). These functions have no biological reality in SReR and SAR and are not members of the
239 sigmoid class as we define it. Other curves defined as sigmoid by some authors do not meet the
240 requirements of our definition either, for example, “sigmoid curves [...] free of upper
241 asymptotes” (Tjørve, 2012).

242

243

244 *Table 1: Some characteristics of sigmoidal functions present in the SAR and SReR literature (see Appendix S1 in Supporting*
 245 *Information for references).*

	Formula	Constraints on parameters to be defined and relevant to macro-ecology	Further constraints required to be in the sigmoid class	Inflection point	Symmetry around the inflexion point	Lower asymptote	Intersects origin	Direction of the relationship
Common logistic	$f(x) = a/(1 + \exp(-b*x + c))$	$a > 0$	/	$x = c/b$ $y = a/2$ In other terms $y = 50\%$ of the upper asymptote	Point symmetry	Zero	No	Increasing (if $b > 0$) or decreasing (if $b < 0$)
Gompertz	$f(x) = a*\exp(-\exp(-b*x+c))$	$a > 0$	/	$x = c/b$ $y = \exp(-1)*a$ In other terms $y = 36.8\%$ of the upper asymptote	Asymmetric	Zero	No	Increasing (if $b > 0$) or decreasing (if $b < 0$)
Extreme value	$f(x) = a*(1 - \exp(-\exp(b*x+c)))$	$a > 0$	/	$x = -c/b$ $y = [1 - \exp(-1)]*a$ In other terms $y = 63.2\%$ of the upper asymptote	Asymmetric	Zero	No	Increasing (if $b > 0$) or decreasing (if $b < 0$)
Champan-Richards	$f(x) = a*(1 - \exp(-b*x))^c$	$a > 0, x \geq 0, c > 0, b > 0$	$c > 1$	$x = \log(c)/b$ $y = a*(1 - 1/c)^c$	Asymmetric	/ (irrelevant since x is non-negative)	Yes	Only increasing

Cumulative Weibull distribution	$f(x) = a*(1-\exp(-b*(x^c)))$	$a>0, b>0, x \geq 0$	$c<0$ or $c>1$	$x=((c-1)/(b*c))^{1/c}$ $y=a*(1-\exp(-1+1/c))$	Asymmetric	/ (irrelevant since x is non-negative)	Yes (if $c>0$)	Increasing (if $c>0$) or decreasing (if $c<0$)
Morgan-Mercer-Flodin (MMF)	$f(x) = a*(x^c)/(b+(x^c))$	$a>0, b>0, x \geq 0$ (with $f(0)=a$ if $c<0$ to be continuous)	$c>1$ or $c<(-1)$	$x=((c-1)*b/(c+1))^{1/c}$ $y=a*(1/2-1/(2*c))$	Asymmetric	/ (irrelevant since x is non-negative)	Yes	Increasing (if $c>0$) or decreasing (if $c<0$)
Cumulative beta-P distribution	$f(x) = a*(1-(1+(x/c)^d)^{-b})$	$a>0, x \geq 0, c>0, b>0$	$d>1$ or $d<(-1/b)$	$x=c*((-d+1)/(-b*d-1))^{1/d}$ $y=a*(1-(1+(-d+1)/(-b*d-1))^{-b})$	Asymmetric	/ (irrelevant since x is non-negative)	Yes (if increasing, $d>0$)	Increasing (if $d>0$) or decreasing (if $d<0$)

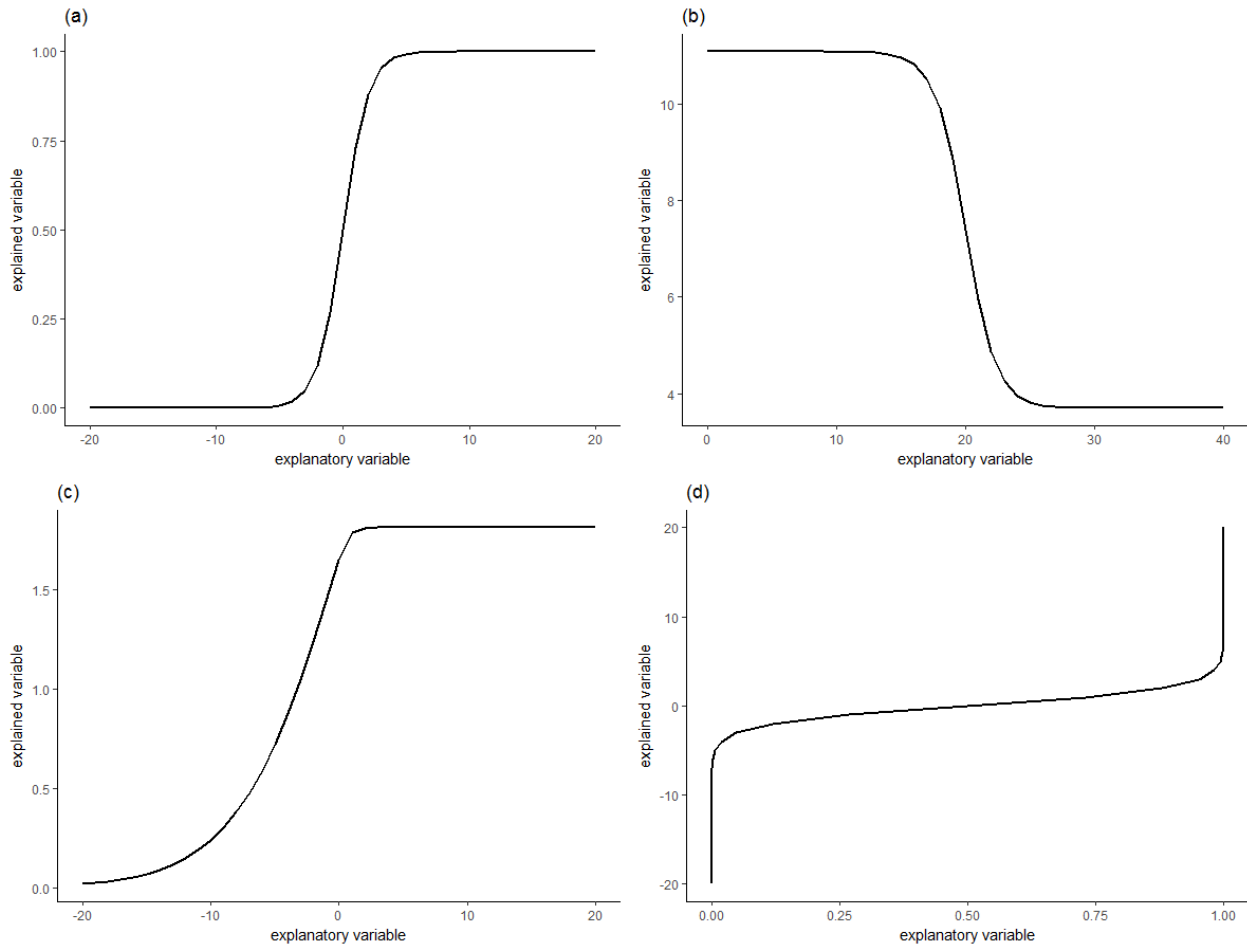
246 *Note that models II and III in Huisman, Olf & Fresco (1993), denoted as $f(x)=M*(1/(1+\exp(a+b*x)))$ and*
247 *$f(x)=M*(1/(1+\exp(a+b*x)))*(1/(1+\exp(c)))$, are particular cases of the Common Logistic Function with, respectively, parameter (a)*
248 *not estimated, and with parameter (a) estimated but with a given maximum value. The Archibald Logistic Function, denoted as*
249 *$f(x)=a/(b+c^x)$, is equivalent to the Common Logistic Function with (b), (c) and (a) in the Common Logistic Function, respectively*
250 *equal to $(-\log(c))$, $(-\log(b))$, (a/b) in the Archibald Logistic Function. The He-Legendre Function, denoted as $f(x)=a/(b+(x^{-c}))$, is*
251 *equivalent to the Morgan-Mercer-Flodin Function with (a) and (b) of the MMF respectively equal to (a/b) and $(1/b)$ in the He-*
252 *Legendre Function. The type III Holling function, denoted as $f(x)=ax^2/(b^2 + x^2)$, is equivalent to the MMF, with (c) and (b) in the MMF*
253 *respectively equal to (2) and (b^2) in the Holling III Function.*

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255

256 *Figure 1: Some possible forms of sigmoids and inverse sigmoids. (a) Simple logistic function, (b)*
257 *decreasing sigmoid, (c) asymmetric increasing sigmoid, and (d) increasing inverse sigmoid.*

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262 **4. Ecological justifications and implications of sigmoid curve characteristics**

263 Although some characteristics of the sigmoid definition are justified mainly by mathematical

264 considerations, many can be related to ecological hypotheses or considerations. First, the

265 presence of an inflection point can be related to the following statement by Lomolino (2000)
266 when he describes the phenomenon underlying the use of sigmoid curves in SARs: “with richness
267 remaining relatively low and apparently independent of area for the smaller islands, increasing
268 rapidly to rise through an inflection point for islands of intermediate size, and then asymptotically
269 approaching, or leveling off at the richness of the species pool for the largest islands”. Of course,
270 many other fields of ecology are interested in models that can depict such phenomena (e.g.
271 ecophysiology; Paine et al., 2012). Another field where sigmoid curves could be useful is the
272 field of ecosystem functioning-biodiversity relationships, where curves adopting such patterns
273 seem frequent (Cardinale et al., 2012). The continuity and differentiability of the curve are related
274 to the existence of an inflection point, and allow us to clearly relate the curve to a mathematical
275 function, that is, to speak of the convexity or concavity of the curve. Continuity and
276 differentiability also allow us to formulate hypotheses not only on the mean value of the response
277 variable, but also on the speed (first derivative) or acceleration (second derivative) of the
278 relationship between the response variable and the gradient being studied.

279 The pattern depicted by Lomolino for SARs might have led us to define sigmoid curves only as
280 increasing curves. Yet we expect that in some areas of ecology, the reversed situation might
281 occur and that such patterns would indeed fall into the domain of the sigmoid curve. For
282 example, a decreasing sigmoid was considered in species-isolation relationships by Hachich et al.
283 (2015). More generally in ecology, the decreasing sigmoidal curve can be used in the case where
284 the gradient studied has a negative effect on the response variable (e.g. Morante-Filho, Faria,
285 Mariano-Neto, & Rhodes, 2015).

286 Second, the existence of asymptotes is also very much related to considerations from ecology.
287 The upper asymptote, implying a threshold above which the mean of the response variable (y)

288 cannot go, theoretically reflects the Liebig law of the minimum in ecophysiology and ecology
289 (Austin, 2007; Paris, 1992). In this case, the limiting factor would first be the predictor studied,
290 and an increase in this limiting factor would lead to an increase in the explained variable. Then,
291 upon reaching the asymptote, the predictor would not be limiting anymore but rather another,
292 unmeasured, environmental factor would be involved, which prevents the explained variable
293 from increasing any further. Inversely, the presence of a lower asymptote implies that the mean
294 of the response variable cannot be lower than this asymptote. The existence of such an asymptote
295 can often be related to the conjunction of the monotonic relationship and of the nature of the
296 variable itself: when the variable is non-negative, the values of the mean cannot be below zero. In
297 studies focusing on the response of a single species, the lower asymptote is therefore usually zero
298 (e.g. Huisman et al., 1993). However, when studying community response, often a lack of a
299 resources does not necessarily imply a total loss of species richness (for example, when species
300 are mobile). In such cases, a logistic function where $f(x)$ is a function of $\log(x)$, whose lower
301 asymptote is located at zero ($y = 0$), is not actually adapted (Godeau et al. In Prep.).

302 The third component of our definition is asymmetry of the curve. Symmetric sigmoid curves, like
303 the logistic function, are widely used, but more for their ease of modelling than for their
304 underlying ecological theory. Indeed, for bell-shaped curves, Austin (1976) stated: “there is no a
305 priori reason to assume that organisms' responses should follow such a symmetrical curve”.

306 Different phenomena can explain asymmetrical curves (Austin 1990 and Austin & Gaywood
307 1994 for phyto-ecology) and theoretically supported asymmetry can also appear with sigmoidal
308 curves (plants with differing initial and final rates of injury in response to temperature stress; c.f.
309 Lim, Arora, & Townsend, 1998).

310

311 Having clear definitions makes it possible to more clearly reflect on the underlying concepts and
312 theories implied by the functions available, and to visualize the most appropriate form of curve to
313 adopt according to the ecological context. After defining and reflecting on the lower asymptote
314 and asymmetry, the researcher naturally questions the choice of link function in the context of
315 binomial logistic regressions. Classically, users of such tools choose canonical link functions
316 such as the logit or the probit function. These two functions belong to the sigmoid class but they
317 are symmetric around the inflection point and they have pre-specified minimum and maximum
318 asymptotes (respectively 0.0 and 1.0). However, the inherent properties of such link functions
319 could have strong ecological limitations, which would restrict their use in some cases. For
320 example, having a maximum of 1.0 (meaning almost sure presence) along the gradient does not
321 reflect biological situations where, even if local habitat conditions are optimal for the organism,
322 the organism could be absent (e.g. due to dispersal limitation inside a metapopulation; Hanski &
323 Gilpin, 1997). Along the same lines, sigmoid and logistic functions are sometimes confused with
324 each other, whereas the latter is nothing more than a particular type of sigmoid (e.g. Hunsicker et
325 al., 2015). Such confusion may prevent researchers from considering other families of functions
326 that fall into the sigmoid class without being logistic.

327 More generally, the shape of the curve must be well integrated in order to properly interpret the
328 results. As put forward by Fattorini, Maurizi, & Giulio (2012), Medellín & Soberón (1999) used
329 a sigmoid model on their data, and then, in order to ensure fit with a logarithmic model, they
330 chose to exclude some of the data corresponding to the first part of the sigmoid curve (where the
331 slope is smaller). Fattorini, Maurizi, & Giulio (2012) point out that Medellín & Soberón (1999)
332 should not have manipulated the data and should have retained a model that fit the entire dataset,
333 the data represented by the first part of the curve being just as important from an ecological point

334 of view as the data represented by the rest of the curve. In fact, the first part of the curve could
335 reflect various ecological mechanisms that deserve to be studied such as – to name but two –
336 sampling problems or biological functions in action (i.e. limiting factors, exclusions, etc.).
337 Through this example, it becomes obvious that, if the sigmoid curve shape and its implications
338 are not acknowledged or defined well enough in the mind of the ecologist, he or she may end up
339 missing important patterns or making wrong assumptions.

340

341 Having a well-established definition of the sigmoid curve and understanding the constraints
342 imposed on the parameter values of the functions which produce sigmoid curves allow us to
343 better apprehend under which conditions a sigmoid function is adapted when one wishes to apply
344 it to a dataset. For example, in the case of the Chapman-Richards function, the curve obtained
345 will be of sigmoid shape only when ($c > 1$). For values of (c) that do not satisfy this condition, the
346 curve will not be of sigmoid shape. A related issue concerns the constraints imposed on the
347 values of (x), which are most often unstated. To keep the same example, the Chapman-Richards
348 function is not defined for ($x < 0$) (cf. Table 1); the function is therefore not relevant in cases
349 where a sigmoidal form of relationship is applied to a dataset where (x) can be negative (e.g.
350 where (x) is a temperature in degrees Celsius or a single latent resource axis). Another, more
351 extreme, example combines these two limitations: the persistence2 function. In fact, this function
352 is sigmoid only if ($x > 0$), ($b = 0$) and ($c > 0$).

353

354 **5. Conclusion and perspectives**

355 Our literature review points out the lack of a clear, stable, universally accepted definition of the
356 sigmoid class of functions in ecology. Some aspects of sigmoid curves are typically ignored
357 (symmetry, direction of the relation, etc.). We also found cases of misuse of convexity to define a
358 curve or a function.

359 As Jeremy Fox stated “words are imprecise, and so purely verbal models and verbal arguments
360 often are ambiguous or even invalid, even if apparently supported by empirical data (like Elton’s
361 verbal arguments about why diversity and complexity beget stability). Mathematics has the virtue
362 of forcing precise definitions of terms, precise and complete specification of assumptions, and
363 rigorous derivation of conclusions” (Fox, 2011). It is therefore unfortunate to accept vague verbal
364 definitions (such as “S-shape” or “J-shape”) when one is using a term derived from mathematics.

365 That is why we have proposed a definition that we hope will allow for better harmonization of
366 what is meant by the term “sigmoid” when describing a curve or a function. In addition to clearly
367 formulating the concept, our definition allows various functions to be united under the same
368 banner (sigmoid class, presented in Table 1). This definition also excludes some functions that
369 were previously considered to belong to the sigmoid family and which, in our opinion, should not
370 be defined as such (sigmoid without an upper asymptote or inverse-sigmoid).

371 This new definition will quite naturally reveal the lack of some other functional shapes to fully
372 represent the sigmoid class. In a future paper, we aim to develop a sigmoid function that
373 incorporates the characteristics retained in this paper and is applicable to an SReR context. Such
374 development of the sigmoid class might be of more general use in ecology, e.g. by broadening
375 the scope of possibilities in binomial logistic regressions.

376 Finally, we hope that in future papers, authors who define a new sigmoid function, or use an
377 already existing one, will take the time to specify the properties of the function and to clearly
378 mention their implications and/or justifications in ecological terms.

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481

482

483 **SUPPORTING INFORMATION.**

484
 485 *Table SI.1: Papers in the SARs and SReRs domains that use functions with a sigmoidal form or*
 486 *that discuss about sigmoidal relationships, with precision about their use of a term.*

Article reference	Use "sigmoid" or "sigmoidal" word in the article	Define or describe sigmoid
Bolgovics et al. 2016	YES	NO
Boomsma et al. 1987	YES	NO
Burbidge et al. 1996	NO	NO
Connor & McCoy 2001	YES	NO
Dengler 2009	YES	NO
Fattorini 2006a	YES	NO
Fattorini 2006b	YES	NO
Fattorini et al. 2012	YES	NO
Gao et al. 2016	YES	NO
Gentile et al. 2005	YES	NO
Hachich et al. 2015	NO	NO
He & Legendre 1996	NO	NO
He & Legendre 2002	YES	NO
Huisman et al. 1993	NO	NO
Kilburn 1963	YES	NO
Kobayashi 1976	YES	NO

Lomolino 2000a	YES	NO
Mashayekhi et al. 2014	YES	NO
Monteil et al. 2004	YES	NO
Natuhara and Imai 1999	YES	NO
Oksanen & Michin 2002	NO	NO
Panitsa et al. 2006	YES	NO
Preston 1962	YES	YES
Simaiakis et al. 2012	YES	NO
Stiles et al. 2007	YES	PARTLY
Tjørve 2003	YES	YES
Tjørve 2009	YES	YES
Tjørve 2012	YES	NO
Tjørve and Tjørve 2011	YES	NO
Tjørve and Turner 2009	YES	NO
Tjørve et al. 2008	YES	NO
Triantis et al. 2012	YES	NO
Turner & Tjørve 2005	YES	NO
Veech 2000	YES	PARTLY
Williams 1995	YES	NO
Williams et al. 2009	YES	NO
Total number : 36	Number of YES : 31	Number of YES or PARTLY : 5

487 “NO” in the second column is for papers that did not use a sigmoid family term. “YES” in the

488 second column and “NO” in the third is for papers that used a sigmoid family term but did not

489 define. “YES” in the second column and “YES” or “PARTLY” in the third is for papers that either
490 entirely or partly defined the sigmoid.

491

492 Bolgovics, Á. et al., 2016. Species area relationship (SAR) for benthic diatoms: a study on
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