Towards a unified functional trait framework for parasites

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Highlights

- Functional traits are morphological, physiological, phenological, and behavioural characteristics of organisms which impact their fitness and are measurable at the level of the individual without using information external to it.
- Parasitology is lagging behind in the application of a functional trait approach to the study of parasite diversity and community ecology. To bridge both disciplines, we introduce a core list of functional traits for parasites.
- In order to cover a large variety of ecological questions, we relate functional traits of parasites with the main challenges faced by organisms: dispersal, establishment, and persistence.

Keywords

functional traits, functional diversity, dispersal, establishment, persistence, community ecology

Abstract

Trait-based research holds high potential to unveil ecological and evolutionary processes. Functional traits are fitness-related characteristics of individuals, which are measured at individual level and defined without using information external to the individual. Despite the usefulness of the functional approach to understand the performance of individuals in ecosystems, and parasitism being the most common life-history strategy on Earth, studies based on functional traits of parasites are still scarce. Since the choice of functional traits is a critical step for any study, we propose a core list of seven functional traits of metazoan parasites, related to three universal challenges faced by organisms (dispersal, establishment, and persistence), and give guidelines to define appropriate functional traits in future parasite community studies.

A Trait-Based Ecology

Ecological studies based on **traits** (see Glossary) have greatly increased over the last three decades to explain ecosystem **properties** under different environments or environmental gradients (Cadotte et al. 2015, Moretti et al. 2017, Weiss & Ray 2019). Among the multiple types of traits that exist (Violle et al. 2007), **functional traits** have widely demonstrated their usefulness to explain or predict a variety of ecological questions about free-living organisms, in particular questions related to the functional facet of diversity, that is, **functional diversity (FD)** of a community (Box 1). Functional traits have also allowed to unveil the mechanisms by which individuals (or their **intraspecific trait variability**, Carmona et al. 2016) scale up to effects on ecosystems and ecosystem processes (Violle et al. 2007). However, the number of studies using functional traits of parasites is still low (Mouillot et al. 2005, Keeney & Poulin 2007, Krasnov et al. 2015, 2016, 2019a, 2019b, Sokolov & Zhukov 2017, Warburton et al. 2017) in comparison with those of free-living organisms. This is perhaps due to three reasons: (i) a general underestimation of the roles played by parasites in ecosystems, despite ample evidence showing their importance (for a review see Gómez & Nichols 2013), (ii) the scarce knowledge on fitness-related traits of parasites in comparison with other organisms, and (iii) the lack of a unified framework of functional traits in parasites.

The selection of functional traits is essential to draw sound ecological conclusions, as the traits chosen must be informative of the target function (Petchey & Gaston 2006) and should be measured using standardised protocols (e.g. Weiher et al. 1999, Moretti et al. 2017). To unveil or predict ecosystem properties and interactions between organisms (even from different trophic levels), functional traits should be explicitly related to individual **performance** (Violle et al. 2007). Our review of the published studies on functional traits of parasites, mainly FD-related studies, suggests that the choice has been often dictated by their relationship with the research questions being asked and/or by their availability, without explicit consideration of their functional value and repeatability in future studies (Table 1). To facilitate comparisons between groups of parasites and promote reproducibility, a unified framework with a common terminology for parasite functional traits is absolutely needed and would parallel frameworks developed for other groups of organisms (e.g. plants Weiher et al. 1999; terrestrial invertebrates Moretti et al. 2017; crustacean zooplankton Barnett et al. 2007; algae Lange et al. 2016). Such a framework would improve and maximise the utility of functional trait approaches in parasitology and contribute to the delineation of the roles of parasites in communities and ecosystems more broadly. Furthermore, it will allow for comparing parasite and host diversities on common terms (see Weiss & Ray 2019 for how to compare functional traits across taxa), thereby paving the way for general ecologists to widely include parasites in community ecology.

Box 1. Taxonomic and Functional Diversity

The way in which diversity is measured is key to understanding species assemblages. Community ecology has relied on species-based measurements (taxonomic diversity, TD), which leads to a loss of ecological (functional) and evolutionary (phylogenetic) information. To solve this limitation, two alternative frameworks to study biodiversity were developed: **phylogenetic diversity** (**PD**) measures the diversity of evolutionary histories of organisms in communities; and functional diversity (FD) quantifies the relative originality of functions provided by each organism in a community (Pavoine & Bonsall 2011). The combined study of these three facets of diversity provides a more complete picture of ecosystem properties. Among the many approaches developed to quantify TD and FD (and PD), we focus on Rao's diversity index (Rao 1982) and Jost's correction of diversity (Jost 2007) given their widespread use in community ecology.

Rao's index is derived from Simpson's index and allows comparisons between TD and FD within the same mathematical framework (Rao 1982). This distance-based diversity measure relies on a matrix of pairwise dissimilarities (d) between species. Species are plotted in an n-dimensional functional trait space (n: number of functional traits) and the pairwise distances between them are calculated (Petchey & Gaston 2006) (Figure IA).

Diversity can be partitioned into spatial components (i.e. α, β, γ), which is key to describe species composition and ecosystem functioning. The α level represents diversity at the sampling unit (usually the host individual), and the Rao's index incorporates the distance between species, i and j (d_{ij}), and the relative abundance (p) of each one with respect to the total number of species in the sampling unit (s) (Figure IB). d_{ij} depends on the kind of data considered, such as functional traits (FD). For TD, $d_{ij} = 1$ for all $i \neq j$ and $d_{ii} = 0$ for all i, so the Rao's index is equal to the Simpson's index of diversity and reaches its potential maximum value (Botta-Dukát 2005).

At γ level, the locality is studied as a single unit by pooling units (hosts) together. P_i and P_j are the local relative abundances for species *i* and *j*, and *S* the total number of species in the locality (de Bello et al. 2010) (Figure IB). β diversity measures the amount of diversity due to differences between units from the same locality (Figure IB). To make β diversity comparable across localities, α and γ diversity values are usually transformed into their **equivalent numbers** (α_{eqv} and γ_{eqv}) (Jost 2007). β Diversity is expressed as a proportion of the local (γ) diversity across all units (α) within a locality. These proportions can be normalised between (0,1) (β_{norm}) to account for a different number of units (*x*) from each locality (de Bello et al. 2010).

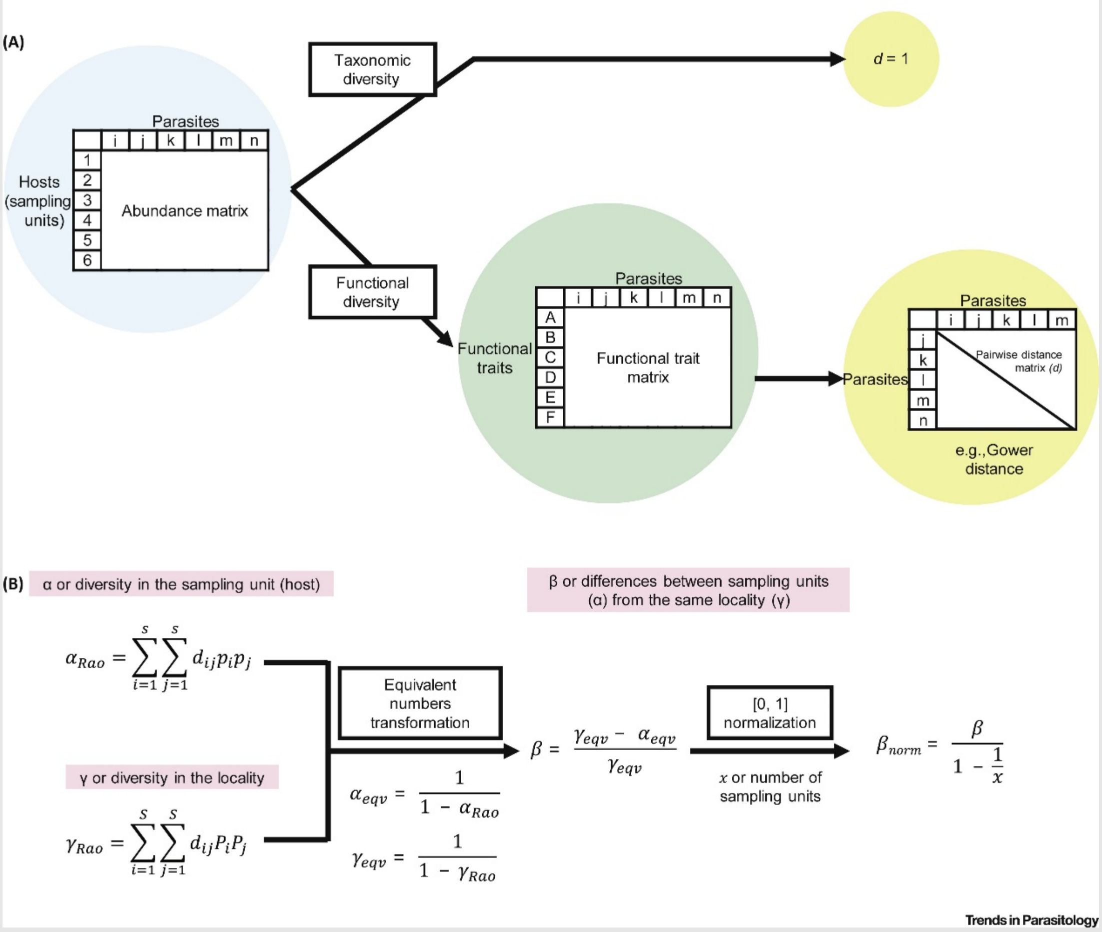

Figure I. Taxonomic and Functional Diversity According to Distance-Based Indices (A) and Rao's Equations for α, β and γ Diversity (B).

Here, we propose a unified functional trait framework for metazoan parasites grounded in the current ecological theory, with the challenge of identifying traits sufficiently general and applicable across phylogenetically distant parasite taxa without losing resolution when characterising the functional groups of parasites.

Table 1. Traits used as functional traits in previous parasitological studies.

Trait	Type of trait[1]	Type of measurement	Level of measurement	External information	References
Body length or size	Functional trait	Quantitative (continuous linear measurements: maximal body length; midline length of the dorsal shield)	Individual	No	Mouillot et al. 2005, Krasnov et al. 2016, 2019a, 2019b
Attachment	Functional trait	Quantitative (continuous standardised linear measurements: haptor's sclerotised parts; ordinal: number of combs)	Individual	No	Mouillot et al. 2005, Krasnov et al. 2016, 2019b
Reproductive organs	Functional trait	Qualitative (categorical: relative length; shape of the vagina armament; shape of the copulatory tube; shape of the accessory piece of the copulatory organ)	Individual (identical for all individuals from the same species)	No	Mouillot et al. 2005
Niche space	Ecological performance	Quantitative (distribution of individuals or biomass of a species in a niche space)	Species	Yes	Keeney & Poulin 2007
Mean characteristic abundance	Demographic parameter	Quantitative (mean number of parasites per individual host; mean abundance on the principal host)	Species	Yes	Krasnov et al. 2015, 2016, 2019a, 2019b
Path of infestation	Ecological performance	Qualitative (cutaneous, percutaneous or alimentary)	Individual (identical for all individuals from the same species)	Yes	Sokolov & Zhukov 2017
Niche preference	Ecological performance	Qualitative (body, burrow/ nest or both)	Individual (identical for all individuals from the same species)	Yes	Krasnov et al. 2015, 2016, 2019b, Warburton et al. 2017
Feeding mode	Functional trait	Qualitative (binary: facultative or obligatory haematophagy; categorical: facultative, non-exclusive obligatory, obligatory haematophagy)	Individual (identical for all individuals from the same species)	No	Warburton et al. 2017, Krasnov et al. 2019a

Seasonality in reproduction	Ecological performance	Qualitative (main reproduction period: warm, cold season or year-round)	Individual (identical for all individuals from the same species)	Yes	Krasnov et al. 2015, 2016, 2019b, Warburton et al. 2017
Host specificity	Ecological performance	Quantitative (mean number of host species on which a given flea species was recorded; mean phylogenetic distinctness of the regional and continental host spectrum; number of hosts on which an ectoparasite species was recorded significantly correlated with the number of individual parasites collected)	Species	Yes	Krasnov et al. 2015, 2016, 2019a, 2019b, Warburton et al. 2017
Degree of sexual dimorphism	Demographic parameter	Quantitative (logarithmic female-to-male body size ratio)	Species	No	Krasnov et al. 2019a, 2019b
Geographic range size	Ecological performance	Quantitative	Species	Yes	Krasnov et al. 2019b
Geographic range latitude	Ecological performance	Quantitative (latitude of the centre of the geographic range)	Species	Yes	Krasnov et al. 2019b

[1] Traits classified following definitions in Violle et al. 2007.

Multiple Solutions, One Lifestyle: Parasite Functional Traits

Since parasitism has arisen several times independently throughout the tree of life, it is difficult to find a common definition, and this leads researchers to disagree on considering some particular groups of organisms as parasites. Regardless of achieving a consensus, the fact is that the same functional traits can be shared by organisms with different life strategies. Hence, our unified framework can be applied to a wide range of metazoans differing in their parasitic way of life and can inspire further extension to non-metazoan parasites.

Core List of Parasite Functional Traits

In order to make the functional trait framework comparable across spatial and temporal scales, collect functionally representative information, share data, and maximise the applicability of results, functional traits in parasitology should conform to the accepted definition in community ecology. They should be fitness-related, measured at the individual level, and without referring to information external to the individual (Violle et al. 2007). The functional traits proposed herein are related to three universal challenges faced by organisms: dispersal, establishment, and persistence (Weiher et al. 1999) (Table 2, Figure 1) and influence fitness through its effects on performance. Most importantly, a requirement for any functional trait is that it can be measured at the individual level, without reference to the environment or any other level of organisation (Violle et al. 2007, Carmona et al. 2016), although in practice **species (or population) mean trait values** are usually employed as surrogates of the original trait (Moretti et al. 2017) (Box 1). In agreement with these criteria, we propose a framework applicable to metazoan parasites based on morphological, life-history, and behavioural characteristics (Table 2, Figure 1).

The following core list includes seven functional traits, which we consider the minimum that can be applied to any metazoan parasite and to address any ecological question.

Attachment

Related to persistence (Table 2, Figure 1). Categorical, continuous, or discrete. As categorical, it is coded as the type of organ used to hold on to their host, whereas as continuous or discrete, metric measurements, (e.g. sucker diameter), or number of attaching structures (e.g. clamps), can be used respectively. Each type of measurement could be combined in a **nested functional trait**.

Egg shape

Related to dispersal and establishment (Table 2, Figure 1). Categorical or continuous. As categorical, it can be approximated to geometrical bodies. As continuous, different shape factors (i.e. dimensionless metrics that depend on the relationship between geometric elements) can be used.

Feeding

Related to persistence (Table 2, Figure 1). Categorical or continuous. As categorical, type of food ingested (e.g. blood). As continuous, examples include amount of food eaten, values of $\delta^{13}C$ and $\delta^{15}N$ isotopes, and time spent feeding.

Life Cycle

Related to dispersal, establishment, and persistence (Table 2, Figure 1). Binary, discrete, or continuous. As binary, it can be coded as organisms with a "one-host" (i.e. monoxenous) or "several-host" (i.e. heteroxenous) life cycle. As discrete, it can be assessed as the number of intermediate, paratenic, or dormant stages, episodes of reproduction or times actively transmitted, among others. Examples of continuous traits include estimates of the longevity of developmental stages. See discussion below.

Egg Size

Related to dispersal and persistence (Table 2, Figure 1). Continuous (Table 3).

Number of Eggs

Related to dispersal, establishment, and persistence (Table 2, Figure 1). Discrete (Table 3).

Body Mass

Related to establishment and persistence (Table 2, Figure 1). Continuous (Table 3).

Table 2. Relationship between functional traits of metazoan parasites and three primary challenges faced by organisms (dispersal, establishment and persistence) found in the literature.

Traits	Dispersal	Establishment	Persistence
Morphological			
Attachment			Different strategies depending on the likelihood of being dislodged. More elaborated organs in individuals with higher risk of being detached (Poulin 2007).
Egg size	Positive relationship. Larger eggs (or transmission stages) enhance the probability of transmission, therefore dispersal (Koehler et al. 2012).		Positive relationship. Larger eggs (or transmission stages) have greater food reserves and thus they can spend longer searching for a suitable host (Costello 2006).
Egg shape	Negative relationship with higher density or presence of appendages in eggs or transmission stages. Individuals with complex egg morphologies are less dispersed (Chambers & Ernst 2005). Positive relationship with complex morphologies when appendix-like structures enhance the transmission to an intermediate host (e.g. Pfenning & Sparkes 2019)	Positive relationship with complex morphologies (Yoshida 1920).	
Mass		Negative relationship with available space. More difficult for larger species (Cramer & Cameron 2006, Koehler et al. 2012).	Positive relationship with fecundity in adult individuals (Poulin & Latham 2003).

Behavioural			
Feeding			Negative relationship. More aggressive habits could damage the host and cause the die-off the parasite. Different degrees of persistence depending on pathogenicity (Poulin & Morand 2004). However, it may be advantageous in terms of competition with other parasites.
Life-history			
Life-cycle	Positive relationship with number of intermediate stages through host migration (e.g. Koehler et al. 2012).	Positive relationship with individuals without intermediate stages when there is a high probability of reaching the definitive host (Parker et al. 2003).	Positive relationship with individuals with intermediate stages counteracting environmental stress (Poulin 1992).
Number of eggs	Positive relationship. Individuals that produce more eggs will be more widespread (Costello 2006).	Positive relationship. More likely to succeed in forming a new generation (Lagrue et al. 2011).	Positive relationship. High number of eggs increases the possibilities of persistence over time (Croll et al. 1982, Roughgarden & Iwasa 1986).

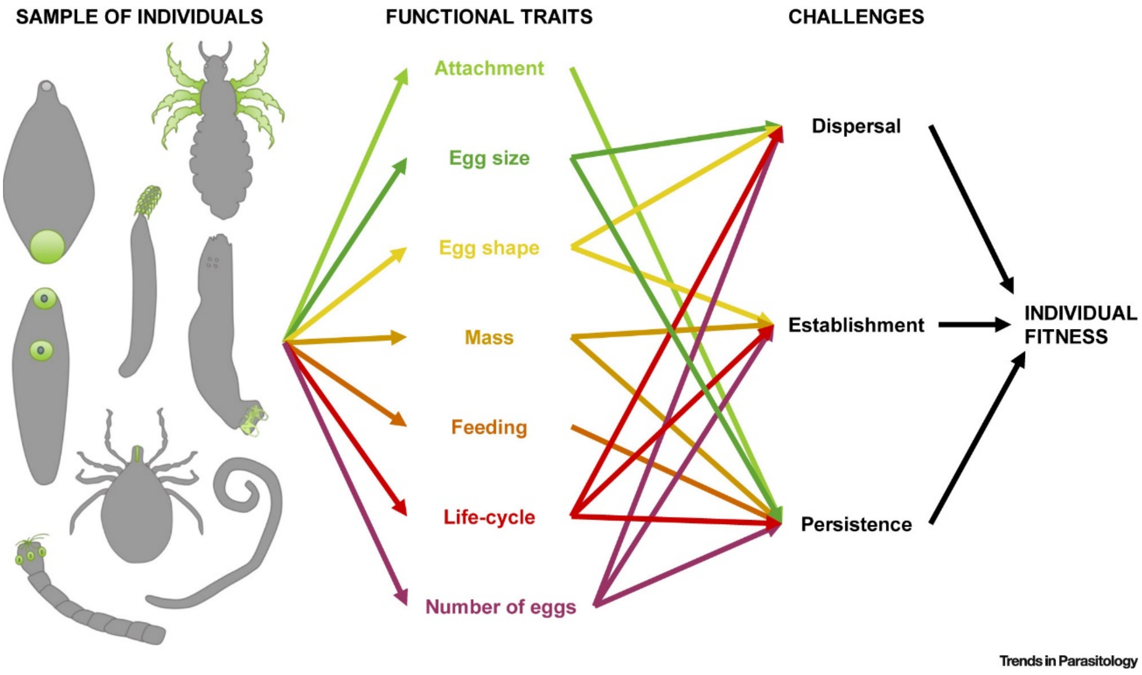

Figure 1. Key Figure. Core list of metazoan parasite functional traits. The term "parasite" can be used to define organisms of distant phylogenetic origins. However, the same functional traits can be shared by organisms with different parasitic strategies. Functional traits are morphological, physiological, phenological, and behavioural characteristics of individuals, measurable at the individual level and that reflect individual performance in ecosystems and its fitness (adapted from Violle et al. 2007).

Measuring Functional Traits

Availability and quality of functional trait data are always an issue, especially for parasites for which information about traits has always been scarce (e.g. Morand 1996). Reliable trait information can be obtained from at least four sources: (i) direct observation, for example, researchers can notice the digestive content of the parasites to establish feeding categories (Moravec 1980); (ii) species descriptions, for example, number of eggs reported (Presswell & Blasco-Costa 2019); (iii) standardised protocols to measure continuous or categorical functional traits, for example, estimation of body mass (Llopis-Belenguer et al. 2018); (iv) proxies, for example, the product of egg length and width as egg size (Poulin 1997). In Table 3, we summarise different approaches previously used in the literature to easily measure some of the proposed traits above.

Analyses based on mean trait values per population or species are acceptable solutions to measure FD in a community (Box 1), albeit they neglect intraspecific trait variability, which is most appropriate to address questions related to responses to environmental gradients, such as climate change (Cadotte et al. 2015, Carmona et al. 2016). In any case, we recommend getting functional trait information from a reasonable number of individuals for reliable estimates of the species (or population) mean trait value (Moretti et al. 2017) and intraspecific trait variability. This is particularly relevant for traits that vary widely among conspecifics, as, for example, the morphology of attachment organs (Rodríguez-González et al. 2015).

Parasites versus Free-Living Organisms

The study of parasite communities entails an obvious difference with respect to free-living organisms: hosts are discrete and natural sampling units. This advantage can lead to the establishment of comparisons and studies being more easily reproducible in parasitology than in other disciplines. Furthermore, we can get a reliable representation of the community by sampling an adequate number of hosts (Walther et al. 1995). However, as any biological organism, hosts differ in their genetic and physiological condition to prevent parasitic infections (Krist 2004) and these are additional effects to control for in the study of natural assemblages of parasites. Although the characteristics of the environment should not be used as traits (see below), providing detailed information about the host where the **attribute** (i.e. value or category) for a functional trait has been measured is essential to interpret its ecological and evolutionary meaning (Violle et al. 2007). Thus, such information should be considered in the analyses and in the discussion of the results.

Caveats for a Functional Trait Framework for Parasites

Select Appropriate Number of Functional Traits

An important challenge is to identify an adequate number of key functional traits (Petchey & Gaston 2002) that reflect the performance of organisms in their ecosystems or in their interaction with other organisms in the community (e.g. Weiher et al. 1999, Lavorel et al. 2013). The number of functional traits that can potentially be assessed in any organism is large (Carmona et al. 2016). But our ability to measure functional traits of parasites is often limited due to sampling biases, lack of information about their life history (Poulin 2010), and unclear evidence of a link between the trait and its impact on individual fitness, among other reasons. The core list of functional traits proposed herein should not be considered complete or closed. In studies of phylogenetically closely related species, for example, traits related to reproductive organs can be used as they tend to diverge to avoid cross-fertilisation among closely related species and are likely to have direct impacts on fitness (e.g. Mouillot et al. 2005). Conversely, when distant phylogenetic groups are studied, traits that tend to converge into few categories should be preferred (e.g. those related to transmission behavior, Thomas et al. 2005).

Furthermore, in some situations, functional traits can be correlated to each other. For instance, a trade-off between egg size and egg numbers has been reported for some parasites (Herreras et al. 2007a, Cavaleiro & Santos 2014). So, when a trade-off is suspected, the opposed traits should be included in the analysis to avoid biased predictions of fitness.

Use Soft Traits

Functional traits should be easy and cheap to measure (soft functional traits *sensu* Weiher et al. 1999). So, when several functional traits are related to the same processes, we should select the softest (Weiher et al. 1999, Violle et al. 2007). For example, the longevity of egg or larval stages relates to persistence (Costello 2006), but longevity is a difficult-to-measure (hard) trait, especially in the wild. In contrast, egg and larval size often reflect longevity and thus represent easy-to-measure (soft) traits. Otherwise, we may not be able to get all the functional information for each species in our sample or we could preclude replication in future studies (Table 3; see matrix of pairwise distances, d_{ij}, in Box 1).

Examples of hard functional traits of parasites include those that involve the life cycle as longevity, since it would require tracking the lifespan of the parasite from hatching to death (e.g. Morand 1996). Likewise, functional traits such as voltinism (number of generations an individual completes in a single year), metabolic rate, or parity (number of times a female lays eggs or gives birth) proposed recently for terrestrial free-living invertebrates (Moretti et al. 2017), are often unknown and very difficult to measure in most parasitic organisms. Researchers should, therefore, focus on soft traits that are correlated with the function to be assessed (e.g. persistence) but easier to measure than the function itself (e.g. egg size). These often have been referred to as **functional markers** (Garnier et al. 2004).

Performance Traits and Ecological Performances

One should abstain from considering as functional traits, features based on information external to the individual or measured at a higher level than the individual (Violle et al. 2007). Particularly, specificity (Table 1), widely used in parasitology, could be considered as a proxy of parasite survival ability (a **performance trait**). As classically defined, specificity cannot be measured at the individual level because it represents the number of different hosts (environmental habitats) in which a parasite species can survive, instead of habitats which every single individual in a sample could inhabit. In addition, it relies on information external to the individual (range of hosts) to be defined. Thus, specificity does not conform to the concept of functional trait currently accepted in ecology (Violle et al. 2007). The range of hosts a parasite can infect is just an environmental variable. Likewise, habitat/niche (e.g. host tissue or location on or in the host, the ecto- and endoparasite dichotomy), the taxonomic identity or features of hosts, and macrohabitat (e.g. freshwater, marine, terrestrial, mixed) are environmental variables (i.e. external to the individual) commonly employed in our field. The response of an organism to these environmental variables can be measured as an **ecological performance**. For instance, given an array of potential hosts in a locality (environmental variable), the survival ability (performance trait) of a parasite can be assessed as classical host specificity, that is, the host range (ecological performance), for the parasite species at that locality.

Table 3. Standardised methods to measure continuous functional traits.

Functional trait	Methods	
Egg size	Volume of geometric morphologies: sphere for copepods; ellipsoid or prolate spheroid for nematodes, trematodes, acanthocephalans or fleas. Proxy of egg size: product of egg length and width for trematodes; maximum length of eggs for monogeneans.	Kearn 1985, Poulin 1997, Fredensborg & Poulin 2005, Herreras et al. 2007a, Cavaleiro & Santos 2014, Khokhlova et al. 2015
Number of eggs	Counts from individuals mounted on permanent slides for trematodes. Counts from aliquots of dissected individuals for nematodes. Number of eggs laid by an individual for a period for monogeneans, trematodes and fleas. Automated counting methods for nematodes.	Kearn 1985, Fredensborg et al. 2004, Herreras et al. 2007b, Khokhlova et al. 2015, Preswell & Blasco-Costa 2019
Mass	Area by Depth by Density for flatworms. Volume of Revolution by Density for nematodes or acanthocephalans. Direct measurements (weighting large parasites on a scale). Approximating body forms to regular geometric morphologies. Generalised regression equations between body length and mass.	Llopis-Belenguer et al. 2018

Although ecological performances can provide valuable insight into community ecology (e.g. Cizauskas et al. 2017), they depend on the coordinated response of multiple traits to environmental factors (Violle et al. 2007) and thus do not represent functional traits. We are not in favour of using ecological performances under a functional-trait perspective because it hinders our understanding of the actual mechanisms driving the fitness responses of the organisms. However, in the absence of knowledge on the traits influencing individual fitness, an ecological performance can be tentatively used as a surrogate of a complex of functional traits.

The use of other features that refer or apply to different levels of organisation (i.e. **demographic parameters**, such as population size, birth, death, immigration, or emigration rates) is discouraged because they do not affect fitness (Violle et al. 2007).

Handling Missing Information

It is difficult to gather a complete or highly resolved dataset of each trait for each taxon (e.g. Barnett et al. 2007). Often, information for a functional trait is either not available or structurally absent (e.g. number of eggs in larval stages). Nonetheless, as many community ecology analyses (such as FD studies) rely on computing a matrix of pairwise distances between parasite species (Box 1), one very common solution is to use the **Gower distance**: pairwise (dis)similarities among taxa based on traits (Gower 1971). Its application is gaining currency as a measure of the pairwise distances among taxa based on traits because of its ability to combine several types of traits (continuous, categorical, binary, etc.) and to allow for missing data when calculating the pairwise dissimilarity matrix of functional traits between species (Botta-Dukát 2005) (Box 1).

Dealing with Different Developmental Stages

Commonly, hosts (i.e. sampling unit, Box 1) harbour parasite species at different developmental stages and, even a parasite species can be represented by adults and larvae in or on the same host. Depending on the aims of the study, it is acceptable to focus on adults, larvae, or both. For instance, one might be interested in unveiling the forces that select certain functional traits of parasites at their definitive hosts exclusively. So, researchers would exclusively focus on adults. If the study considers incorporating larvae and adults jointly, the first question is whether they represent the same or different functional entities. The answer depends on the previous knowledge on each parasite species involved and the scope of the study. Below, we contemplate three potential scenarios:

(i) Adults and larvae of the same species in/on the same organ. Host role: definitive. Larvae that arrived recently and still have to develop to the adult stage share host with adult stages (e.g. ticks (Parasitiformes)). Adults and larvae can be considered as the same functional entity when computing pairwise dissimilarity matrix. For continuous functional traits, we propose to average individual values (regardless of the adult or larval condition) by the total number of individuals.

(ii) Adults and larvae of the same species in/on the different organs. Host role: definitive and intermediate, respectively.

This can occur in species with multiple developmental stages and complex life cycles (e.g. *Trichinella* spp.). Adults and larvae can be considered as different functional entities holding different functional traits. For instance, feeding can be set as "tissue" or "latent" depending on its developmental stage. Furthermore, functional traits related to adults, such as size and number of eggs, will be set to zero for the larval stages.

(iii) Only larvae of a given species occur. Host role: intermediate.

A species only uses the target host during its larval stage. As in (ii), the larvae would represent an independent entity in terms of functional trait characterization.

Finally, as a note of caution, decisions on what to include must be consistent across both the functional and taxonomic facets of diversity (Box 1). Thus, if, for instance, adults and larvae of species A are considered as separate functional entities, the same criterion should apply in the analysis of **taxonomic diversity**.

Concluding Remarks

This framework sets the basis for the selection of adequate functional traits (fitness-related, measurable at the individual level, and without information external to the individual, Violle et al. 2007) and promotes novel insights into the mechanisms of parasite community assembly and dynamics. Studying parasite ecology from a functional perspective is lagging behind other disciplines and this is hindering our fine understanding of the multitude of roles that parasites play in ecosystem properties. As in other disciplines, we hope that this ready-to-use core list of functional traits of metazoan parasites inspires further efforts in defining and understanding functional traits of parasitic organisms.

To date, most functional trait studies have been based on species (or population) mean trait values. However, focussing on intraspecific trait variability could be especially insightful (Carmona et al. 2016) because conspecifics can occupy different positions in the **functional trait space** or individuals of different species can overlap in it (see Outstanding Questions).

In consequence, it can prove extremely rewarding for revealing cryptic (i.e. unrelated or overlapped positions) functional roles and mechanisms, which are masked in the mean value approach. As it was previously demonstrated (Carmona et al. 2016), this approach entails computing functional trait information of a statistically meaningful number of individuals in the sample at the same time. This seems especially challenging in parasitology because of the patchy distribution of parasites on or in their hosts. The issue of intraspecific trait variability also brings to light the need to perform more experimental studies to unveil the relationship between potential functional and performance traits and the components of individual fitness. Furthermore, the development of new functional markers can prove fruitful to understand complex ecosystem properties. For example, the proportion of the chemical elements C:N:P in parasite individuals can be a proxy of the performance of the individual nutrient consumption, and, finally, an indicator of the nutrient flux at a locality (Bernott & Poulin 2018). Ultimately, the expansion of this core list of functional traits relies on the availability of species information. Thus, the creation of a public-access database of functional traits of parasites compiled by international and multidisciplinary parasitologists, from taxonomists to ecologists, is highly encouraged, as it exists for other groups of organisms.

Outstanding questions

- How do different environmental filters select for parasite functional traits in communities?
- How do species interactions select for parasite functional traits?
- Can we predict species abundances within communities based on trait variation, environmental conditions, and competitive interactions?
- What are the mechanisms selecting for particular traits at different stages of parasite community assemblies?
- Under a functional trait perspective, what can we learn from parasite biological invasions? Which functional-trait attributes of introduced parasites can foster the success of an invasion? Which attributes of native parasites can hamper host invasions?
- How do functional-trait attributes determine the position and role of parasites in the interaction network of the community?
- How can intraspecific functional trait variability inform of ecoevolutionary responses in parasite communities?

- What hidden patterns in parasite community ecology could be revealed by the combined analysis of the facets of diversity (taxonomic, functional, and phylogenetic diversity)?

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Glossary

Attribute: value or category taken by a trait at any place and time.

Demographic parameter: population-level feature based on aggregation of features of individuals.

Ecological performance: optimum and/or the breadth of distribution of performance traits along an environmental gradient.

Equivalent numbers (or effective number of species): value of a diversity index that would result if all the species of the assemblage were equally likely (equally abundant and evenly distributed) and maximally dissimilar.

Functional diversity (FD): a measure of richness and abundance of functional traits in a community or ecosystem.

Functional marker: trait correlated with a function that is easier to measure than the function itself. For example, in Acanthocephala the complex-to-measure function dispersal ability of an individual has been assessed by egg morphology (Pfenning & Sparkes 2019).

Functional trait: trait (see below) which impacts the fitness of individuals and reflects their performance in ecosystems.

Functional trait space: *n*-dimensional space where *n* is the number of functional traits considered. Typically, species are plotted in such space according to their species mean functional trait value. Under the recent "intraspecific trait variability" approach (Carmona et al. 2016), individuals are plotted according to their own values, without averaging by species.

Gower distance (d_{ij}): a measure of the pairwise distances among taxa based on traits. It ranges from zero (identical taxa) to one (maximum dissimilarity between taxa). It allows different types of variables and missing data. It is associated with some properties of the Euclidean distance.

Intraspecific trait variability: range of variation in the same trait among conspecifics within a sample.

Nested functional trait: functional trait that can be measured at different self-contained levels. Levels can combine different types of attributes. For example, "attachment", a categorical functional trait can be combined with morphometric (continuous) measures of the organ involved.

Performance: the ability of individuals to grow, reproduce, or survive in a particular ecological habitat.

Performance traits: traits that measure one of three components of the fitness (survival, growth, or reproduction). They can be measured in a cohort that reflect average fitness of individuals.

Phylogenetic diversity (PD): measure of the richness and abundance of genetically different entities in a community or ecosystem.

Property: feature or process at community or ecosystem level.

Species (or population) mean trait value: mean value of a trait for a species or population of the species. These values are used in the functional trait matrix (Box 1) to calculate the distances between species/populations.

Taxonomic diversity: a measure of the richness and abundance of taxonomic entities in a community or ecosystem.

Trait: morphological, physiological, phenological, or behavioural feature measurable at the individual level, from the cell to the whole organism, without reference to the environment or any other level of organisation. Traits can be of various types: continuous, discrete, ordinal, categorical, binary, fuzzy, multiple choice, or circular.