THE ECLIPSE OF SPECIES RANGES

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ABSTRACT

This paper distinguishes four recognisably different geographical processes in principle causing species to die out. One of these processes, the one we dub "range eclipse", holds that one range expands at the expense of another one, thereby usurping it. Channell and Lomolino (2000a, Journal of Biogeography 27: 169–179; 2000b, Nature 403: 84–87; see also Lomolino and Channell, 1995, Journal of Mammalogy 76: 335–347) measured the course of this process in terms of the proportion of the total range remaining in its original centre, thereby essentially assuming a homogeneous distribution of animals over the range. However, part of their measure seems mistaken. By giving a general, analytical formulation of eclipsing ranges, we estimate the exact course of this process. Also, our formulation does not partition a range into two spatially equal parts, its core and its edge, but it assumes continuity. For applying this model to data on the time evolution of species, individual time series should be available for each of them. For practical purposes we give an alternative way of plotting and interpreting such time series. Our approach, being more sensitive than Channell and Lomolino's, gives a less optimistic indication of range eclipses than theirs once these have started.

Key Words: range, biogeography, conservation, extinction

1. INTRODUCTION

Decreases in the extent of geographical species distributions are of main concern to present-day conservation biology, because species are (dynamically) distributed non-homogeneously over their (dynamical) ranges, when responding to ecological conditions. The size of a range is delimited by energetic requirements, by interactions with other organisms or climate, or by other factors (for a more extensive review see Hengeveld, 1990; Rodríguez, 1999; Case *et al.*, 2005). Range limits are, however, only part of the problem. They are extreme values of the general response of the species to varying ecological conditions that determine the density profile over the species' entire range. The dynamics of this profile in an expanding or contracting range are described in Hengeveld and Hemerik (2002) in

terms of an extension of an invasion model formulated previously (Bosch *et al.*, 1990, 1992). Ranges can also be determined by special combinations of ecological factors (Haeck and Hengeveld, 1981) making these either both small, rare and ecologically vulnerable, or large, abundant and more or less stable.

In this paper, we only give analytical solutions to the process according to which the geographical range of a species can contract, where one species over-runs and usurps the range of another, causing the latter to die out completely. Channell and Lomolino (2000a, b) call this process range collapse. However, what they call range collapse is in fact one out of four different processes of decline that can be imagined, resulting either in local or in total extinction. All four processes can be considered demographic decline, but the first two with unequal (a) and with equal vulnerability (b), respectively, in the central and the marginal parts of the range can be induced by overrunning species and climatic changes (Figure 1a, b). The third and fourth processes (Figure 1c, d) are purely demographic and are supposed to happen by predominantly human influences. Of these two, the third process, Figure 1c, concerns the eclipse of one range as caused by the expansion
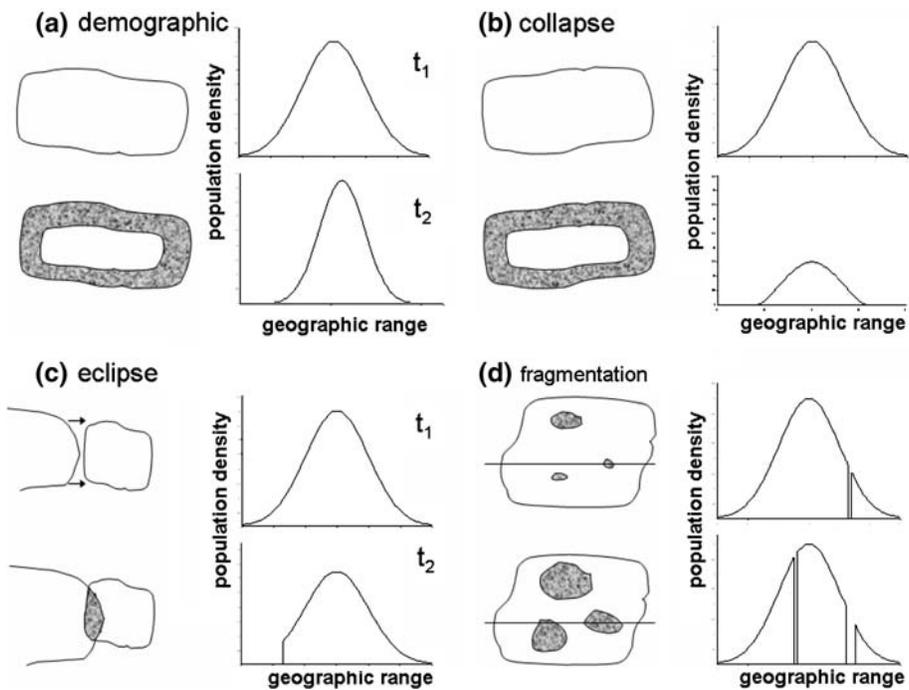
Figure 1. Four possibilities of range decline: (a) demographic decline, (b) range collapse, (c) range eclipse, and (d) fragmentation. In (c), one species invades the area of another one, thereby eventually wiping out the latter (grey shades represent areas already invaded). Each picture on the left shows the area not yet invaded at times t_1 and t_2. The graphs on the right show the effect the invader has on the density profile of the invaded species. The density profile for range fragmentation is the profile at the line transect given in the figures of the area not yet invaded.

of another one, so that the species is from one side of its range wiped out bit by bit. Finally, a fourth type (Figure 1d) concerns a compound process, where one or more spots of demographic destruction grow to all sides, and are located throughout the range; this is known as fragmentation.

Earlier, one of us (RH) distinguished two geographical processes according to which species can decline (Figure 1a, b; see also Haeck and Hengeveld, 1981). Channell and Lomolino (2000a) distinguished demographic extinction from range collapse, without, however, considering the processes (a) and (b) as distinct, as Haeck and Hengeveld (1981) proposed. Also, they considered the process of range collapse to be contagious, which seems confusing. A contagious process, namely, is one in which chain reactions occur, which does not necessarily happen in the invading species. Furthermore, one would especially not expect a chain reaction to happen in the reducing range of the victim species. If a chain reaction would occur, it is only in the expanding species overrunning the range of the eclipsing species. Given Haeck and Hengeveld's (1981) original distinction between Figure 1a, b, and also considering the passive nature of a range getting overrun (Figure 1c), it would be advisable to re-name these three processes. We therefore call the processes in Figure 1b, c *range collapse* and *range eclipse*, respectively. As usual, the process in Figure 1d is called *fragmentation*. Figure 1a still concerns the *demographic decline* from Channell and Lomolino (2000a). In demographic decline, the range becomes smaller, whereas the densities in the core area remain the same; in range collapse, both the range gets smaller and the central densities decline (Rodríguez, (2002) calls this melting away of ranges). In range fragmentation, several areas decline at random across the range, often causing local extinction of the species. Finally, in range eclipse extinction occurs from one part of the margin only, spreading from there homogeneously across the range. Our paper concerns a description of the process of range eclipse only.

The problem of recognising a process from the course of an extinction curve is thus still open. Here, we approach this problem by first modelling presumed processes of decline without assuming contagiousness. Thereafter, we give directions of how to interpret curves based on hypothetical time series of declining ranges. We model range eclipses analytically, deriving formulas for a few different cases, whereby a circular invaded range is either (a) small or (b) large compared to that of the invader (Figure 2a, b, respectively). Thus, mathematically, we consider a linear range front, or a circular one. Using this model, we calculate the invaded part of the eclipsing range, both for unstructured ranges with a spatially uniform density of individuals (homogeneous), as well as for structured ranges, whereby the highest density of individuals is found in the central parts (peaked). We have done this because there still seems to be uncertainty about the validity of the abundant centre hypothesis (see Sagarin and Gaines, 2002). Results are discussed within a practical context.

2. MODELS

Let us first define the problem and then concentrate on two special cases for the calculation of the invaded part of the range. We first calculate the range overlap for the case where the circular invaded range overlaps with that of the invader. More in particular, we derive formulas for the cases where the circular

Table I. Definition of the symbols used in the text

Symbol	Definition
α	Angle BOA = angle BOC, see Figure 2
$d(t)$	|OB|, see Figure 2
$d'(t)$	|O'B|, see Figure 2
h	Density of individuals in the circular invaded range
h_{max}	Maximum height of the cone-shaped and homogeneous density profile
Ω	Size of the invaded area
O	Centre of the area to be invaded
p	Distance between the centres of the invading and invaded circles (O' and O, resp.)
r'	Radius of the invading range
r, r_0	Constant radius of the circular range to be invaded
ρ_0	Beginning of the radius of the circular invading range
s	Distance from the centre

invaded range is invaded (a) by the species with a straight front (Figure 2a), and (b) by one with a circular front (Figure 2b). In the Appendix, we derive the formulas for the invaded area Ω of unstructured ranges; in Figure 2, we give some definitions of variables used. Table I contains definitions of these variables.

2.1. Homogeneous abundance distribution

For both situations with homogeneously distributed individuals of, say, h individuals per unit surface area across the range, the formulas (A1) and (A6) for the area translates directly into the number of individuals that the invader exterminates [see formulas (1a) and (1b)]. When we assume that the radius of the area to be invaded is constant $r(0) = r_0 = d(0)$, then for a front approaching linearly over time, it holds that $r = r_0$, and $d(t) = r_0 - at$ [case (a)]. In case (b), p and r are constant, and we take $r(t) = r_0$, $r'(t) = \rho_0 + at$, so that $d(t)$ and $d'(t)$ are also functions of time (see A5).

$$N = h\Omega = h\text{Re}(f(d(t), r(t))) = h\text{Re}\left\{r(t)^2\arccos\left(\frac{d(t)}{r(t)}\right) - d(t)\sqrt{r(t)^2 - d(t)^2}\right\}$$
$$(1a)$$

$$N = h\Omega = hg(p, r(t), r'(t)) = h\text{Re}\{f(d(t), r(t)) + f(d'(t), r'(t))\}$$
$$= h\text{Re}\left\{f\left(\frac{p^2 + r(t)^2 - r'(t)^2}{2p}, r(t)\right)\right\} + h\text{Re}\left\{f\left(\frac{p^2 + r'(t)^2 - r(t)^2}{2p}, r'(t)\right)\right\}$$
$$(1b)$$

2.2. Peaked abundance distributions

Now, consider a non-homogeneous, spatially structured range with a peaked distribution of individuals in the range centre, as is commonly found (Hengeveld and Haeck, 1982; Caughley *et al.*, 1988; Hengeveld, 1990; Lomolino and Channell, 1995; Donald and Greenwood, 2001; Rodríguez, 2002; Rodríguez and Delibes, 2002; Williams *et al.*, 2003). Let us assume a density of h_{max} individuals per surface unit in the range centre. In that case, the derivation of the number of individuals exterminated by invaders with circular ranges is hard to obtain. Therefore, we consider invaders with a linear front into the density h of individuals in the circular range to be invaded (with radius r_0), which depends on the distance from the centre s, according to $h(s) = h_{max}(1-(s/r_0))$, a cone-shaped density profile. For fixed r and d, formula (2) gives the number of exterminated animals in the volume V above $\Omega = Re(f(d,r))$. However, the radius of the invaded area remains constant during time $r(t) = r_0$, but d, for example, varies with time $d(t) = r_0 - at$.

$$N = \iiint\limits_V \mathrm{d}x\mathrm{d}y\mathrm{d}z = \int\limits_{\phi=-\arccos(d/r)}^{\phi=\arccos(d/r)} \int\limits_{s=d/\cos(\phi)}^{s=r} \int\limits_{z=0}^{z=h_{max}(1-(s/r))} s\,\mathrm{d}z\mathrm{d}s\mathrm{d}\phi$$

$$= h_{max} \int\limits_{\phi=-\arccos(d/r)}^{\phi=\arccos(d/r)} \frac{r^2}{6} - \frac{d^2}{2\cos^2(\phi)} + \frac{d^3}{3r\cos^3(\phi)}\,\mathrm{d}\phi$$

$$= \mathrm{Re}\left\{ h_{max}\left(\frac{d^3}{6r}\ln\left(\frac{r+\sqrt{r^2-d^2}}{r-\sqrt{r^2-d^2}}\right) + \frac{\pi r^2}{6} - \frac{r^2}{3}\arcsin\left(\frac{d}{r}\right) - \frac{2}{3}d\sqrt{r^2-d^2}\right)\right\}$$

$$(2)$$

2.3. Channell and Lomolino's index C

For invaded circular ranges with radius R_0, Channell and Lomolino (2000a, b) considered half of the surface area with radius $\frac{1}{2}\sqrt{2}\,R_0$ to be the range centre, and the other half the range margin. Their centrality index C represents that part of the original centre that remains at a certain stage of the invasion, divided by the remainder of the original range. We define C' for the homogeneous and peaked density distributions as the remaining number of individuals in the original range centre, divided by the total number of individuals in that part of the range that still remains. This implies that for the homogeneous case C and C' coincide.

3. RESULTS

Using these formulas, we compare the dynamics of the range size and the number of individuals of the invaded species during invasion. According to formula (A1), the proportion of exterminated individuals grows slower at first and then faster in peaked ranges than in spatially homogeneous ones (Figure 3). For

OB=|d|, OA=OC=r, O'B=|d '|, O'A=O'C=r', OO'=p
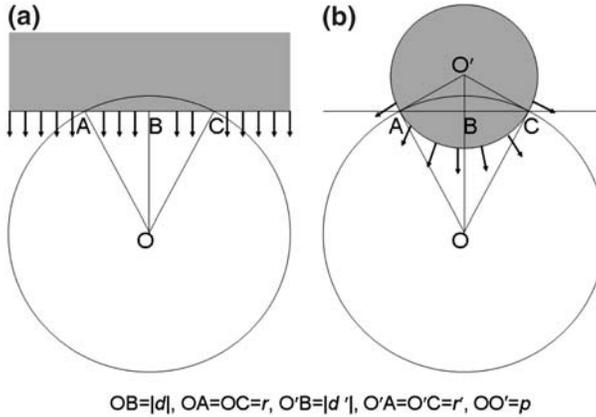
Figure 2. The original range of the invaded species is located within the circle with centre O. (a) the invader occupies the area above the line AC; (b) the invader occupies the grey area that is the overlap between the expanding circle with centre O′ and the invaded circle with centre O.
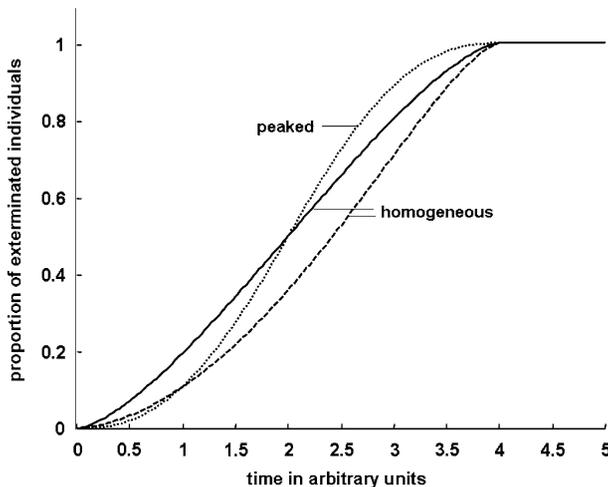
Figure 3. Number of exterminated individuals over time according to formula A1, for homogeneous (drawn curve) and peaked (dotted) density distributions, both for $r = 2$, $d(t) = 2−t$, $h_{max} = 6$, and for homogeneous density distributions with $p = 3$, $r = 2$, $r'(t) = 1 + t$, $h = 2$ (dashed curve).

expansions of invaders with circular ranges, rather than those with a straight front, the process of decline is considerably slower.

 The same formula A1 can be used for the extermination of species with straight range limits by invaders with radial expansion fronts for $r(0) = d(0) = R_0$, $d(t) = R_0$, and $r(t) = R_0 + at$. Since the invaded area is

large, it grows exponentially as long as no other borders of this area are crossed (Figure 3).

3.1. Channell and Lomolino's index C

Channell and Lomolino (2000a) used their index C, calculated as the remaining surface area of the original centre divided by the remaining part of the original range. To distinguish range collapse from range eclipse, they took the theoretical curve of the range collapse indicated by "contagion" (their Figure 2) and motivated the choice between these processes by the number of points in the lower right corner of their graph. These points represent the cases in which all the ranges were completely exterminated, so that $C = 0$. The points of many species, though, have intermediate values for the percentage contraction and are more or less symmetrically distributed around the 50% starting value (see dashed triangle in our Figure 4a, b).
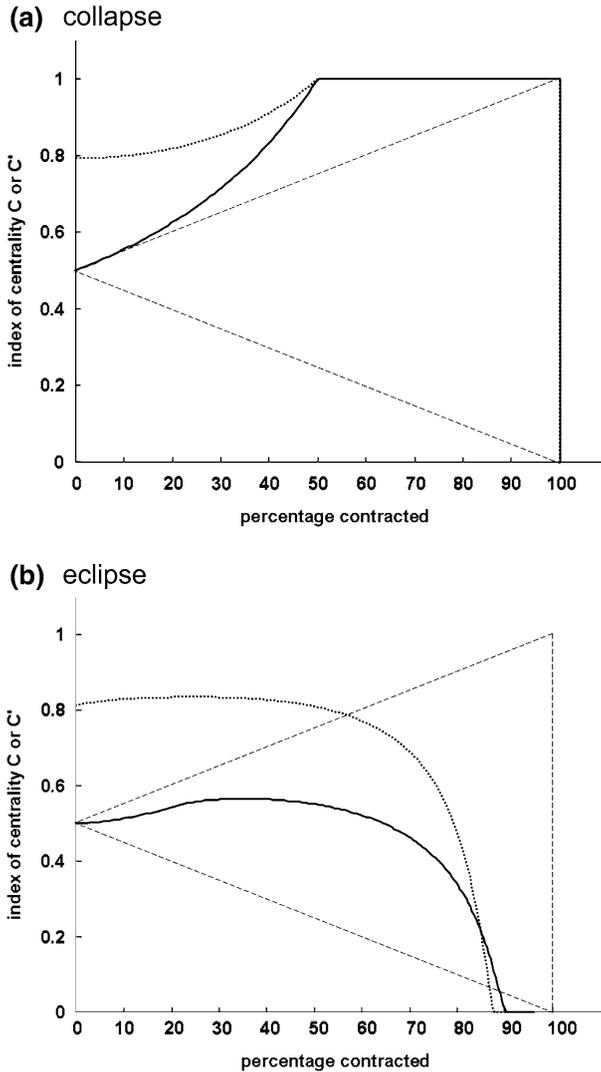
3.2. The new centrality index C'

Figure 4a shows the calculation results for our centrality index C' for range collapses with a homogeneous ($=$ Channell and Lomolino's C) and for those with a peaked density profile, respectively, and Figure 4b those of a similar comparison for the range eclipse hypothesis. Obviously, their centrality index C and our centrality index C' both start at the value of 0.5 in homogeneous situations. In range collapses, the invader comes from all sides, so that the centrality index first increases to 1, up to the moment of total extinction. In contrast, when the invader comes only from one side, as in range eclipses, the centrality index initially changes slightly, after which it declines gradually to zero just before total extinction. The peaked abundance distribution changes this general picture only slightly. Figure 4b shows that for declines of between 80% and 90% range loss the initially very high central abundances in peaked distributions are exhausted faster than in homogeneous ones.

So far, we only looked at invaders travelling at a constant rate, but constant expansion velocities obviously cause the invaded area to increase exponentially over time. Moreover, expansion with the same surface area per unit of time results in a linearly increasing invaded area. Unfortunately, the derived dynamics concerning the proportion of individuals exterminated over time cannot easily be compared statistically with each other.

4. DISCUSSION AND CONCLUSIONS

We modelled range eclipses analytically and obtained an impression of the time evolution of the proportion of individuals the invader already exterminated. However, from this time evolution, we cannot distinguish between causes of decline.

Channell and Lomolino (2000a) gave a number of scattergrams, which also contain polynomial regression curves intended to characterise general trends in range contraction. The curves in their Figure 2 essentially delimit that part of the plane where range collapses and range eclipses are indistinguishable, as can be seen from the increasing scatter in their Figures 5, 6 and 7 (here represented as the

(a) collapse

(b) eclipse

Figure 4. The centrality index C' as a function of the percentage contraction of the invaded species for (a) range collapse and (b) range eclipse. Cases with homogeneous and peaked densities over the original range are shown as drawn and dotted curves, respectively. The triangle with dashed borders depicts the area in which the majority of dots from Channell and Lomolino (2000) fall.

dashed triangle in our Figure 4a, b). These curves also suggest that roughly half the number of species (the upper half of the scatter) tends towards range collapse, whereas only the other half seems to be in the process of being eclipsed.

All this, of course, concerns statistical aspects of the problem of range eclipse. Another aspect is partly statistical and partly biological: it is not always feasible to allot 50% of the range to the ecologically marginal part of the range and the other

50% to the range centre. It is therefore important to look carefully for possible causes of bias, either in the analysis or in the data, just because this may result in a different interpretation. On the whole, the models of demographic decline (Figure 1a) and range collapse (Figure 1b) indicate climatic or demographic causation, whereas causes of range eclipse (Figure 1c) are usually biotic, being due to direct or indirect human action or expansion (Channell and Lomolino, 2000a, b; Fisher *et al*., 2003; Laliberte and Ripple, 2004). Yet, such an explanation need not always apply in seeming cases of range eclipse, because species ranges, being dynamic entities, can also shift extensively in geographic space for climatic reasons, eventually reaching the sea or any other unfavourable area. Then, the last of the remaining populations become marginal by definition, because optimal conditions to be expected in the range centre can no longer be physically realised. For example, in their Figure 3b, Channell and Lomolino (2000a) consider the last remnant of the range of the Red Wolf, *Canis rufus*, in North America as marginal. This does not convince, as its range is truncated by the Caribbean Sea. Ecologically, this remnant might as well be either the marginal or optimal, potentially central part of its range. Alternatively, former range margins may also have become central as a result of a shift in range location. Yet another variable at the geographical level is that, because of a rapid shift, the former range centre now becomes its margin, where it can die out subsequently, and this according to the demographic decline of Figure 1a. All cases should be checked on such points to know whether range shifts and truncations could have biased the overall results.

For all practical purposes, we are convinced that the time evolution of species should preferably be based upon time series of both the number of individuals remaining and the size of the remaining range (see also Rodriguez, 2002). Moreover, some species are more vulnerable than others, whereas over the range the vulnerability varies within each species, as expressed in the non-homogeneity of their densities. With our analysis we advise to concentrate conservation measures for eclipsing species on the central part of its original historically known range. If the central part is already exterminated, then the species becomes very vulnerable or is even doomed to extinction. Indeed, the process of extinction is almost a step function: once the decline has set in, it can hardly be stopped (Figure 4b), a scenario that is worse than that of Channell and Lomolino (2000). Successful conservation of an eclipsing species can therefore only be based on an early-warning system for their declining numbers.

5. APPENDIX

Consider one circular expanding range usurping another range. The easiest way to derive an analytical solution to the problem of the dynamics of this process is to start with a static circular range that overlaps part of another range, either with a straight front (1a), or with a circular one (1b).

1a. Invasion of a circular range by an invader with a straight range front

In Figure 2a, the invaded area Ω is the grey circle segment above the line AC within a circle with centre O and radius r, representing the range limit of the invaded species. We need some definitions for calculating the size of area Ω: as point B lies halfway between A and C, the line OB as a part of a radius is

perpendicular to the line AC. The length of the line OB is denoted as $|d|$, which allows d to be negative. At the time the range limits of the invaded and the expanding species touch, $d = r$, whereas d is positive as long as the centre of the invaded circle is outside the invaded area. The lines OA and OC are radii of the circle with length r, and the angle α of BOC equals that of BOA. Thus, $\cos \alpha = d/r$ and $\alpha = \arccos(d/r)$. The area of the circle sector between AO and OC equals $r^2 \alpha$ subtracting the area of the triangle AOC from this value, we obtain the formula for Ω (note that in a dynamic approach d is varying in time):

$$\Omega = \mathrm{Re}(f(d,r)), \text{ with } f(d,r) = r^2 \arccos(d/r) - d\sqrt{r^2 - d^2} \qquad (A1)$$

when d lies in the interval $[-r, r]$, this function has a real value, and for values of d outside this interval, the result is complex-valued. Of these, we take the real part, since the invaded area should always be real-valued. The invaded area increases when d goes from r to $-r$ (Figure 5).

A different, possibly helpful parameterisation of the same area, increasing as α changes from 0 to 2π, is $g(\alpha, r) = r^2\left(\alpha - \frac{1}{2}\sin(2\alpha)\right)$.

1b. Calculation of the invaded area for two circular ranges

For two circular ranges, the invaded area Ω in Figure 2b is the part between arc AC of the circle with centre O and arc AC of the circle centred at O′. The circle with centre O′ and radius r' is assumed to be the expanding area. Let the radius of the upper circle be r', that is the length of both O′A and O′C, and that of the lower circle r, i.e. the length of OA and OC. The lengths of the line segments OB and O′B are called d and d' respectively, and the distance between O and O′ is called p. The area of overlap Ω of the two circles can be calculated using the formula derived previously:

$$\Omega = f(d,r) + f(d',r') \qquad (A2)$$
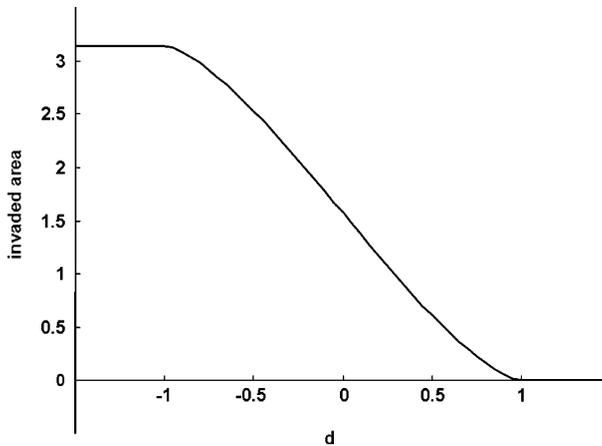
Figure 5. Graph showing the real part of $f(d, r)$ with $r = 1$. Note that from $d = 1$ to $d = -1$, the invader wipes out an increasingly larger part of the range of the eclipsing species.

The only unknowns are d and d', which, however, can be calculated from p, r and r' (from these d, d', r' are time dependent). Because OAB and O'AB are both rectangular triangles sharing the line segment AB, we have

$$r^2 - d^2 = (r')^2 - (d')^2 \tag{A3}$$

Furthermore, we know that

$$d + d' = p \tag{A4}$$

From formulas A3 and A4, we derive A5:

$$d = \frac{p^2 + r^2 - r'^2}{2p} \Lambda\, d\prime = \frac{p^2 + r'^2 - r^2}{2p} \tag{A5}$$

For touching circles, it can easily be shown that $d = r$ and $d' = r'$. For overlapping ranges with invaded area Ω, we find

$$\Omega = \mathrm{Re}\{g(p, r, r\prime)\} = \mathrm{Re}\left\{f\left(\frac{p^2 + r^2 - r'^2}{2p}, r\right) + f\left(\frac{p^2 + r'^2 - r^2}{2p}, r\prime\right)\right\} \tag{A6}$$

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