

REVIEW

On the development of a predictive functional trait approach for studying terrestrial arthropods

Pierre-Marc Brousseau¹  | Dominique Gravel²  | Ira Tanya Handa¹ ¹Département des Sciences
Biologiques, Université du Québec à
Montréal, Montréal, QC, Canada²Département de Biologie, Canada Research
Chair on Integrative Ecology, Université de
Sherbrooke, Sherbrooke, QC, Canada

Correspondence

Pierre-Marc Brousseau
Email: brousseau.pierre-marc@courrier.uqam.ca

Handling Editor: Catherine Parr

Abstract

1. The characterization of ecological communities with functional traits allows to consider simultaneously the ability of a species to survive and reproduce in an environment, its interactions with other species and its effects on the ecosystem.
2. Functional traits have been studied mainly by plant ecologists, but are increasingly common in the study of other taxa including arthropods. Arthropods represent a group for which a functional trait approach could be highly profitable because of their high diversity, abundance, ubiquity and role in many important ecological processes.
3. This review synthesizes two decades of functional trait research on terrestrial arthropods. We show that while the approach has gained popularity, particularly in the last decade, the **absence of clearly postulated hypotheses is a recurrent problem limiting generalization**. Furthermore, studied traits are often poorly related to studied functions. To address these problems, we propose a step-by-step protocol to postulate clear hypotheses prior to trait selection and emphasize the need for a common set of more generalizable traits in future studies.
4. Extending the functional trait approach to arthropods opens the door to improving our understanding of interspecific interactions and potential links between response and effect traits. We present the concept of trait-matching with several examples of arthropod traits known to be effective predictors of consumer–resource interactions.
5. The development of a successful functional trait approach for terrestrial arthropods will necessitate an understanding of relevant traits, standardized measurement protocols and open access databases to share this information. Such progress will provide ecologists with a new set of tools to answer broad questions in several fields including the study of community assembly, ecological networks and multitrophic functionality.

KEYWORDS

biotic interactions, food webs, functional ecology, insects, intraspecific trait variation, spiders

1 | INTRODUCTION

The use of traits to understand the relationship of an organism to its environment has been fundamental to ecology. While early studies on traits were limited to qualitative assessments of community structure (Raunkjær, 1934), a new generation of studies is building on a wide range of quantitative indices (Mouillot, Graham, Villegier, Mason, & Bellwood, 2013), providing a more predictive approach (Webb, Hoeting, Ames, Pyne, & Poff, 2010) and allowing for a greater emphasis on functions within ecosystems (Lavorel, 2013). A “trait” refers to any morphological, physiological, phenological or behavioural characteristic measurable at the individual level (Pey, Nahmani et al., 2014; Violle et al., 2007). “Functional traits” are “traits” either related to the performance (growth rate, survival or reproduction probability) of the organism (*response traits*), to an ecological process (*effect traits*) (Violle et al., 2007), or, in some cases, to both (Lavorel et al., 2013). **While taxonomic studies typically describe changes in community composition, functional trait studies aim to reveal the mechanisms behind these changes and their consequences for ecological processes (Culp et al., 2011; Shipley, 2010). The concept transcends the notion of species, making trait-based studies more generalizable than taxonomic studies by providing a common currency to compare similar communities from different regions or environments with few species in common (McGill, Enquist, Weiher, & Westoby, 2006).**

The response trait approach is based on the hypothesis that the environment (landscape, abiotic conditions and biotic interactions) acts as a filter, selecting individuals based on their traits (Diamond, 1975; Keddy, 1992) (Figure 1). As such, response traits represent an indirect link between the environmental filters (e.g. humidity level, available food) and the performance (growth, survival, fecundity) of an organism (McGill et al., 2006). Thus, species with the right traits in a given situation will be more likely to increase their population size through higher performance (McGill et al., 2006) and immigration rate (Pulliam, 2000).

Effect traits determine the impact of an organism on ecosystem processes (Díaz & Cabido, 2001). For example, the hairiest pollinators are expected to transport a larger amount of pollen (Stavert et al., 2016). It has been proposed that communities composed of species with high dissimilarity between their effect trait values could result in complementary interactions through niche partitioning or facilitation (Loreau & Hector, 2001). Such effects were demonstrated with plants, bacteria and invertebrates (Cadotte, Cardinale, & Oakley, 2008; Coulis et al., 2015; De Oliveira, Haettenschwiler, & Handa, 2010; Gravel et al., 2011; Heemsbergen et al., 2004) and have helped gain understanding of how biodiversity influences ecosystem functions.

While the functional trait approach has an important history in plant ecology (Cadotte et al., 2008; Cornelissen et al., 2003; Wright et al., 2004), there has been an increasing interest to adapt the approach to study animals (Luck, Lavorel, McIntyre, & Lumb, 2012; Moretti et al., 2017; Pey, Nahmani et al., 2014) and microbes (Larkin & Martiny, 2017), so as to improve our understanding of multitrophic

interactions (de Bello et al., 2010; Gravel, Albouy, & Thuiller, 2016; Lavorel et al., 2013). Although in theory, very broad trait axes (or economic spectra) reflecting resource acquisition, growth, dispersal, etc., are common to all organisms (Litchman, Ohman, & Kjørboe, 2013; Salguero-Gómez et al., 2016), moving beyond plants requires defining new types of traits. For example, some aspects of animal ecology can only be assessed by including behavioural functional traits (Luck et al., 2012; Pey, Nahmani et al., 2014). Extending these reflections will also require a better understanding of trait syndromes, that is correlations or trade-offs between traits caused by physiological or evolutionary constraints. Trade-off patterns in the investment towards reproduction vs. survival are expected to be similar for plants and animals (Litchman et al., 2013; Paniw, Ozgul, & Salguero-Gómez, 2018), but will require continued thought on various dimensions. For example, antipredator traits are currently underrepresented for terrestrial invertebrates, but their study will be beneficial to our understanding of predator-prey interactions, population dynamics and ecosystem functions.

Our objective with this review was to survey published research on functional traits of terrestrial arthropods to determine how the functional trait approach has been integrated to date. We have chosen to focus on terrestrial arthropods as they are ubiquitous, exceptionally diverse, and are involved in key ecological processes including decomposition (Handa et al., 2014; Kočárek, 2003) and pollination (Schleuning, Fruend, & Garcia, 2015). As such, arthropods represent a broad group from which learning should be transferable to apply functional trait approaches to other terrestrial animals. In this review, we highlight progress made in the study of functional traits of terrestrial arthropods and we propose solutions to challenges with the hope to improve future research in this field. To do this, we conducted a literature review (1) to understand which functional traits and which taxa have been studied and (2) to determine whether published studies postulated hypotheses leading to a better understanding of the mechanisms involved in community assembly or ecosystem functioning, as originally intended with this approach. We also illustrate how this approach is being extended to understand interspecific interactions (e.g. consumer resource) through the matching of traits.

2 | MATERIALS AND METHODS

The literature review was carried out by searching publications on the Web of Science and Google Scholar with the criteria “traits” + “function*” + all principal classes and orders of terrestrial arthropods (e.g. “arthropods”, “insects”, “spiders”, “beetles”). Citations were also tracked across article. Only studies that were explicitly trait-oriented were retained, that is studies that used arthropod functional traits (according to the above definition) to study the response to a disturbance or to an environmental filter (response traits) or their impact on ecosystem processes (effect traits). We deliberately concentrated our review on studies referring to the functional trait approach and therefore excluded studies focusing on particular aspects

of organisms, such as morphology, but that were not relating traits to performance or an ecosystem process. We did not include studies where the guild (or trophic level) was the only trait, as these typically describe a group of species rather than a functional attribute per se. We also rejected studies based exclusively on body size due to its commonness and the difficulty to formulate hypotheses relating this trait to a single environmental filter (see Section 4.2). The literature review included studies published before January 2017.

For studies that included response traits, we evaluated whether the elements present in the introduction, material and methods and supplementary materials permitted to identify how the studied traits were mechanistically related to the subject of the study (explicit examples in Table S1). For this task, we excluded studies dealing with broader questions regarding conservation (Maes & Van Dyck, 2001) or guild definitions based on shared traits (Silva & Brandão, 2010), for which hypotheses could not be evaluated based on our

criteria. We answered three questions (Figure 2). First, we validated whether environmental filters (abiotic, biotic and geographic) were clearly identified (Bremner, 2008). To assess this aspect, we verified whether environmental gradients that were expected to vary and thus act as filters were presented. Identified filters across studies were diverse and included humidity level, temperature, available food, diversity of predators and landscape fragmentation. Cases where filters were clearly identified often had a sentence in the form of “We hypothesized a direct effect of [filter w] on the community structure of [taxa x].” Other accepted forms were “[Disturbance v] is known to influence [filter w].” Cases where the disturbance was related to the communities without identifying any clear filters (e.g. “Land use will impact the community structure of [taxa x]”) were rejected. When a gradient was identified, but that this gradient did not allow to identify the filtering mechanism involved, the filter was also considered as unidentified. For example, a failed case would be if a gradient of floristic composition was identified, but no further detail was provided to determine whether the gradient affected vegetation structure, diversity of available food, microclimate, etc.

Secondly, we evaluated whether a clear hypothesis linking environmental filters to organismal functions was postulated (Naeem & Wright, 2003). Functions were diverse and included dispersal ability, feeding interactions, thermal tolerance and fecundity (Table 1 for summary, Table S2 for full list). For this aspect, we looked for sentences in the form “We hypothesized that [filter w] will influence the [function y].” We also considered this aspect fulfilled in sentences such as “[Filter w] can have a negative/positive impact on species with a low/high ability in [function y].” It was considered as unfulfilled if the function was directly related to the disturbance, but the filters were not clearly identified.

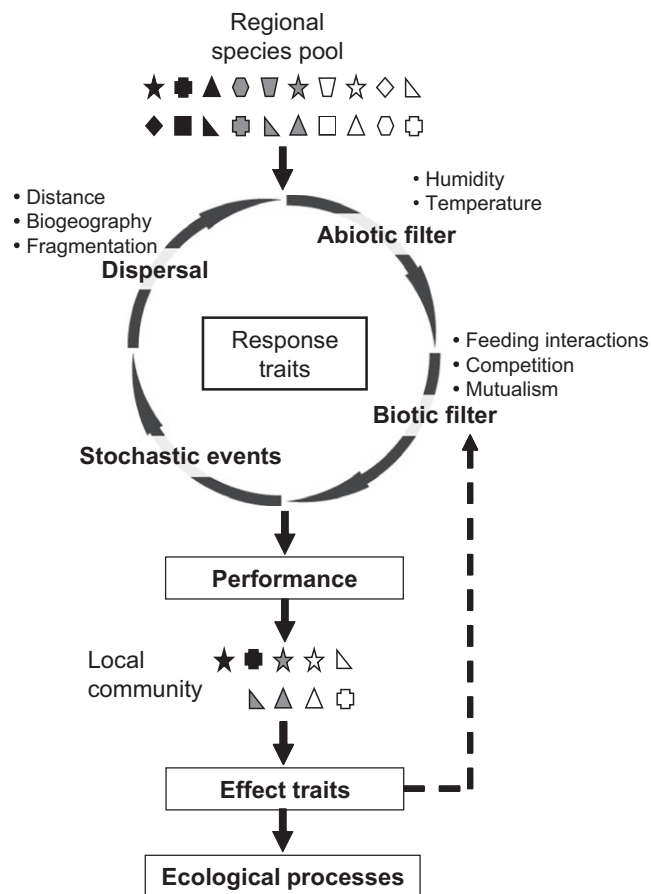


FIGURE 1 Hypothesized processes leading to a local species and trait assemblage from a regional pool. The regional species pool is first determined by evolution, biogeography and immigration/emigration with other regions. To establish themselves in the local community, species need to go through three filters acting simultaneously (represented as a cycling process with examples of limiting factors) and selecting species based on their response traits. Performance represents growth rate, survival rate and fecundity. A feedback loop is expected between effect traits and the biotic filter (represented as a dashed line)

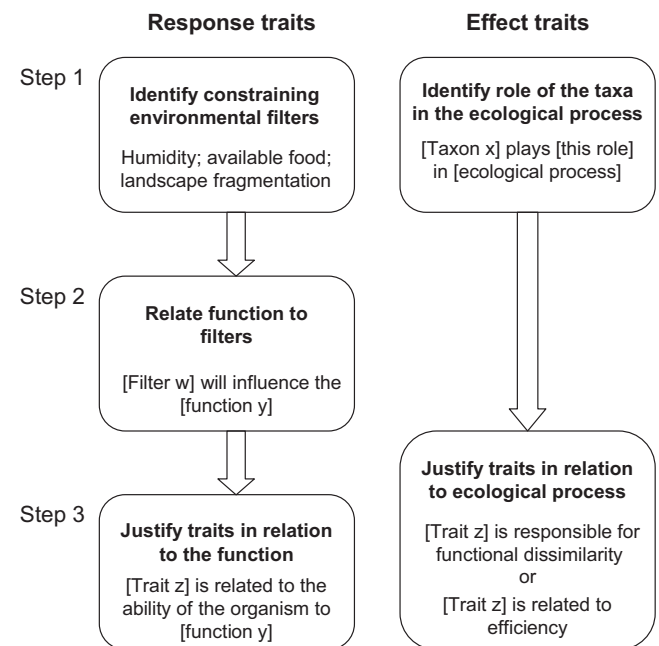


FIGURE 2 Schematized representation of a step-by-step protocol to postulate clear hypotheses in response and effect trait studies of arthropods

Finally, we evaluated whether the selection of all traits was explicitly justified by linking them to functions and performance (Luck et al., 2012). We did not evaluate whether the traits were well selected, but only if they were adequately justified. When adequately justified, the information was often shown in a table with a column "Traits" and a column "Role" or "Hypothesized mechanism." Alternatively, it was shown in the text as a sentence of the form "[Trait z] is related to the ability of the organism to [function

y]." Cases where justifications were considered as vague and thus unfulfilled were examples such as "These traits are known to impact organism performance" or "[Trait z] is related to [function y]" without providing any reference. Only references explicitly demonstrating the mechanistic link between the trait and the function were accepted as a valid justification.

For studies based on effect traits of arthropods, we evaluated two questions (Figure 2). First, we checked whether the studied taxa were clearly related to the ecological process. This generally appeared in a sentence of the form "[Taxon x] is known to play a role in [ecological process y]." We also accepted cases where "taxon x" was replaced by "guild x" when the taxon was clearly related to this guild. Secondly, we checked whether the hypothesis relating selected traits and the ecological process was formulated. Justification of effect traits could be at two levels. We acknowledged that effect traits could represent traits contributing to the functional dissimilarity of a community and thus susceptible to create synergistic effects when combined (e.g. pollinators with different phenology can provide services throughout the growing seasons) or that effect traits could be used to compare the efficiency of different organisms. Trait justification was evaluated with the same criteria as for the response traits.

TABLE 1 Examples of functional traits found in terrestrial arthropod literature and their hypothesized function. This list presents the most commonly found traits in the monitored literature for each environmental filter (dispersal, abiotic and biotic) and ecosystem processes. A complete list of traits found in the reviewed terrestrial arthropod literature including a reference list can be consulted in Table S2

Function	Traits
Dispersal	
Aerial dispersal	Presence/absence of wings
	Ballooning
	Migratory statue
Foraging distance	Intertegular distance
	Wing length
Ground dispersal	Femoral length
	Leg length
Abiotic filters	
Habitat structure	Position of nest
	Head width
	Eye position
Habitat complexity	Tibial length
Resistance and tolerance	Body pigmentation
	Oviposition place
Biotic filters	
Resource used	
Toughness	Head width
	Mandible length
	Head length
Localization	Eye size
	Antennae length
Competition	
Phenology	Overwintering stage
	Circadian activity
	Breeding season
Fecundity	Voltinism
	Sexual vs. parthenogenesis
Effect traits	
Efficiency	Time spent per flower
	Number of flowers visited per min.
Resource partitioning	Hunting strategy
	Eye size

3 | RECENT PROGRESS IN THE STUDY OF FUNCTIONAL TRAITS

3.1 | Message 1: Functional traits in arthropod ecology are gaining popularity. Despite a clear motivation to adhere to this approach, we still struggle to work towards a predictive ecology

Our review criteria yielded a total of 171 published studies spanning a variety of terrestrial arthropod taxa, particularly spiders, springtails, ground beetles, ants and bees (Table 2 and Table S2). The earliest study was in 1996 (Castella & Speight, 1996), and the subject remained marginal until 2012 (Figure 3). Since then, over three-quarters (135) of the studies were published showing almost an exponential increase (Figure 3). Studies on effect traits were underrepresented in the literature with only 18 published studies found. However, admittedly, traits are sometimes considered in the study of ecological processes, particularly pollination, without using explicit reference to a functional trait approach (Ibanez, 2012; Stang, Klinkhamer, & van der Meijden, 2006).

Some studies have shown that using a functional trait approach with arthropods made it possible to identify mechanisms that would not have been possible to identify based on a taxonomic approach. For example, large bees with long hair and relatively short wings were more cold-tolerant in laboratory trials and bee communities sampled in colder environments in the field reflected these same response traits (Peters, Peisker, Steffan-Dewenter, & Hoiss, 2016). In turn, Stavert et al. (2016) showed that pollination efficiency was related to the hairiness of bees and the morphological structure of flowers, which could mean that temperature indirectly structures pollination networks. In another study, the

TABLE 2 Number of studies per taxa for the 171 publications and the number of response traits related to each ecological filter type (dispersal, abiotic, biotic) or the number of effect traits. “Undescribed” represent traits we were unable to relate to a particular filter in the reviewed publications

Taxa	Studies	Dispersal	Abiotic	Biotic	Effect	Undescribed	Total
Multitaxa	14	4	2	9	9	1	25
Acari	6	0	6	4	0	2	12
Araneae	21	3	7	10	1	0	21
Isopoda	1	1	4	3	0	1	9
Diplopoda	1	0	0	0	2	3	5
Collembola	13	2	4	6	0	5	17
Hemiptera	2	2	0	6	0	1	9
Orthoptera	8	4	1	6	4	1	16
Carabidae	36	7	3	15	6	8	39
Coleoptera	21	6	4	8	1	7	26
Lepidoptera	20	5	1	11	0	1	18
Apoidea ^a	20	2	2	9	11	3	27
Formicidae	19	3	8	16	1	9	37
Syrphidae	3	1	1	6	0	0	8

^aIncludes pollinators at large.

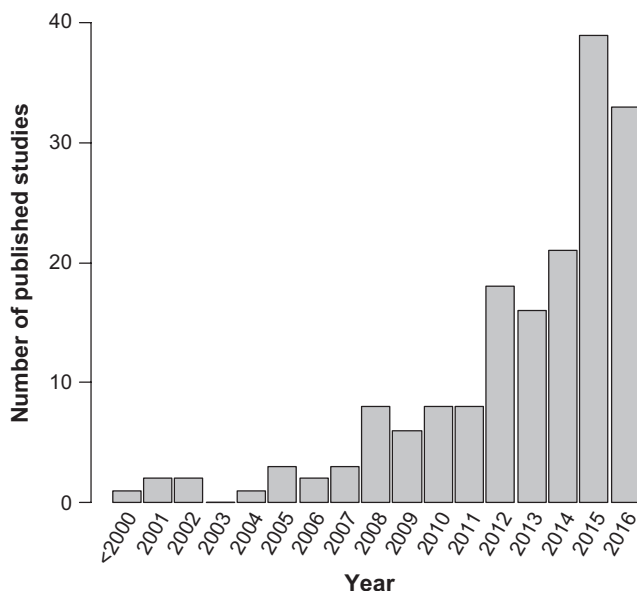


FIGURE 3 Temporal progression of the number of published studies using the functional trait approach with terrestrial arthropods

length of ant legs was shown to decrease with the complexity of the environment where they forage, which could be a trade-off between foraging speed and manoeuvrability (Wiescher, Pearce-Duvet, & Feener, 2012).

Nonetheless, our analysis of whether studies were clearly hypothesis-driven revealed that only 19% of response trait studies ($n = 139$) clearly met all three criteria (i.e. identifying environmental filters and postulating hypotheses linking traits, functions and filters). Over the years, this percentage did not vary much, except for a peak of 33% in 2011–2012 (Figure 4). When each criterion was considered individually, 61% of the articles clearly identified environmental filters, 37% offered hypotheses linking traits to environmental filters

and responding organismal functions, and 37% provided a justification for selected traits (Figure 5). Effect trait studies ($n = 18$) showed a more consistent approach with ecological processes and hypotheses being clearly identified in 61% of the cases.

These results suggest that moving towards a predictive science is challenging. The functional trait approach could help in developing a predictive ecology (Shipley, Vile, & Garnier, 2006); however, it can only be carried out if common goals are identified and underlying assumptions are understood (Shipley et al., 2016). While these assumptions were well identified in the past (Loreau, 2010; McGill et al., 2006; Naeem & Wright, 2003; Reich, Walters, & Ellsworth, 1997; Shipley, 2010), they are often forgotten, even in plant ecology (Didham, Leather, & Basset, 2016; Shipley et al., 2016). This aspect can be easily resolved by going back to the basics and by postulating hypotheses allowing to identify ecological mechanisms (Figure 2).

3.2 | Message 2: We are documenting a diverse set of traits indicating more creativity, but we are having trouble identifying a common set

For all 171 published studies, we summarized functional traits in relation to hypothesized dispersal, abiotic and biotic environmental filters or associated ecosystem processes (summary presented in Tables 1 and 2 and details in Table S2). We also classified each trait as per the five categories (morphology, physiology, life history, behaviour and feeding) described by Moretti et al. (2017). We excluded from the trait list all “traits” related to ecological preference, that is traits describing the habitat preference of the species (e.g. “preferred altitude”, “open vs. forested habitat”) (Pey, Nahmani et al., 2014; Violle et al., 2007).

Overall, we distinguished 156 different response or effect traits associated with 49 different functions demonstrating a will to explore several aspects of arthropod ecology with functional traits

(Table S2). These advances represent substantial and valuable exploratory work, and we recognize that such exploration sometimes makes justifying traits and postulating clear hypotheses more challenging. Some traits were largely studied across taxa, such as body size, dispersal ability (based on presence/absence of wings), overwintering stage and voltinism (Table S2). These traits provide a common currency leading to a possible generalization across taxa. Nonetheless, only 31 traits were repeated in at least five studies and with at least two taxa, demonstrating a limit to generalization. A common set of traits will be helpful to address broad questions about community assembly or ecosystem functioning (Moretti et al., 2017). However, it is noteworthy to mention that when studying a specific taxon, specific traits can sometimes be more informative. In this respect, traits such as femoral length of ants and nest position of bees are also well documented (Table S2).

The literature review also revealed a bias in the types of traits we are measuring (Table S2). Half of the inventoried traits were morphological traits (81), while only 11 physiological traits were found. The three other categories (life history, behaviour and feeding) were represented with c. 25 traits. Thirty-five traits, of which 33 were morphological traits, were impossible to relate to a clear function based on given information and were set apart in the category “function undescribed” (Table S2). Morphological traits are interesting as they can easily be measured on a high number of specimens and species in a relatively short time. However, they do not always represent functionally important traits and should be used with caution (Didham et al., 2016; Shipley et al., 2016). Furthermore, often, they cannot be generalized as they are associated with different functions across taxa. For example, length of the front legs of ground beetles can be associated with running speed (Forsythe, 1983), while the same trait is related to prey type in orb-weaver spiders (Olive, 1980) and to catching distance of mantis (Michaels, Prindle, & Turvey, 1985). A functional trait approach needs to rely on functionally meaningful (i.e. related to fitness) and consistent traits (Moretti et al., 2017; Shipley et al., 2016).

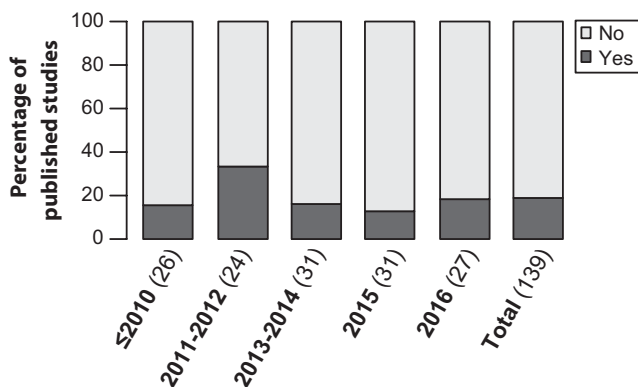


FIGURE 4 Percentage of published studies on response traits of terrestrial arthropods postulating all hypotheses presented in Figure 2 allowing to identify mechanisms relating traits to filters across publication years. Numbers in parentheses are the number of published studies per taxa

We also observed a lack of standardized measurement protocols. For example, in some taxa, the length of the legs can be related to their foraging speed; however, it is measured either as the whole leg length or as the length of the femur only depending on the study (Table S2). Establishing standardization in trait measurement will be necessary to facilitate generalizations across studies.

3.3 | Message 3: There is an improvement in available tools to study functional traits

A first important step towards generalization and standardization was made with the publication of a list of core traits and “handbook” with standardized protocols to measure traits for terrestrial invertebrates (Moretti et al., 2017). We encourage future studies to build on this list as much as possible; however, this list is not exhaustive and other traits will be required in some circumstances. Undoubtedly, the “handbook” will continue to evolve so as to expand the list of

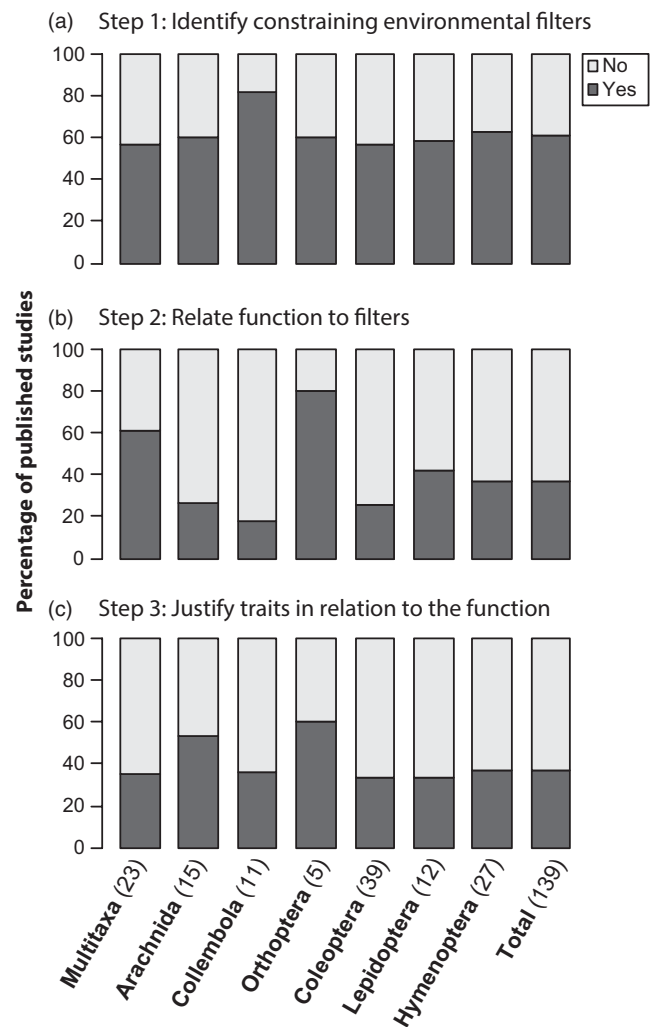


FIGURE 5 Percentage of published studies on response traits of terrestrial arthropods that (a) identify constraining environmental filters, (b) relate functions to filters and (c) justify traits in relation to the function. Numbers in parentheses are the number of published studies per taxa

core traits and refine measurement protocols. Particularly, we noted the need for a list of traits related to different types of interactions (trophic, symbiotic, competition, etc.).

An important improvement has been the development of some open databases for invertebrates. National (e.g. Canadian Repository of Invertebrate Traits and Trait-like Requirements—CRITTER; Handa, Raymond-Léonard, Boisvert-Marsh, Dupuch, & Aubin, 2017) and international (e.g. BETSI database for soil invertebrates; Pey, Laporte et al., 2014) initiatives have emerged. Taxon-specific databases such as Carabids.org for ground beetles of the Palearctic region (Homburg, Homburg, Schaefer, Schuldt, & Assmann, 2014) or GlobalAnts for ants (Parr et al., 2017) have stimulated reflections among specialists. While these databases include only a small part of the diversity of terrestrial arthropods, they represent valuable tools to synthesize the large amount of information available in specialized literature (Luck et al., 2012; Pey, Nahmani et al., 2014).

The development of databases characterizing multiple traits, species and environments will also help to resolve questions related to traits and performance of organisms at large scales (Reich et al., 2014; Shipley et al., 2016). So far, the link between traits of arthropods and their performance in varying abiotic and biotic conditions is lacking. Links are merely hypothetical and were tested at local scales, subjecting them to locally dependent effects that can impede robustness, generalization and predictive ability (Violle, Reich, Pacala, Enquist, & Kattge, 2014). Ideally, the effect of the studied filter should be removed from any other filter, but this is not always possible (Kraft et al., 2015). Another complication is that in some circumstances, a combination of multiple traits will better determine the relationship of organisms to an environmental gradient than a single trait (de Bello et al., 2010; Violle et al., 2012). Consequently, it can be hard to isolate the independent contribution of specific traits to a function, particularly for traits correlated with body size. Integrating large scale datasets including many sites with different sets of species will allow to extract the correlation between traits and filters, while minimizing locally dependent effects (Violle et al., 2014; Wright et al., 2004).

Databases also have the complementary beneficial effect to promote the use of standardized measurements of traits (Homburg et al., 2014) and the establishment of a common language (thesaurus) to describe traits and ancillary data (e.g. see Pey, Laporte et al., 2014). As databases continue to develop, thesauruses are being expanded to include a larger diversity of traits and taxa and this common language will help to prevent misinterpretation of available data (Shipley et al., 2016). However, while the importance of common databases is generally well accepted, the philosophy behind open databases could impede their development as they are highly profitable to users, but less profitable to contributors. This problem could be resolved by encouraging data citations and other measures for the recognition of contributions (Baird et al., 2011; Poisot, Mounce, & Gravel, 2013).

Beyond the development of standardized protocols and data repositories for arthropods, another important general advance has been the development of statistical tools to investigate

trait-environment relationships (Ovaskainen et al., 2017; Peres-Neto, Dray, & ter Braak, 2017). Trait-environment relationships were often quantified in the past with statistical models relating community weighted means (CWMs) of response traits with either abiotic or biotic variables (Lavorel et al., 2013; Shipley et al., 2006). While these analyses helped advance functional ecology considerably, other techniques are now recommended as CWMs can inappropriately represent the variance in trait composition, leading to incorrect statistical inference (Peres-Neto et al., 2017). Alternatively, methods such as the fourth corner analysis (Legendre, Galzin, & Harmelin-Vivien, 1997), a multivariate model quantifying the correlation between traits and the environment, can be useful. Another promising method builds on the strengths of hierarchical models and Bayesian statistics to include traits and phylogenies in joint species distribution models (JSDMs; see Warton et al., 2015; Ovaskainen et al., 2017). JSDMs offer a new approach to represent multivariate data, quantifying not only the relationship between species distribution and the environment, but also the covariation between them. The hierarchical structure of the model allows to constrain parameters such that species with similar functional traits will respond similarly to the environment. The development of such methods is currently an active field of research in community ecology, and new methods are expected in the coming years that will benefit arthropod functional ecology. These methods will help us uncover general relationships between arthropod traits and the environment, irrespective of the regional species pool, that could prove useful to predict species distributions in the context of global change.

4 | DEALING WITH HIGH INTRA- AND INTERSPECIFIC TRAIT VARIATION OF ARTHROPODS

One principal challenge to find generalizable traits with arthropods is to identify the ones that can be measured across the high diversity in species, shape and morphological structures. The challenge becomes even bigger if one wants to consider communities including other invertebrates such as detritivorous food webs with nematodes and earthworms (Moretti et al., 2017). Also, in many arthropod taxa, adults and immature organisms are dissimilar with each stage possessing its own set of traits. To a lesser extent, such dimorphism can also be true for males and females. The implications of such intraspecific variation in the application of the functional approach with arthropods have rarely been discussed. Nonetheless, exploring the implication of intraspecific trait variation (ITV) of arthropods will be required in the near future.

Traditionally, mean species trait values were used to calculate functional diversity metrics (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011), but research in plant ecology has demonstrated that including ITV can improve the ability to infer community structure (Jung, Violle, Mondy, Hoffmann, & Muller, 2010; Volf et al., 2016). ITV can represent more than 30% of

community trait variation across gradients for plant traits such as height and leaf N concentration (Siefert et al., 2015) and is likely to play an important role if it is large compared with interspecific variation (Siefert et al., 2015). Identified factors influencing the importance of ITV include the scale of the study (Albert et al., 2011) and the type of traits measured; for example, leaf chemical traits are more variable within species than leaf morphological traits (Siefert et al., 2015). **With animals, it is expected that behavioural traits may be more variable than morphological traits (Duckworth, 2009).** For example, 30% of community-level trait variation was explained by ITV for web-building behaviour of spiders in urban areas (Dahirel, Dierick, De Cock, & Bonte, 2017). Temperature can also influence ITV as it affects the expression of many life-history traits of arthropods including fecundity, growth rate and feeding rate (Arias, Poupin, & Lardies, 2011; Römbke, Römbke, & Russell, 2011). To encourage future studies on ITV, we recommend reporting mean trait values with their standard deviation in publications (Moretti et al., 2017) and providing data for each measured individual in databases.

4.1 | Immature vs. adult stages

Hypotheses in functional trait studies should be postulated such that traits associated with the appropriate life stage are considered when studying taxa with varying ecology or morphology throughout their development (e.g. Odonata, Coleoptera, Lepidoptera, some Acari). **Very few of the reviewed studies included traits related to immature stages except for Lepidoptera and Syrphidae, and in these cases, only traits related to diet and habitat were included.** Nonetheless, in some cases, response traits of immature organisms could better explain the distribution of the organisms than those of adults, particularly for capital breeders, that is species for which important traits such as size and fecundity are determined by the resources they accumulate during the immature stages (Tammaru & Haukioja, 1996). Such considerations are also true for effect traits of defoliators as immature organisms (e.g. caterpillars) generally cause the most damage to plants. Including traits from a stage that is not associated with an environmental filter or active in the studied ecological process will not only be meaningless, but may lead to misinterpretation. Intraspecific variation caused by life stage differences can be considered by treating both stages separately in the analyses (Bolnick et al., 2003).

Similar problems can be encountered with sex dimorphism. In some cases, only few traits will be affected such as a larger body size for females or hypertrophied mandibles of males. Nonetheless, these sexual differences can create a distinct niche for both sexes (Mason, 1977). When dimorphism creates a bimodal distribution for one of the studied traits, it would also be advisable to treat sex distinctly as for immature life stages.

4.2 | Treating high interspecific variation

Dealing with a high diversity implies the need to establish standard traits that will increase our capacity to infer across taxa and

processes and improve predictive ability (e.g. biting force, dispersal distance, water loss rate). Traits such as body size and phenology are commonly used across taxa (Hedde, van Oort, Renouf, Thénard, & Lamy, 2013; Moretti & Legg, 2009), but are difficult to relate to a particular filter. For example, body size has been a useful trait to summarize complex ecological networks (Gravel, Poisot, Albouy, Velez, & Mouillot, 2013) and is also central to the metabolic theory of ecology (Brown, Gillooly, Allen, Savage, & West, 2004). **However, the predictive ability of body size varies enormously across ecosystems (Brose et al., 2006).** Even when considering metabolic theory, body size alone explained only between 2% and 20% of the observed variation in metabolic functions for species across a 10-fold size range (a scale corresponding to that typically observed in arthropod communities) (Brown et al., 2004).

Another aspect to consider is that different strategies can evolve to resolve the same problem; thus, different trait values can result in the same niche (Young, Haselkorn, & Badyaev, 2007). Thus, **traits should be selected to reflect the outcome (e.g. feeding niche) of the trait instead of the trait per se.** In some cases, the same trait, for example biting force, will be measured differently depending on the type of mouthparts (mandibles vs. chelicerae), but will still have the same outcome (Moretti et al., 2017; van der Meijden, Langer, Boistel, Vagovic, & Heethoff, 2012). In other cases, different traits may be at play. For example, two different strategies can be used to eat a snail: crushing the shell with strong mouthparts or attacking through the aperture with long appendices (Nyffeler & Symondson, 2001). In this example, biting force and length of mouthparts are both describing the same feeding niche.

5 | TRAIT-MATCHING: A PROMISING PERSPECTIVE

Considering traits of arthropods (beyond plants) opens the door to the emerging field of interaction ecology, where their complexity and their consequences are widely acknowledged (Brousseau, Gravel, & Handa, 2018; Gravel et al., 2013). The functional trait approach could be highly interesting to solve the challenge of documenting interaction networks (Bartomeus et al., 2016; Gravel et al., 2016; Morales-Castilla, Matias, Gravel, & Araújo, 2015). In turn, the structure of ecological networks is seen as an important component determining species distributions (Araújo & Rozenfeld, 2014) and ecosystem processes (Loreau, 2010).

The particularity of traits involved in the occurrence of interactions is that they influence both the response (the performance of the consumer will depend on the occurrence of resources with appropriate traits) and the effect (by trophic regulation). Traits related to interactions can be used in a one-dimensional way (i.e. considering only the consumer's point of view) or in a bidimensional way through **trait-matching (i.e. by considering traits of both interacting organisms).** In theory, trait-matching can be applied to any kind of species interaction (Morales-Castilla et al., 2015); however, its study has been limited to feeding and mutualistic

interactions. In these cases, foraging traits of the consumer (e.g. body size, strength, length of the tongue) can be matched to vulnerability/palatability traits of the resource (e.g. body size, toughness, depth of the corolla) to determine the probability of interaction between two organisms (Brousseau et al., 2018; Ibanez, 2012). **An interesting aspect of trait-matching is that the same traits can be used to answer questions related to response and effect traits. For example, the variance of mean biting force of the grasshopper community responds to the mean leaf toughness of the plant community** (Le Provost et al., 2017). In turn, biting force predicts the effect of grasshoppers on plant biomass (Deraison, Badenhauer, Börger, & Gross, 2015).

Trait-matching can be used in effect trait studies by providing information on the efficiency of an organism in a particular task (Schleuning et al., 2015). This aspect was principally studied in pollination networks, where the matching of the proboscis length of the pollinator and the depth of the corolla of the flower is well demonstrated (Ibanez, 2012; Inouye, 1980). This trait-matching is a good predictor of species interactions (Ibanez, 2012) and of the handling time and thus of the number of visited flowers and pollination efficiency (Herrera, 1989; Inouye, 1980). It was also suggested that the location of the hairs on the body of the pollinator can be matched to the morphology of the flower to determine the efficiency to pollinate a flower (Stavert et al., 2016).

In some instances, trait-matching can be used to relate more than two trophic levels. A study on leaf litter decomposition demonstrated that increasing the functional diversity of both decomposers and leaf litter traits increased the decomposition rate (Coulis et al., 2015). This could be related to resource preference shown by decomposers (David, 2014) and by a matching of their traits with physical and chemical traits of leaf litter affecting their assimilation efficiency. In turn, the traits of the decomposers (Frouz & Šimek, 2009; Köhler & Alberti, 1990) and of the leaf litter (Coulis, Hättenschwiler, Coq, & David, 2016) can influence the characteristics of the faeces of decomposers (e.g. C:N ratio, fragmentation of plant material), microbial activity and the relation to the decomposition rate (Hedde, Bureau, Akpa-Vinceslas, Aubert, & Decaëns, 2007). Thus, we can hypothesize that trait-matching could help to better understand the impact of functional diversity on decomposition rate, but further work will be needed.

6 | CONCLUSIONS

The use of functional traits to study plant community structure and dynamics is highly profitable for community ecologists, as well as for applied ecology. Studies of arthropod functional traits should be just as promising. Nevertheless, we must keep in mind that a trait-based approach is a simplification of a species-based approach. The strength is in the capacity to generalize and offer clear mechanisms, thus emphasizing the importance to apply a hypothesis-based framework for studies. As active heterotrophs, the reality of arthropods is tremendously different from the reality of sessile autotrophs

as plants. This reality needs to be considered by giving a higher importance to the traits related to their interspecific interactions as well as their movement ability. Identifying the right set of traits to study arthropods will be a long challenge because of their diversity and the lack of data for many taxa. However, with the understanding of meaningful traits and the development of databases to share this information, it could become a powerful tool in the future.

ACKNOWLEDGEMENTS

We are grateful for stimulating exchanges with multiple colleagues and comments by L. Raymond-Léonard as well as those of several anonymous reviewers to improve the quality of this article. Our research was financed by the Natural Sciences and Engineering Research Council of Canada (NSERC) and le Fond de recherche du Québec – Nature et technologies (FRQNT).

AUTHORS' CONTRIBUTIONS

P.-M.B. led the writing of the manuscript. All authors participated in the development of the ideas, contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All data used are present in the manuscript.

ORCID

Pierre-Marc Brousseau  <http://orcid.org/0000-0002-0699-3299>

Dominique Gravel  <http://orcid.org/0000-0002-4498-7076>

Ira Tanya Handa  <http://orcid.org/0000-0002-7272-031X>

REFERENCES

- Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G., & Violle, C. (2011). When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics*, 13, 217–225. <https://doi.org/10.1016/j.ppees.2011.04.003>
- Araújo, M. B., & Rozenfeld, A. (2014). The geographic scaling of biotic interactions. *Ecography*, 37, 406–415. <https://doi.org/10.1111/j.1600-0587.2013.00643.x>
- Arias, M. B., Poupin, M. J., & Lardies, M. A. (2011). Plasticity of life-cycle, physiological thermal traits and Hsp70 gene expression in an insect along the ontogeny: Effect of temperature variability. *Journal of Thermal Biology*, 36, 355–362. <https://doi.org/10.1016/j.jtherbio.2011.06.011>
- Baird, D. J., Baker, C. J. O., Brua, R. B., Hajibabaei, M., McNicol, K., Pascoe, T. J., & de Zwart, D. (2011). Toward a knowledge infrastructure for traits-based ecological risk assessment. *Integrated Environmental Assessment and Management*, 7, 209–215. <https://doi.org/10.1002/ieam.129>
- Bartomeus, I., Gravel, D., Tylianakis, J. M., Aizen, M. A., Dickie, I. A., & Bernard-Verdier, M. (2016). A common framework for identifying linkage rules across different types of interactions. *Functional Ecology*, 30, 1894–1903. <https://doi.org/10.1111/1365-2435.12666>

- Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, 161, 1–28. <https://doi.org/10.1086/343878>
- Bremner, J. (2008). Species' traits and ecological functioning in marine conservation and management. *Journal of Experimental Marine Biology and Ecology*, 366, 37–47. <https://doi.org/10.1016/j.jembe.2008.07.007>
- Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L.-F., ... Cohen, J. E. (2006). Consumer-resource body-size relationships in natural food webs. *Ecology*, 87, 2411–2417. [https://doi.org/10.1890/0012-9658\(2006\)87\[2411:CBRINF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2)
- Brousseau, P.-M., Gravel, D., & Handa, I. T. (2018). Trait-matching and phylogeny as predictors of predator-prey interactions involving ground beetles. *Functional Ecology*, 32, 192–202. <https://doi.org/10.1111/1365-2435.12943>
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789. <https://doi.org/10.1890/03-9000>
- Cadotte, M. W., Cardinale, B. J., & Oakley, T. H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences of the USA*, 105, 17012–17017. <https://doi.org/10.1073/pnas.0805962105>
- Castella, E., & Speight, M. C. D. (1996). Knowledge representation using fuzzy coded variables: An example based on the use of Syrphidae (Insecta, Diptera) in the assessment of riverine wetlands. *Ecological Modelling*, 85, 13–25. [https://doi.org/10.1016/0304-3800\(95\)00015-1](https://doi.org/10.1016/0304-3800(95)00015-1)
- Cornelissen, J. H. C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D. E., ... Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51, 335–380. <https://doi.org/10.1071/bt02124>
- Coulis, M., Fromin, N., David, J.-F., Gavinet, J., Clet, A., Devidal, S., ... Hättenschwiler, S. (2015). Functional dissimilarity across trophic levels as a driver of soil processes in a Mediterranean decomposer system exposed to two moisture levels. *Oikos*, 124, 1304–1316. <https://doi.org/10.1111/oik.01917>
- Coulis, M., Hättenschwiler, S., Coq, S., & David, J.-F. (2016). Leaf litter consumption by macroarthropods and burial of their faeces enhance decomposition in a Mediterranean ecosystem. *Ecosystems*, 19, 1104–1115. <https://doi.org/10.1007/s10021-016-9990-1>
- Culp, J. M., Armanini, D. G., Dunbar, M. J., Orlofske, J. M., Poff, N. L., Pollard, A. I., ... Hose, G. C. (2011). Incorporating traits in aquatic biomonitoring to enhance causal diagnosis and prediction. *Integrated Environmental Assessment and Management*, 7, 187–197. <https://doi.org/10.1002/ieam.128>
- Dahirel, M., Dierick, J., De Cock, M., & Bonte, D. (2017). Intraspecific variation shapes community-level behavioural responses to urbanisation in spiders: From traits to function. *Ecology*, 98, 2379–2390. <https://doi.org/10.1002/ecy.1915>
- David, J. F. (2014). The role of litter-feeding macroarthropods in decomposition processes: A reappraisal of common views. *Soil Biology and Biochemistry*, 76, 109–118. <https://doi.org/10.1016/j.soilbio.2014.05.009>
- de Bello, F., Lavorel, S., Diaz, S., Harrington, R., Cornelissen, J. H. C., Bardgett, R. D., ... Harrison, P. A. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, 19, 2873–2893. <https://doi.org/10.1007/s10531-010-9850-9>
- De Oliveira, T., Haettenschwiler, S., & Handa, I. T. (2010). Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. *Functional Ecology*, 24, 937–946. <https://doi.org/10.1111/j.1365-2435.2010.01694.x>
- Deraison, H., Badenhauer, I., Börger, L., & Gross, N. (2015). Herbivore effect traits and their impact on plant community biomass: An experimental test using grasshoppers. *Functional Ecology*, 29, 650–661. <https://doi.org/10.1111/1365-2435.12362>
- Diamond, J. M. (1975). Assembly of species communities. In M. L. Cody, & J. M. Diamond (Eds.), *Ecology and evolution of communities* (pp. 342–444). Cambridge, MA: Harvard University Press.
- Díaz, S., & Cabido, M. (2001). Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16, 646–655. [https://doi.org/10.1016/S0169-5347\(01\)02283-2](https://doi.org/10.1016/S0169-5347(01)02283-2)
- Didham, R. K., Leather, S. R., & Basset, Y. (2016). Circle the bandwagons – challenges mount against the theoretical foundations of applied functional trait and ecosystem service research. *Insect Conservation and Diversity*, 9, 1–3. <https://doi.org/10.1111/icad.12150>
- Duckworth, R. A. (2009). The role of behavior in evolution: A search for mechanism. *Evolutionary Ecology*, 23, 513–531. <https://doi.org/10.1007/s10682-008-9252-6>
- Forsythe, T. G. (1983). Locomotion in ground beetles (Coleoptera: Carabidae): An interpretation of leg structure in functional terms. *Journal of Zoology*, 200, 493–507. <https://doi.org/10.1111/j.1469-7998.1983.tb02811.x>
- Frouz, J., & Šimek, M. (2009). Short term and long term effects of bibionid (Diptera: Bibionidae) larvae feeding on microbial respiration and alder litter decomposition. *European Journal of Soil Biology*, 45, 192–197. <https://doi.org/10.1016/j.ejsobi.2008.09.012>
- Gravel, D., Albouy, C., & Thuiller, W. (2016). The meaning of functional trait compositions of food webs for ecosystem functioning. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 371, 1–14. <https://doi.org/10.1098/rstb.2015.0268>
- Gravel, D., Bell, T., Barbera, C., Bouvier, T., Pommier, T., Venail, P., & Mouquet, N. (2011). Experimental niche evolution alters the strength of the diversity-productivity relationship. *Nature*, 469, 89–92. <https://doi.org/10.1038/nature09592>
- Gravel, D., Poisot, T., Albouy, C., Velez, L., & Mouillot, D. (2013). Inferring food web structure from predator-prey body size relationships. *Methods in Ecology and Evolution*, 4, 1083–1090. <https://doi.org/10.1111/2041-210x.12103>
- Handa, I. T., Aerts, R., Berendse, F., Berg, M. P., Bruder, A., Butenschoten, O., ... Haettenschwiler, S. (2014). Consequences of biodiversity loss for litter decomposition across biomes. *Nature*, 509, 218–221. <https://doi.org/10.1038/nature13247>
- Handa, I. T., Raymond-Léonard, L., Boisvert-Marsh, L., Dupuch, A., & Aubin, I. (2017). CRITTER: Canadian Repository of invertebrate traits and trait-like ecological records. Natural Resources Canada, Canadian Forest Service, Sault Ste. Marie, ON, Canada. Retrieved from www.nrcan.gc.ca/forests/research-centres/glfrc/20303
- Hedde, M., Bureau, F., Akpa-Vinceslas, M., Aubert, M., & Decaëns, T. (2007). Beech leaf degradation in laboratory experiments: Effects of eight detritivorous invertebrate species. *Applied Soil Ecology*, 35, 291–301. <https://doi.org/10.1016/j.apsoil.2006.08.002>
- Hedde, M., van Oort, F., Renouf, E., Thénard, J., & Lamy, I. (2013). Dynamics of soil fauna after plantation of perennial energy crops on polluted soils. *Applied Soil Ecology*, 66, 29–39. <https://doi.org/10.1016/j.apsoil.2013.01.012>
- Heemsbergen, D. A., Berg, M. P., Loreau, M., van Haj, J. R., Faber, J. H., & Verhoef, H. A. (2004). Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science*, 306, 1019–1020. <https://doi.org/10.1126/science.1101865>
- Herrera, C. M. (1989). Pollinator abundance, morphology, and flower visitation rate: Analysis of the “quantity” component in a plant-pollinator system. *Oecologia*, 80, 241–248. <https://doi.org/10.1007/bf00380158>
- Homburg, K., Homburg, N., Schaefer, F., Schuldt, A., & Assmann, T. (2014). Carabids. org – a dynamic online database of ground beetle species

- traits (Coleoptera, Carabidae). *Insect Conservation and Diversity*, 7, 195–205. <https://doi.org/10.1111/icad.12045>
- Ibanez, S. (2012). Optimizing size thresholds in a plant–pollinator interaction web: Towards a mechanistic understanding of ecological networks. *Oecologia*, 170, 233–242. <https://doi.org/10.1007/s00442-012-2290-3>
- Inouye, D. W. (1980). The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees. *Oecologia*, 45, 197–201. <https://doi.org/10.1007/bf00346460>
- Jung, V., Violle, C., Mondy, C., Hoffmann, L., & Muller, S. (2010). Intraspecific variability and trait-based community assembly. *Journal of Ecology*, 98, 1134–1140. <https://doi.org/10.1111/j.1365-2745.2010.01687.x>
- Keddy, P. A. (1992). Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science*, 3, 157–164. <https://doi.org/10.2307/3235676>
- Kočárek, P. (2003). Decomposition and Coleoptera succession on exposed carrion of small mammal in Opava, the Czech Republic. *European Journal of Soil Biology*, 39, 31–45. [https://doi.org/10.1016/S1164-5563\(02\)00007-9](https://doi.org/10.1016/S1164-5563(02)00007-9)
- Köhler, H.-R., & Alberti, G. (1990). Morphology of the mandibles in the millipedes (Diplopoda, Arthropoda). *Zoologica Scripta*, 19, 195–202. <https://doi.org/10.1111/j.1463-6409.1990.tb00255.x>
- Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 29, 592–599. <https://doi.org/10.1111/1365-2435.12345>
- Larkin, A. A., & Martiny, A. C. (2017). Microdiversity shapes the traits, niche space, and biogeography of microbial taxa. *Environmental Microbiology Reports*, 9, 55–70. <https://doi.org/10.1111/1758-2229.12523>
- Lavorel, S. (2013). Plant functional effects on ecosystem services. *Journal of Ecology*, 101, 4–8. <https://doi.org/10.1111/1365-2745.12031>
- Lavorel, S., Storkey, J., Bardgett, R. D., de Bello, F., Berg, M. P., Le Roux, X., ... Harrington, R. (2013). A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science*, 24, 942–948. <https://doi.org/10.1111/jvs.12083>
- Le Provost, G., Gross, N., Börger, L., Deraison, H., Roncoroni, M., & Badenhauer, I. (2017). Trait-matching and mass effect determine the functional response of herbivore communities to land use intensification. *Functional Ecology*, 31, 1600–1611. <https://doi.org/10.1111/1365-2435.12849>
- Legendre, P., Galzin, R., & Harmelin-Vivien, M. L. (1997). Relating behavior to habitat: Solutions to the fourth-corner problem. *Ecology*, 78, 547–562. [https://doi.org/10.1890/0012-9658\(1997\)078\[0547:rbthst\]2.0.co;2](https://doi.org/10.1890/0012-9658(1997)078[0547:rbthst]2.0.co;2)
- Litchman, E., Ohman, M. D., & Kiørboe, T. (2013). Trait-based approaches to zooplankton communities. *Journal of Plankton Research*, 35, 473–484. <https://doi.org/10.1093/plankt/fbt019>
- Loreau, M. (2010). *From populations to ecosystems: Theoretical foundations for a new ecological synthesis*. Princeton, NJ: Princeton University Press. <https://doi.org/10.1515/9781400834167>
- Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76. <https://doi.org/10.1038/35083573>
- Luck, G. W., Lavorel, S., McIntyre, S., & Lumb, K. (2012). Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. *Journal of Animal Ecology*, 81, 1065–1076. <https://doi.org/10.1111/j.1365-2656.2012.01974.x>
- Maes, D., & Van Dyck, H. (2001). Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biological Conservation*, 99, 263–276. [https://doi.org/10.1016/S0006-3207\(00\)00182-8](https://doi.org/10.1016/S0006-3207(00)00182-8)
- Mason, L. G. (1977). Prey preferences and ecological sexual dimorphism in *Phymata americana* Melin. *The American Midland Naturalist*, 97, 293–299. <https://doi.org/10.2307/2425095>
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Michaels, C. F., Prindle, S., & Turvey, M. T. (1985). A note on the natural basis of action categories: The catching distance of mantids. *Journal of Motor Behavior*, 17, 255–264. <https://doi.org/10.1080/00222895.1985.10735348>
- Morales-Castilla, I., Matias, M. G., Gravel, D., & Araújo, M. B. (2015). Inferring biotic interactions from proxies. *Trends in Ecology & Evolution*, 30, 347–356. <https://doi.org/10.1016/j.tree.2015.03.014>
- Moretti, M., Dias, A. T. C., de Bello, F., Altermatt, F., Chown, S. L., Azcárate, F. M., ... Berg, M. P. (2017). Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, 31, 558–567. <https://doi.org/10.1111/1365-2435.12776>
- Moretti, M., & Legg, C. (2009). Combining plant and animal traits to assess community functional responses to disturbance. *Ecography*, 32, 299–309. <https://doi.org/10.1111/j.1600-0587.2008.05524.x>
- Mouillot, D., Graham, N. A. J., Villeger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, 28, 167–177. <https://doi.org/10.1016/j.tree.2012.10.004>
- Naeem, S., & Wright, J. P. (2003). Disentangling biodiversity effects on ecosystem functioning: Deriving solutions to a seemingly insurmountable problem. *Ecology Letters*, 6, 567–579. <https://doi.org/10.1046/j.1461-0248.2003.00471.x>
- Nyffeler, M., & Symondson, W. O. C. (2001). Spiders and harvestmen as gastropod predators. *Ecological Entomology*, 26, 617–628. <https://doi.org/10.1046/j.1365-2311.2001.00365.x>
- Olive, C. W. (1980). Foraging specialization in orb-weaving spiders. *Ecology*, 61, 1133–1144. <https://doi.org/10.2307/1936833>
- Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F. G., Duan, L., Dunson, D., ... Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, 20, 561–576. <https://doi.org/10.1111/ele.12757>
- Paniw, M., Ozgul, A., & Salguero-Gómez, R. (2018). Interactive life-history traits predict sensitivity of plants and animals to temporal autocorrelation. *Ecology Letters*, 21, 275–286. <https://doi.org/10.1111/ele.12892>
- Parr, C. L., Dunn, R. R., Sanders, N. J., Weiser, M. D., Photakis, M., Bishop, T. R., ... Gibb, H. (2017). GlobalAnts: A new database on the geography of ant traits (Hymenoptera: Formicidae). *Insect Conservation and Diversity*, 10, 5–20. <https://doi.org/10.1111/icad.12211>
- Peres-Neto, P. R., Dray, S., & ter Braak, C. J. F. (2017). Linking trait variation to the environment: Critical issues with community-weighted mean correlation resolved by the fourth-corner approach. *Ecography*, 40, 806–816. <https://doi.org/10.1111/ecog.02302>
- Peters, M. K., Peisker, J., Steffan-Dewenter, I., & Hoiss, B. (2016). Morphological traits are linked to the cold performance and distribution of bees along elevational gradients. *Journal of Biogeography*, 43, 2040–2049. <https://doi.org/10.1111/jbi.12768>
- Pey, B., Laporte, M.-A., Nahmani, J., Auclerc, A., Capowiez, Y., Caro, G., ... Hedde, M. (2014). A thesaurus for soil invertebrate trait-based approaches. *PLoS ONE*, 9, e108985. <https://doi.org/10.1371/journal.pone.0108985>
- Pey, B., Nahmani, J., Auclerc, A., Capowiez, Y., Cluzeau, D., Cortet, J., ... Hedde, M. (2014). Current use of and future needs for soil invertebrate functional traits in community ecology. *Basic and Applied Ecology*, 15, 194–206. <https://doi.org/10.1016/j.baee.2014.03.007>
- Poisot, T., Mounce, R., & Gravel, D. (2013). Moving toward a sustainable ecological science: Don't let data go to waste!. *Ideas in Ecology & Evolution*, 6, 11–19. <https://doi.org/10.4033/iee.2013.6b.14.f>
- Pulliam, H. R. (2000). On the relationship between niche and distribution. *Ecology Letters*, 3, 349–361. <https://doi.org/10.1046/j.1461-0248.2000.00143.x>

- Raunkjær, C. (1934). *Life forms of plants and statistical plant geography*. Oxford, UK: Oxford University Press.
- Reich, P. B., Luo, Y., Bradford, J. B., Poorter, H., Perry, C. H., & Oleksyn, J. (2014). Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proceedings of the National Academy of Sciences of the USA*, 111, 13721–13726. <https://doi.org/10.1073/pnas.1216053111>
- Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the USA*, 94, 13730–13734. <https://doi.org/10.1073/pnas.94.25.13730>
- Römbke, T., Römbke, J., & Russell, D. (2011). Effects of temperature increases on the feeding activity of two species of isopods (*Porcellio scaber*, *Porcellionides pruinosus*) in laboratory tests. *Soil Organisms*, 83, 211–220.
- Salguero-Gómez, R., Jones, O. R., Jongejans, E., Blomberg, S. P., Hodgson, D. J., Mbeau-Ache, C., ... Buckley, Y. M. (2016). Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences of the USA*, 113, 230–235. <https://doi.org/10.1073/pnas.1506215112>
- Schleuning, M., Fruend, J., & Garcia, D. (2015). Predicting ecosystem functions from biodiversity and mutualistic networks: An extension of trait-based concepts to plant–animal interactions. *Ecography*, 38, 380–392. <https://doi.org/10.1111/ecog.00983>
- Shipley, B. (2010). *From plant traits to vegetation structure: Chance and selection in the assembly of ecological communities*. Cambridge, UK: Cambridge University Press.
- Shipley, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, 180, 923–931. <https://doi.org/10.1007/s00442-016-3549-x>
- Shipley, B., Vile, D., & Garnier, E. (2006). From plant traits to plant communities: A statistical mechanistic approach to biodiversity. *Science*, 314, 812–814. <https://doi.org/10.1126/science.1131344>
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., ... Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18, 1406–1419. <https://doi.org/10.1111/ele.12508>
- Silva, R. R., & Brandão, C. R. F. (2010). Morphological patterns and community organization in leaf-litter ant assemblages. *Ecological Monographs*, 80, 107–124. <https://doi.org/10.1890/08-1298.1>
- Stang, M., Klinkhamer, P. G. L., & van der Meijden, E. (2006). Size constraints and flower abundance determine the number of interactions in a plant–flower visitor web. *Oikos*, 112, 111–121. <https://doi.org/10.1111/j.0030-1299.2006.14199.x>
- Stavert, J. R., Liñán-Cembrano, G., Beggs, J. R., Howlett, B. G., Pattemore, D. E., & Bartomeus, I. (2016). Hairiness: The missing link between pollinators and pollination. *PeerJ*, 4, e2779. <https://doi.org/10.7717/peerj.2779>
- Tammaru, T., & Haukioja, E. (1996). Capital breeders and income breeders among Lepidoptera: Consequences to population dynamics. *Oikos*, 77, 561–564. <https://doi.org/10.2307/3545946>
- van der Meijden, A., Langer, F., Boistel, R., Vagovic, P., & Heethoff, M. (2012). Functional morphology and bite performance of raptorial chelicerae of camel spiders (Solifugae). *The Journal of Experimental Biology*, 215, 3411–3418. <https://doi.org/10.1242/jeb.072926>
- Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., ... Messier, J. (2012). The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology & Evolution*, 27, 244–252. <https://doi.org/10.1016/j.tree.2011.11.014>
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. *Oikos*, 116, 882–892. <https://doi.org/10.1111/j.2007.0030-1299.15559.x>
- Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences of the USA*, 111, 13690–13696. <https://doi.org/10.1073/pnas.1415442111>
- Volf, M., Redmond, C., Albert, Á. J., Le Bagousse-Pinguet, Y., Biella, P., Götzenberger, L., ... de Bello, F. (2016). Effects of long- and short-term management on the functional structure of meadows through species turnover and intraspecific trait variability. *Oecologia*, 180, 941–950. <https://doi.org/10.1007/s00442-016-3548-y>
- Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. C. (2015). So many variables: Joint modeling in community ecology. *Trends in Ecology & Evolution*, 30, 766–779. <https://doi.org/10.1016/j.tree.2015.09.007>
- Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I., & Poff, N. L. (2010). A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters*, 13, 267–283. <https://doi.org/10.1111/j.1461-0248.2010.01444.x>
- Wiescher, P. T., Pearce-Duvet, J. M. C., & Feener, D. H. (2012). Assembling an ant community: Species functional traits reflect environmental filtering. *Oecologia*, 169, 1063–1074. <https://doi.org/10.1007/s00442-012-2262-7>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827. <https://doi.org/10.1038/nature02403>
- Young, R. L., Haselkorn, T. S., & Badyaev, A. V. (2007). Functional equivalence of morphologies enables morphological and ecological diversity. *Evolution*, 61, 2480–2492. <https://doi.org/10.1111/j.1558-5646.2007.00210.x>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Brousseau P-M, Gravel D, Handa IT. On the development of a predictive functional trait approach for studying terrestrial arthropods. *J Anim Ecol*. 2018;87: 1209–1220. <https://doi.org/10.1111/1365-2656.12834>