

Review articles

New trends in research on parasite host specificity: a survey of current parasitological literature[1]

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ABSTRACT. The main goal of this article is to attract attention of junior scientists interested in evolutionary and ecological parasitology, to some very interesting articles dealing with the methodology of such investigations. The authors review some problems related to terminology used in the studies of host-parasite relationships and then recapitulate the subjects of five articles, in which new indices of the range and characters of hosts specificity are proposed. These are: the article of Caira et al. (2003), Poulin et Mouillot (2003, 2005), Krasnov et al. (2011) and Poulin et al. (2011).

Key words: ecological aspect, geographical aspect, host specificity, indices of specificity, methodology, phylogenetical aspect, terminology

Introduction

The problem of host specificity – exploitation of a defined circle of living organisms by parasites, as the environment of their life – is still in the centre of the scientific interest of parasitologists. Trials are still undertaken to improve both: terminology showing various aspects of this phenomenon, and the methods of its measurement by various indices, which describe the complex relationships between the parasite and their hosts better and more precisely than verbal definitions. Both tasks are not easy, mainly because of different factors – ancient as well as contemporary, which act in various host-parasite relationships. In this article we would like to draw attention of our junior colleagues who are interested in evolutionary and ecological parasitology, to some very interesting articles dealing with the methodology of such investigations.

Terminology

The formulation of terms describing some features of host specificity arises from the great diversity of interrelations between parasite and their hosts, such as a size of host circle, the position of each host in the hierarchy of animal kingdom, the distribution of parasite among different hosts, as well as current opinions about the factors which model the characteristics of host specificity. This last aspect was discussed at the First Symposium on Host Specificity Among Parasites of Vertebrates (Neuchatel 1957). As a result several terms have been proposed which show the sources of the origin of this phenomenon [1]. Two main types of hosts specificity were defined: **ancient** or **phylogenic specificity** – very narrow, „connected with the systematic position of the hosts", and three categories of **recent specificity** (independent of host systematic): **ecological** – very large, related to alimentary regime of hosts; **physiological** – large, connected with metabolic activity of hosts, and **neogenic** – narrow, arising from ecological or physiological factors, when the plasticity of parasite has been lost. It is worth to notice a weak precision of defining the range of specificity: narrow, large, very large, as well as multitude of other designations describing this range. For

[1] This article was presented at the XX Wroclaw Parasitological Conference.

example, in the articles presented during this Symposium we have found following examples of terms defining narrow and large specificity: less host specific – most host specific; strongly specific – wide specific, strict specific – week specific; high specificity; low degree of specificity and so on. There were several attempts to find more precise terms, based on the number of host species. The first was probably Sandground [2] who proposed in 1929 the term „**monoxenous**" for parasites which were connected with only one host species, or several related (representing one genus) hosts. Then Euzet et Combes [3] proposed using three terms: **monoxenous**, for parasites with one host species, **stenoxenous** – with more than one, but strictly related hosts, and **euryxenous** – for parasites with several, not related host species. These terms are currently used, but there exist also some others, quite common in the literature, equivalent to the categories proposed by Euzet et Combes: parasites which have only one host species – **oioxenous**, **monoxenous**, **species-specific**, **host-specific**, **specialists**; parasites with more than one, but closely related host species: **stenoxenous**, **monoxenous**, **oligoxenous**, **specialists**; parasites with several, not related host species: **euryxenous**, **polixenous**, **generalists**.

None of these terms defines the strict limits (number of hosts) of parasite categories. Moreover, two of them are used for two categories. They also do not show that, independently of the degree of relation between the hosts, they can be unevenly exploited by parasite. This phenomenon was experimentally studied by Michajłow [4] already in 1932. On the basis of prevalence and intensity of colonization of different Copepode species by *Triaenophorus nodulosus* oncospheres, he distinguished two categories of hosts in which these larvae developed to the next stage – procercoid: **main** or **proper** hosts – in which the prevalence and intensity of infection were very high, and **auxiliary** hosts – in which these two indices of infection were lower. Kisielewska [5], who studied the structure of parasite communities in hosts, proposed in 1968 the terms for three categories of parasites composing the community: **dominants** – a stable component of parasite community, having the highest index of infection, **influents** – also a stable component of parasite community, but with lower index of infection, and **accessory** species – parasites rare and with very low index of infection. In 1986 (almost 20 years later) Bush et Holmes [6] proposed also three terms for the description of parasite community: **core** species, **satellite** species (two terms used by Hansky [7] in ecological studies of free living organisms) and **intermediate** (or **centrifugal**) species. These three categories are quite similar to those proposed by Kisielewska. Bush et Holmes also used two other terms, proposed by Price in 1980 [8] and very popular today – namely **specialists** and **generalists**. All these terms are not precise, and without clear limits of their ranges. There were at least two attemps to propose unified ecological terms in parasitology: one in 1982, by a special committee appointed by the President of American Society of Parasitologists [9], second in 1999 by Busch et al. [10] (in Polish literature Pojmańska [11] presented in 1993 a critical review of common ecological terms used in Anglo-Saxon and Polish languages).

Indices of specificity

Two indices used by Michajłow [4,12] for the description of a „host value" for the development of *Triaenophorus nodulosus*: mean intensity of infection and prevalence are still used in parasitological studies. Similarly, index of relative density, which is the derivative of intensity and prevalence are often used. The higher value of these indices, the closest relation between parasite and its host. There are ongoing searches of more and more adequate indices, showing not only the range of host specificity, but also its character and factors influencing parasite specialization. Very often the methods proposed by ecologists in relation to free living organisms are adapted for describing the interrelations between parasites and their hosts. The number of host circle was introduced in the index of infection employed by Kisielewska [13]. Rohde [14], who employed the indices of intensity and prevalence of infection, proposed also the third one, which was based not only on the number of real hosts, but also on the number of potential ones. Following more recent articles published between 2003–2011 attract our special attention.

Caira et al. [15] focused on phylogenetic aspect of host-parasite relationships. Their ***HS*** (host specificity) index is based on host range (number of hosts species parasitized) and the position of each host on the taxonomic ladder of animal kingdom (genus, family, order, class), but not on a prevalence or intensity of infection. The number of hosts occupying each step of this ladder is important in index calculation. The lower the level of step common for all hosts (in which parasite loses its specificity) the higher a specificity of parasite. The computation is rather complicated, but described in detail in the article. Index value is presented as a decimal fraction, the first digit showing the level common for all hosts. The range of this value is from 0 (for parasites which have only one host species) to 10. For example: ***HS*** of *Aphanurus stossichi* which has only one host species = 0, ***HS*** of *Lepidopedon cascadensis*, with 2 host species representing 1 genus = 0.3010300, and ***HS*** of *Bunodera luciopercae*, which has 35 host species, representing 25 genera, 12 families, 10 orders and 1 class = 8.60020316. The authors computed ***HS*** for about 700 species of parasites representing several systematic groups of invertebrates and discussed its usefulness in comparative studies, especially for testing some hypotheses and generalizations. For us one result of their works is especially interesting and important. For the first time in the history of studies on host-parasite relationship it has been proposed to specify some ecological terms by the values of ***HS***. These authors proposed the following ***HS*** values for three basic categories of parasites (with slight modifications) suggested by Euzet et Combes [3].

1) Oioxenous (one host only): ***HS*** = 0;

2) Mesoxenous (divided into two subcategories):

a) mesostenoxenous (more than one host, but restricted to one genus): ***HS*** greater that 0 and less than 3.000434077;

b) metasteoxenous (more than one hosts, but restricted to one family): ***HS*** greater than or equal 3.000434077 and less than 5.574321858;

3) Euryxenous (more than one family of hosts): ***HS*** equal or greater than 5.574322.

They also proposed to restrict two terms so commonly used nowadays: to consider **oioxenous** (= monoxenous) and **mesostenoxenous** parasites as **specialists**, with ***HS*** less than 3.0004, while **metastenoxenous** and **euryxenous** – as **generalists**, with ***HS*** equal or greater than 3.0004.

According to the authors this quantitative index is more precise than that verbal description of parasite specificity. The only limitation is that one has to be sure, that the host taxon under study belongs to a monofiletic group.

In the same year **Poulin et Mouillot** [16] proposed a new index of host specificity, marked as $\mathbf{S_{TD}}$, which also takes into account the phylogenetic aspect of specificity. The phylogenic distance between pairs of host species is measured on taxonomic ladder of animal kingdom, their values ranging from 1 (genus common for all hosts) to 5 (only type is common for all hosts). Measuring variance $\mathbf{VarS_{TD}}$ provided additional information on phylogenetic structure of a host circle (taxonomic distances between hosts on lower steps). Developing this index the authors used methods employed by ecologists (for example those of Clark et Warwick [17,18]) in studies of biodiversity. Similar, as in the ***HS*** index of Caira et al. [15], the lower the value of $\mathbf{S_{TD}}$, the higher host specificity of a parasite. The asymmetry of hosts specificity structure (shown by $\mathbf{VarS_{TD}}$) reduces its value. According to the authors this new index „is independent of study effort, e.g. the number of published records of a parasite" and is useful in comparative studies on host specificity, as well as a parasites' evolution and their power of colonization. One of advantages of this index is also the facility of its computation (the authors mention suitable equations and examples of index application).

In the next paper **Poulin et Mouillot** [19] proposed one more new index, marked as $\mathbf{S_{TD}*}$, in which two aspects („facets") of host specificity were taken into account: host phylogenic distance and distribution of parasites among the hosts. In this index the average taxonomic distinctnesses of all pairs of host species are weighted by the parasite prevalence in the different hosts. Similar as in the case of $\mathbf{S_{TD}}$, the index $\mathbf{S_{TD}*}$ is inversely proportional to specificity level. As to its computation, the authors present the detail for computer program they used. They proposed to use it as a standard procedure in comparative studies.

Another new index proposed by **Krasnov et al**. and marked as beta-specificity $\mathbf{\beta_{SPF}}$ [20] is based on a spatial or geographic factor. It has to show host species turnover (replacement of some host species – parasitological vicariate) or differences in distribution of parasites among hosts across localities. Referring to the studies on spatial patterns in free living organisms they remind that the research on biodiversity can be carried out on three scales: alfa (local), beta (between localities), and gamma (global), and proposed to employ the corresponding terms: alfa-specificity, beta-specificity and gamma-specificity in parasitological researches. The authors precisely describe the complicated computation of $\mathbf{\beta_{SPF}}$ employed by them for testing spatial specificity of some fleas parasitizing small mammals. According to the authors such comparative studies can be useful in anticipating the ability of parasites for expansion and colonization new territories and new hosts. We think that this aspect is especially important today, when the phenomenon of natural or „anthropological" expansions of living creatures is more and more often observed.

All these problems are discussed once again and summarize in the article of **Poulin et al.** [21]. The authors emphasize „the multifaceted nature" of hosts specificity, and describe its three categories influenced by ecological, phylogenetical or geographical factors. We strongly recommended this article, as the authors widely discuss the implications of each index for understanding various questions of parasites' evolution and ecology, and indicate the best indices for specific problems (with accurate equations and computer programms).

Structural specificity describes the distribution of parasite species among different host species and is also called – **basic specificity**. It is defined not only by the number of hosts, but also by abundance and prevalence of parasite in each host species. Uneven distribution of parasites (different values of these indices), especially their accumulation in one or few hosts species, indicates high structural specificity. The authors proposed to use the Simpson or Shannon indices.

For measurement of the **phylogenetic specificity** (based on the phylogenic distances among the hosts at all subsequent taxons in taxonomic range of animal kingdom – just to that common for all hosts species) the authors recommended their $\mathbf{S_{TD}}$ and $\mathbf{S_{TD}}$* indices but also some phylogenetical and ecological indices applied by the ecologists in relation to free living organisms. The index $\mathbf{S_{TD}}$* presents the combined phylo-structural aspect of hosts specificity.

The authors precisely describe the measurement of **specificity in geographic space**. The most characteristic feature of this specific category is that beta- and gamma-specificities are the resultants of many basic alfa-specificities. Any parasite could experience different environmental conditions and different sets of potential hosts across its geographic range, the factors which can regulate the number and composition of host circle (turnover of host species), as well as the quantitative distribution of parasite species among their host populations. Apart from $\mathbf{ß_{SPF}}$ index the authors recommend to employ some method for biodiversity measurements. They present a method for measuring combined phylogentic and geographic specificity (phylogenetic beta-specificity), which assesses „phylogentic relatedness of host species and their different use across localities".

The authors point out advantages of studying the phenomenon of host specificity deconstructing into its structural components. It allows to generate more precise and better targeted hypotheses, find suitable „tool-kit" to test them, and increases the value of comparative analyses. It allows to evaluate the role of various factors in building host-parasite relationships and „precisely match a putative selective factors with the specific facets of host specificity". It should be very useful in prediction of environmental processes, including epidemiological ones.

In concluding remarks the authors pointed out the urgent need of studying the parasite specializations at different levels, but warn: „whatever the question we pose, we must make sure to use the proper analytical tools to answer it". They encouraged to apply some methods used by ecologists for studies on biodiversity for parasitological studies. We would like to encourage our colleagues to get familiar in great detail with those, cited here, very interesting articles, and to introduce some of the ideas into their own investigations.

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