Simulation of Rapoport’s rule for latitudinal species spread

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Abstract:
Rapoport’s rule claims that latitudinal ranges of plant and animal species are generally smaller at low than at high latitudes. However, doubts as to the generality of the rule have been expressed, because studies providing evidence against the rule are more numerous than those in support of it. In groups for which support has been provided, the trend of increasing latitudinal ranges with latitude is restricted to or at least most distinct at high latitudes, suggesting that the effect may be a local phenomenon, for example the result of glaciations. Here we test the rule using two models, a simple one-dimensional one with a fixed number of animals expanding in a northern or southerly direction only, and the evolutionary/ecological Chowdhury model using birth, ageing, death, mutation, speciation, prey-predator relations and food levels. Simulations with both models gave results contradicting Rapoport’s rule. In the first, latitudinal ranges were roughly independent of latitude, in the second, latitudinal ranges were greatest at low latitudes, as also shown empirically for some well studied groups of animals.

1 Introduction

This paper on the spread of species in North-South direction deals with "Rapoport’s rule" for land, freshwater and marine surface animals. Stevens (1989), who named it and provided some examples, used it to ”explain” the greater species diversity in the sense that latitudinal gradients in species diversity and Rapoport’s rule have coincidental exceptional data and therefore have to be the ”outcome of the same process.”. The rule claims that latitudinal ranges of species are generally narrower at low than at high latitudes,
which would facilitate coexistence of more species in the tropics. It was
named after Rapoport (1982) who had earlier described this phenomenon
for subspecies of mammals. Subsequently, many papers on the rule were
published, some supporting and many providing evidence against it (there
are more than 300 citations of Stevens’ paper). The first papers that pro-
vided evidence against the rule are those by Rohde (1992) and Rohde et al.
(1993), using marine teleosts (excluding deepwater and migratory species).
In the same papers, however, support for the rule was found for freshwater
teleosts, although only above a latitude of about 40 degrees North. Indeed,
support for the rule for most groups that have been examined and used as
evidence for the rule is strongest above a latitude of about 40 to 50 de-
grees, and Rohde (1996) therefore concluded that the rule describes a local
phenomenon, restricted to high latitudes. He explained this by the extinc-
tion of species adapted to narrow temperature ranges during the ice ages,
an explanation also given by Brown (1995). Another explanation is given
by the ”climatic variability ” or ”the seasonal variability hypothesis”, first
proposed by Letcher and Harvey (1994) and Stevens (1996), according to
which the greater seasonal temperature fluctuations at high latitudes select
for greater climatic tolerances and therefore greater latitudinal ranges (for
a recent discussion see Fernandez and Vrba 2005). Stevens (1992) extended
the rule to elevational gradients, claiming that species tend to have greater
altitudinal ranges toward mountain tops, and Stevens (1996) extended the
rule further to depth gradients in the oceans. Gaston et al. (1998) concluded
that support for a general pattern described by the rule is ”at the very least”
equivocal. Rohde (1999) has reviewed papers for and against the rule.

One problem with the rule is the methods used to support it. Usually,
means of the ranges in a particular latitudinal band are plotted against lat-
titude, although Roy et al. (1994) and Rohde and Heap (1996) used median
and modal ranges as well. Stevens (1989) counted all the species occurring
in each 5 degree latitudinal band, i.e. a species with a range of 50 degrees
appears in 10 or 11 bands. Rohde et al. (1993) have shown that this method
leads to an artificial inflation of latitudinal ranges of high latitude species.
The reason is that species diversity at low latitudes is greater, and if only a
few tropical species have large latitudinal ranges extending into higher lat-
titudes with their much lower diversity, the average latitudinal range there
will be greatly inflated (the few high latitude species extending into the
tropics would hardly have any effect). They therefore proposed the midpoint
method, in which only those species are counted which have their midpoint
in a particular 5 degree band. The midpoint method also has been criticised. Indeed, there is a certain arbitrariness in using midpoints: it may not always be the case that a species has originated in what is now its midpoint, and so a species extending far into the tropics may in fact be an originally high latitude species.

Also, Rapoport’s rule does intuitively not make sense. The tropics have far the largest latitudinal range (about 23 degrees South to 23 degrees North) with more or less uniform and high temperatures. Since temperature is one of the most important (and probably the most important) environmental parameter affecting communities, one would expect the largest latitudinal ranges in the tropics (as indeed shown by Rohde et al. 1993 for marine teleosts). In the marine environment, the trend described as ”Thorson’s rule” would counteract Rapoport’s rule. According to Thorson’s rule, tropical marine benthic invertebrates, such as molluses and echinoderms, tend to produce very large numbers of small eggs and pelagic larvae that disperse widely, whereas high latitude species tend to produce few and large offspring, often by viviparity or ovoviviparity, that are often brooded, i.e. stay close to the parent animal (Thorson 1950). That the trend is not restricted to benthic invertebrates, was shown by Rohde (1985) who demonstrated the same phenomenon for monogenean gill parasites of marine fishes.

Nevertheless, even application of the midpoint method sometimes shows a Rapoport effect. The question is: why do some species have narrow and others large latitudinal ranges in the tropics? Rohde (1998) has suggested that newly evolved species and species with little vagility and dispersal abilities should have narrow latitudinal ranges, and because most species originate in the tropics, the effect would be Rapoport’s rule. In contrast, species that disperse widely would have the widest ranges in the tropics, because uniform temperature over wide ranges provides suitable habitats.

In this paper, we try to test Rapoport’s rule with two different models: A one-dimensional simple model with a fixed number of animals expanding in northern or southern direction only, and the two-dimensional Chowdhury model involving birth, ageing, death, mutation, speciation, prey-predator relation and food levels (Chowdhury et al 2003, Chowdhury and Stauffer 2005, Stauffer et al 2005). The simple model is used to clarify some definition problems for the latitudinal spread of a species. The Chowdhury model, which earlier gave results compatible with the higher density of animals species in the tropics (Rohde and Stauffer 2005), is then used for a more realistic simulation. In the simple model we assume that a species originates in a
temperature region for which it is particularly fit, and then moves to other
temperatures. In contrast to simulations of Arita (2005) we treat each animal
separately.

2 Simple model

2.1 Width definition

If an animal species occurs mainly at some geographical latitude \( x \) but is
spread over an interval from \( x - \Delta \) to \( x + \Delta \) in North-South direction, how
do we define this width \( \Delta \)? We could determine the northernmost and the
southernmost occurrence of the species, excluding records of individuals that
have been carried by wind, currents or other external agents into obviously
abnormal habitats where the species cannot survive (e.g., penguins are occa-
sionally carried to the beaches of Rio de Janeiro only to die there). Alter-
natively, only nesting places or other evidence that the species can survive
and produce offspring there, could be used. The choice will depend on the
group, the question asked and the data available. Again \( 2\Delta \) could be the
difference between the most northern and the most southern latitude. How-
ever, although both definitions are useful for the analysis of real data sets,
which very rarely give information on animal numbers at different latitudes,
they are not optimal for computer simulations and are in principle wrong
(though unavoidable) also for reality.

Let us assume that a species centered at about the equator has a prob-
ability of one in a million to survive at some colder northern latitude \( \Delta \).
Then, if only 100,000 such animals exist, presumably none would reach that
latitude. The same effect occurs if there are a million animals, but only ten
percent are observed. If, on the other hand, the species has 1000 million
animals, and almost all those up north are found, then the northernmost
latidude observed for this species would be larger than \( \Delta \). (This criticism
also applies, if all species occurring in some band are checked).

To avoid this dependence of the observed width on the number of animals,
the quality of observations, and the randomness of rare and extreme events,
we instead define the width \( \sigma \) through the standard deviation of the latitude
of the animals:

\[
\sigma^2 = \langle (x - x_c)^2 \rangle
\]

as customary in statistics. Here \( x_c \) is the center latitude, often taken as
< x > and in our case defined as the latitude in the centre of distribution, which in nature often will be the centre of origin and is treated in the model as such. (See below for a correction due to tunneling across the equator.) The brackets < . . . > indicate averages over all animals \( i = 1, 2, \ldots, N \), like

\[
< x > = \sum_{i=1}^{N} x_i .
\]

For a "normal" (Gaussian) distribution it means that about 2/3 of the animals live in the interval between \( x_c - \sigma \) and \( x_c + \sigma \). If with this definition the population changes from large to very large, then \( \sigma \) is determined more accurately, without changing in a systematic way to larger values. But, as pointed out above, this definition of ours is applied much more easily to computer simulations where we can track all animals, than to real data sets.

### 2.2 Model definition

Following Stevens, we use 35 bands of 5 degree latitude each, with the first near the South Pole, the central band around the equator, and the last band near the North Pole. In each band, one typical species of \( N \) animals has its origin, and later these animals spread northwards and southwards to the other bands. If an animal in the first band wants to move further south, it is put into the second band instead. Symmetrically, an animal in the last band 35 wanting to move north is put into band 34. The animals neither die nor give birth and thus represent a whole sequence of generations, in the bad old tradition of theoretical biology of working with a constant number of animals. The width is measured in bands, i.e. in units of 5 degrees latitude.

If the probability of an animal to move is constant (taken as 1/2) and (apart from the reflexions at the first and last band) the animals move North or South with equal probability, then after some time all animals are spread homogeneously over most of the bands, except near the extremes. This is hardly realistic; polar bears have not expanded to the equator.

Thus instead we use biased wandering: The probability to move in the direction of the band of origin is higher than for the opposite direction. We take this bias as \( (x - x_c)/5 \), where \( x = 1, 2, \ldots, 35 \) now is the band number. Thus if an animal has moved five bands northwards from its origin, then the next move with certainty goes South.

However, this model also has to take into account the tunneling from the northern to the southern hemisphere to the mirror latitude \(-x_c\) correspond-
ing to the latitude of origin. With our definition of bands, the latitude is $5(x - 18)$ degrees, negative in the South and positive in the North. Then instead of averaging over $(x - x_c)^2$ as defined above, and of using a bias proportional to $x - x_c$, we take $(x - x'_c)^2$ and $x - x'_c$ whenever an animal is on the hemisphere which is not that of its origin. Here $x' = 36 - x$ is the mirror band corresponding to the same latitude as $x$ on the other hemisphere. In other words, the bias favours motion towards the same temperature as the temperature of origin, and we measure distances only from the closer of the two temperature bands. Thus if half of the animals live at 20 degree South, where the species has originated, and the other half have crossed the equator and live at 20 degree North, then the width is zero and not 20 degrees.

Finally, instead of assuming a vagility independent of latitude, we also allow the moving probability to diminish linearly with increasing latitude, from unity at the equator to zero at the poles, depending on the current latitude of the animal (justified by Thorson’s rule, see above).

2.3 Results

Fig. 1 shows in its top part the animal distributions for selected bands of origin (southern hemisphere) and in its bottom part the resulting widths versus time. Equilibrium is seen here already after 10 to 100 time steps. Except near the two poles, the widths are about the same, and the distributions are Gaussian. Fig.1 uses a constant vagility, while for Fig.2 it is higher near the equator than near the poles; in Fig.2 we now see clear differences in the time development of the width, but still the same equilibrium widths. The animal distribution is about the same as in Fig.1, and is therefore not shown in Fig.2.

3 Chowdhury model

3.1 Model definition

The simulations with the more realistic Chowdhury model, based on individual births and deaths, is more complicated in some and simpler in other aspects. It represents a whole ecosystem; we took the number of food levels as six; tests with nine levels gave similar results. Self-organization of minimum reproduction age, litter size, and prey-predator relations is achieved through
random mutations. Speciation happens with a probability $p$ per iteration by occupation of empty ecological niches through a species from an occupied niche. And each site of an $L \times L$ square lattice carries a whole such ecosystem; a species in one ecological niche can invade an empty corresponding niche on a neighbouring lattice site, with probability $d$ (= diffusivity in physics). These two parameters $d$ and $p$ are varied here (mostly $d = 0.001$, $p = 0.0001$); the other parameters are fixed as in Rohde and Stauffer (2005). We refer to that paper or recent summaries (Chowdhury and Stauffer 2005; Stauffer, Kunwar and Chowdhury 2005) for more details on the Chowdhury model. The Fortran program is available from stauffer@thp.uni-koeln.de (species23n.f, nearly 500 lines). It requires nearly 100 Megabytes of memory for six food levels.

Now we set $L = 35$ for easy comparison with the 35 latitude bands above, and assume a birth rate proportional to $(17 - |\ell|)/17$ where $\ell = x - 18$ (= latitude in 5 degree units) is the number of the band, $-17 \leq \ell \leq 17$. (These birth rates count how many animals reach maturity, and life in the cold is more difficult.) Again the width is measured in units of 5 degrees latitude.

### 3.2 Results

The resulting Fig.3 shows that there are much more animals (per unit area) near the equator than near the poles, as wanted. The widths $\sigma$ are again defined through $\sigma^2 = \langle (\ell - \ell_c)^2 \rangle$ where $\ell_c$ is the band of origin of the species (not of birth of the individual). Figure 4 shows how these widths increase slowly (logarithmically?) with time $t$. Ten samples had to be averaged over to give a clear trend larger than the statistical fluctuations. For the longest time of 2 million (line in Fig.4) perhaps this increase stopped, but anyhow such long times are not very realistic biologically since in a million generations the climate changes. The important result is that these widths are smaller than one band, less than in the preceding section. Thus animals do not spread all over the world, and we did not have to introduce a bias pushing them back to the latitude where the species originated. Thus also no tunneling was possible. In this sense the Chowdhury simulation was simpler than the one of the previous section.

Fig. 5 shows that an increase of the vagility $d$ also increases the widths; high $d$ values, however are unrealistic according to Rohde and Stauffer (2005). Finally, Fig.6 shows the variation with speciation probability $p$; again high $p$ are unrealistic.
4 Conclusion

Our results for both the simple model and the Chowdhury model contradict Rapoport’s rule that latitudinal ranges are smallest at low latitudes. For the simple model, ranges were more or less independent of latitude, for the Chowdhury model, they were largest near the equator for the parameters used. This confirms empirical findings by various authors who did not find support for the rule in most taxa (see above, e.g. Rohde 1993, Gaston et al. 1998). The fact that the rule was found to hold for several groups, particularly at high latitudes, does not contradict the results of our simulations. A general model like ours is not meant to account for all historical and geographical contingencies, for example those resulting from glaciations. If a Rapoport effect is indeed a local phenomenon due to glaciation or other local effects, as suggested by Brown (1995) and Rohde (1996), it would not be expected to be revealed by such a general model. The Chowdhury model has recently been shown to give results for latitudinal gradients in species diversity which conform to reality (Rohde and Stauffer 2005); nevertheless, our results concerning Rapoport’s rule need confirmation from simulations using different models.

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Figure 1: Top: Distribution of animals originating at 80, 60, 40, 20, and 0 degrees South. We see South-North tunneling from the 20 degree band, but not from latitude 40 and higher. The curves for animals originating in the North are symmetric and omitted for clarity. Bottom: Time developments for the width, including the northern species.
Figure 2: As Fig.1 bottom, but with high vagility near equator (upper lines) and low vagility near the poles (lower lines).

Figure 3: Latitudinal variation of the number of animals (upper data) and species (lower data) in Chowdhury model, summed over ten samples run for 240,000 time steps, of which the first 40,000 were ignored in the sums.
Figure 4: Slow increase of the widths $\sigma(\ell)$, when time $t$ increases by factors of ten, from bottom to top. As for Fig.3 we omitted the initial sixth of the time from the averages, but increased the time five times by a factor 10. For the longest time, shown by the line, only one instead of ten samples was simulated.
Figure 5: Strong increase from bottom to top with increasing diffusivity $d$ of the widths $\sigma(\ell)$; $p = 0.0001$, statistics as for Fig.3.

Figure 6: Increase with speciation probability $p$ of the widths $\sigma(\ell)$; $d = 0.001$, statistics as for Fig.3. Two higher curves still missing.