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# „OUTLAWS": SOME EVOLUTIONARY ASPECTS OF RARITY IN INSECTS

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*Disorder is limited; the only question is the size of its box (I)*

**Abstract**. The term „rare" must always have a practical and operative meaning. The discussion is introduced by consideration of some trivialities: 1) potential and actual population sizes are as important properties of an evolving species as any morphological, physiological or other features; 2) every species is rare at rise; 3) most insect species are rare. The importance of distinguishing the ecological and the evolutionary meaning of rarity is stressed. Their incongruence is a consequence of a number of reasons, e.g. there is no direct correlation between local rarity and the niche dimensions, the mean size of populations and the size of distribution area, etc.

Speciation (of an abundant species) is a process of maturation. In *statu nascendi* every new species is isolated (and exists in low numbers), but having left isolation its potentials and constraints (competitive, predator-prey, etc. relationships with the extant species) will determine further steps of speciation. From this viewpoint rare species are premature species: they have never reached the phase (population size) of confrontation (competition, etc.). However, under the umbrella of abundant species, rare species are released from most community constraints and hence they are objects in the laboratory of Nature: „hopeful monsters" are possibly derivatives of rare species.

*Key words: evolution, speciation, population size, rarity.*

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The notion of „rarity" has become rather popular in ecology. This is a recent development, though. It was only four years ago when the first modern book on rarity as such was published. The significance of Gaston's (1994) work cannot be overestimated, I am certain.

The first question, as it is always so — what is rarity. (I think it would be disadvantageous to base any further discussion on the difference in the meaning of „rare" and „scarce", obviously existing in English). What I think of this term is that we must not think of a clear and clear-cut notion if we mention rarity. This is very much of a weak, relative (comparative) notion, though it seems important for various reasons. No wonder that there is much confusion about the meaning of „rare".

Although there are theoretical problems with rare species, the delimitation of the term „rare" must always be very practical and operative. This is why I would propose a cut-off point of 1 %, 0.5 % or 0.1 % of species frequency in a given sample, or, 1 %, 0.5 % or 0.1 % of the frequency of the dominant species in the sample; depending of the aims of the study and on the taxonomic group under study. Much to my regret, I have to say that Gaston's otherwise very good book has not made things stand better at all. He suggested „that a useful cut-off point is the first quartile of the frequency distribution of species abundances or range sizes" (i.e. a cut-off of 25 %).

I am not going to discuss all the controversial consequences of such a cut-off, and I do not want to provoke a debate on criteria of rarity: a practical term is under the permanent test of the practice. I would rather show an example from my works, a frequency distribution of a given sample of flies on elephant dung in Africa (Fig. 1). The 49 dipterous species (a total of 3 677 specimens) are ranked from the commonest to rarest, frequencies being given on a logarithmic scale. The two horizontal lines are at the 1 % and 0.1 % level of the relative frequency; the dotted line is at the 1 % level of the dominant species. The vertical line is Gaston's cut-off of the first/last quartile, which results in some of the species represented by singletons being regarded as *not rare*!

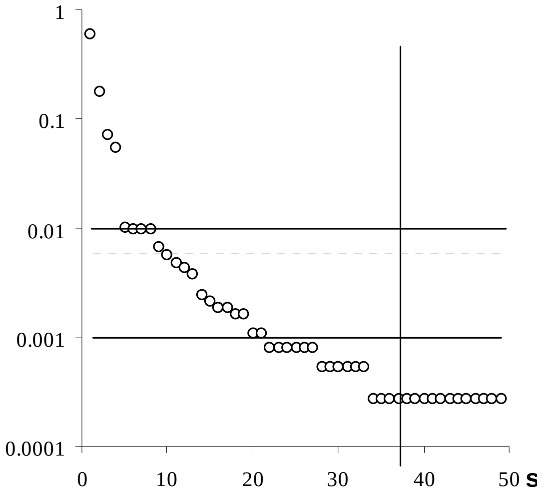

Fig. 1. Frequency distribution in a sample of dipterous species observed on elephant dung in Tanzania (relative frequencies of 49 species, logarithmic scale; s: serial number of species in frequency; explanation in text)

Gaston's argumentation for his definition is weak, I think, but otherwise his book is of an historically important scientific value. (An interpretation of the frequencies from common to rare as a continuum does not hinder but rather facilitates studies on the causes of rarity. On the other hand, it is true that it is always the researcher who must decide on the level of rarity, but I think this necessity of decision as unavoidable).

I believe, D. Rabinowitz's (1981) paper on the seven forms of rarity is a mile-stone in the scientific approach to rarity. Since her works are so well-known, I do not repeat their summarizing table here (with examples of flowering plants in order to remind you the „three traits” etc.). I can only admit that the eighth box is not empty for flies, though the rare species are not inclined to be specialists, or at least they are not exclusively so. If we conceive those three traits as three continua (and modify local population size „somewhere large” to „large”), we obtain a three-dimensional space or rather a cube; let me call that cube „DebRa's cube”. It is easy to understand that there is only one negative apex on that cube, where all the three traits have their maxima (globally thinking; of course, negative for rarity). And it is easy again to realize that not only the other apices, but an infinite number of other points on the sides of the cube and inside the cube may represent rare species. It is useless to say that one can find also other traits for similar consideration.

There has been much confusion about the interpretation of rarity. This is why I think Gaston's book is so important. I do not want to discuss those misinterpretations in details, only I must mention Hanski's core-and-satellite species model (Hanski 1982, for some other respects see Nee *et al.* 1991), which was misinterpreted for the rare-and-abundant continuum, very much against the original aims of its author.

In my opinion the main cause of the confusion is a lack of distinction of the ecological and evolutionary meaning of rarity. I emphasize the importance of such a distinction. The incongruence of the ecological and the evolutionary meaning of rarity is a consequence of a number of reasons, e.g. there is no direct correlation between local rarity and the niche dimensions, mean size of the populations and the size range of distribution, just to refer to DebRa's cube. Consequently, my definitions are:

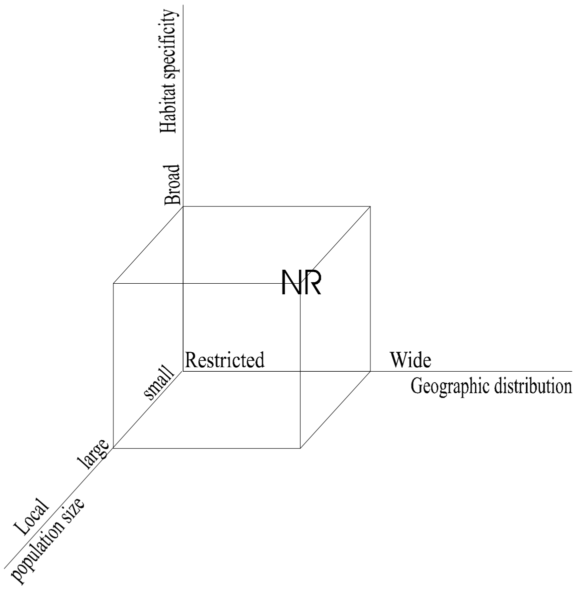

Fig. 2. From the „Seven forms of rarity” to DebRa's cube: to illustrate that an immense number of forms or rarity exists (cf. Rabinowitz *et al.* 1986).

*The ecological meaning of „rarity” is no more than a low relative frequency in the samples as a consequence of any cause.* The level of cut-off is always determined by the researcher based on practical criteria.

*The evolutionary meaning of rarity is that the species is extant globally in low numbers* (population size in any context of population biology is better interpretable as effective population size). The two kinds of meaning are rarely congruent and it is so for species just before their extinction. Paraphrazing the title of Rosenzweig's (1995) excellent book, we may speak about „rarity in space and time”.

Considering the above reasons, rarity needs to be interpreted for every species and in every actual case, since it is interpretable *only in concrete cases*. For such an interpretation we must have sufficient information on the bionomics, phenology and other traits of the given species.

If there is so little to be generalized about the „rare” species, is there any reason to seek for general considerations about their phylogeny? Well, in the meagre discussion below I would rather stress some *common ecological features of the rare insects, which may have evolutionary relevances.*

As regards rarity in insects, the starting point of the discussion is a consideration of some trivialities: 1) the potential and actual population sizes are just as important properties of an evolving species like any morphological, physiological, etc. features; 2) the majority of the insect species are rare*;* 3) every species is rare at rise. One may say that the third point is not always true; that is, there are evolutionary situations when the transformation of the species occurs in large populations. I am aware of that but those cases are not the topic of the present paper.

As for the evolutionary factors affecting gene frequencies in rare species, of course mutations and meiotic drift must have the same role as in the abundant species. *Migration is important in those species only* that *exploit permanent resources, since dispersal for new evanescent resources (like small dead animals, fresh dung etc.) makes consideration of migration in the usual sense inoperative.* As McKinney *et al.* (1996) showed generally and convincingly „rare species having a patchier (less uniform) distribution in both time and space”.

Actually I think that genetic drift plays the most important role in their speciation by producing *extremely fit* populations by chance. The probability of such an event is very low, but the number of the possible cases is high. The main role of selection is to maintain the fittest ones, as always so.

The ecologically interpretable general traits of the rare species are as follows:

Quite contrary to the abundant species, where predation by *definite* predatory populations, or parasitism by more or less specialised parasites are major factors in control of population size, the majority of the specimens of rare species are lost in the course of their quest for finding „new” resources; and *if it is so, their main limiting factors are out of the community they belong* (in other words, for a high number of rare species: minute sources, very large sinks, cf. Pulliam (1988)). Therefore the stochastic processes in dispersal are far more important for them than even a strong selective pressure *at some given points* of their range. On the other hand, such kind of a rare species must have good potentials of spreading and strong bases in its recognition system. So most of what is said in this paper applies to flying insects only.

They are not involved in competitive processes at all. I would call them „outlaws”, since — with some exaggeration I would say — they are under a single community constraint only: they must not exceed a given level of abundance. Their local extinction and local recolonisation are not only common processes but *this is their way of existence*. It is useless to say, all these cause a lot of problems when we want to determine their range of distribution etc.

It is well-known that rare species form the majority, not only within a given guild, but even within the taxonomic groups. This phenomenon is known under various „laws” in ecology, like Monard's law, Monard-Balogh's law, namely, there is only a single abundant species from every genus in a community and most of the species in a genus are rare (Papp 1993). And just the populations of the abundant species *with similar ecological traits, with the same predators and parasites form an umbrella over the rare ones*. They are predated and parasitized in proportion to their relative frequencies, which results in the outlaw — in some respects a constraintless — position of the rare species (cf. eg., Lawton 1984). It is incorrect to think of the rare insect parasitoids as parasitoids of rare species. That would be too costly.

The speciation processes which produce rare species from rare species are common and take place easily, but they are mostly negligible for the main directions of global macroevolution. From our viewpoint those evolutionary situations are interesting when a rare species becomes abundant, or when an abundant species gives birth to numerous rare ones.

Of course, there must have been cases in the evolutionary history of insects when a rare species became abundant. However, an abundant species has to be fit in competitive, predatory, and other interactions. We have to acknowledge that numerous species or even the majority of the species do not accept the challenge and hence they remain rare.

Speciation (of an abundant species) is a process of maturation. *In statu nascendi* every new species is isolated in the physical or in the ecological space (and exists in low numbers), but having left isolation its potentials and its constraints (competitive, predator-prey and other relationships with the extant species) will determine the further steps of speciation. From this viewpoint the rare species are premature species: they have never reached the phase (population size) of confrontation (competition with other species etc.). However, under the umbrella of abundant species, rare species are released from most community constraints and hence they are objects in the laboratory of Nature: the „hopeful monsters" are derivatives of rare species. Indeed, Nature's „extension laboratory" works at least partly on the principle of trial-and-error. Or if that is a game, this game is played by high number of players and with very high number of cards (so there is a chance for a royal flush for some).

I can stress again that the main directions of macroevolution are markedly determined by the abundant species, but „hopeful monsters" are more likely to evolve from rare ones. Rarity is a proper condition for endeavours. Among those circumstances the efforts are not limited by competition and are rather little constrained by predation and parasitism.

Although it is not always so, it must be a common phenomenon that the evolving „new" species exist in low numbers, even if they are derivatives of an abundant one, or even if later they become abundant. Several isolated populations of a widespread and abundant species can transform into separate species within a given period. Since an abundant species has a better chance to produce a new branch within a given period than a rare one, branches that include abundant species are less likely bifurcating; their multifurcation must be far more frequent than those of the rare species. An assumption of multifurcations in several heleomyzid genera (Diptera) during the Ice Ages is surely a better hypothesis than bifurcations exclusively.

In the case when several rare species are formed from an abundant one consecutively, or the alternative case, where the present day abundant species has an intermediate position among rare ones (in this case some important change must have happened sometime in that evolutionary period), are analysed in a subsequent paper.

I must stress that I do not want to pose a new hypothesis here but *a new simple test in the evolutionary analysis,* however, it needs better elaboration.

As it may be seen on Rabinowitz's table, species with wide geographic distribution, broad habitat specificity and somewhere large local population size may be found rare locally (for instance at the edge of its distribution, in habitats representing extreme values of its niche, etc.). Again, an infrequent question among the problems of low abundances is that species which are able to live in abundant numbers, may also occur and live in a number of other communities *at low frequencies.* (A well-known example is the occurrence of the house fly in pastures of Central Europe: it is extremely rare there). I think this is an important component of their evolutionary strategy. In those „alien" communities populations of other species form the umbrella above them. In several communities there is a „shift system" among the species that are able to exist as abundant. This is an important balance to yearly, seasonal or other changes of environmental factors by which the community is capable to react dynamically. An example is given in Table 1, where the frequencies of agromyzid species in cereal fields of Hungary are shown in three consecutive years.

Recall that the neodarwinian synthesis had considerations of the abundances (actually the population sizes), though I think the different population sizes have not been properly analysed from the viewpoints of speciation. Cladistic theory does not and *cannot* take the different frequencies of the species into consideration. This is one of its weakest points. (Some consequences to cladistics are discussed in a forthcoming paper.)

Table 1. Percentile frequencies of agromyzid species in cereals in three consecutive years in Hungary (100 net sweeps/sample, on the average five samples per county; from Papp 1993)

| species | 1987 | 1988 | 1989 |
|---|---|---|---|
| *Agromyza intermittens* | 0.11 | 1.75 | 1.51 |
| *luteitarsis* | 58.71 | 1.57 | 1.62 |
| *megalopsis* | 0.83 | 8.89 | 1.57 |
| *nigrella* | 9.07 | 85.43 | 93.68 |
| *nigrociliata* | 2.31 | 0.96 | 0.25 |
| *rondensis* | 28.40 | 0 | 0.09 |
| *Phytomyza fuscula* | 0.22 | 0.68 | 0.85 |
| other species | (4 spp.) | (5 spp.) | (9 spp.) |
| % combined | 0.35 | 0.72 | 0.43 |
| total number of individuals | 2768 | 2801 | 8953 |
| total number of samples | 63 | 46 | 57 |

In summary, the present paper is aimed at a discussion of the basic concept of „rarity" in evolutionary studies and to serve as „food for thought" for a better approach.

The problems in generalisation of the meaning of „rarity", the extremely high diversity in life habits, life history strategy and other evolutionary biological features of the rare insect species make it difficult to establish laws of wide validity in the evolutionary aspects of rare species (or even to risk statements of generalization). What we really know by now is that „big" ecological invariance principles, the general models in population biology and the prevailing theories of speciation are hardly valid for them. This statement will not mean that prevailing theories (and models) are actually to be revised. *All those theories are valid for the abundant species which control the main biotic processes on Earth, the matter and energy flows and biotic constraints*. On the other hand, the generalizations for all the species are surely invalid.

The majority of the species on Earth (at least so for the insects) are rare and insignificant as for the ecological processes. Nevertheless when one investigates the revolutionary changes in macroevolution, one must more frequently think of the rare species, the outlaws, the chips of macroevolution. Or simply but more generally, if we are really concerned about the knowledge of biodiversity on Earth (I mean its quality, quantity and its evolution), they must not be neglected.

## Acknowledgements

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