



# Body size and the behavioral ecology of insects: linking individuals to ecological communities

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The role of body size as a key feature determining the biology and ecology of individual animals, and thus the structure and dynamics of populations, communities, and ecosystems, has long been acknowledged. Body size provides a functional link between individual-level processes such as physiology and behavior, with higher-level ecological processes such as the strength and outcome of trophic interactions, which regulate the flow of energy and nutrients within and across ecosystems. Early ecological work on size in animals focused on vertebrates, and especially mammals. More recent focus on invertebrates, and insects in particular, that spans levels of organization from individual physiology to communities, has greatly expanded and improved our understanding of the role of body size in ecology. Progress has come from theoretical advances, from the production of new, high-resolution empirical data sets, and from enhanced computation and analytical techniques. Recent findings suggest that many of the allometric concepts and principles developed over the last century also apply to insects. But these recent studies also emphasize that while body size plays a crucial role in insect ecology, it is not the entire story, and a fuller understanding must come from an approach that integrates both size and non-size effects. In this review we discuss the core principles of a size-based (allometric) approach in insect ecology, together with the potential of such an approach to connect biological processes and mechanisms across levels of organization from individuals to ecosystems. We identify knowledge gaps, particularly related to size constraints on insect movement and behavior, which can impact the strength and outcome of species interactions (and especially trophic interactions) and thus link individual organisms to communities and ecosystems. Addressing these gaps should facilitate a fuller understanding of insect ecology, with important basic and applied benefits.

## Addresses

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## Introduction

‘In scaling, as in so many other areas of biology, we know far more about homeotherms than about poikilotherms or unicells. Since most organisms are not homeotherms, a great deal of work is required before our knowledge would be proportional to animal abundance.’ [Peters, 1983]

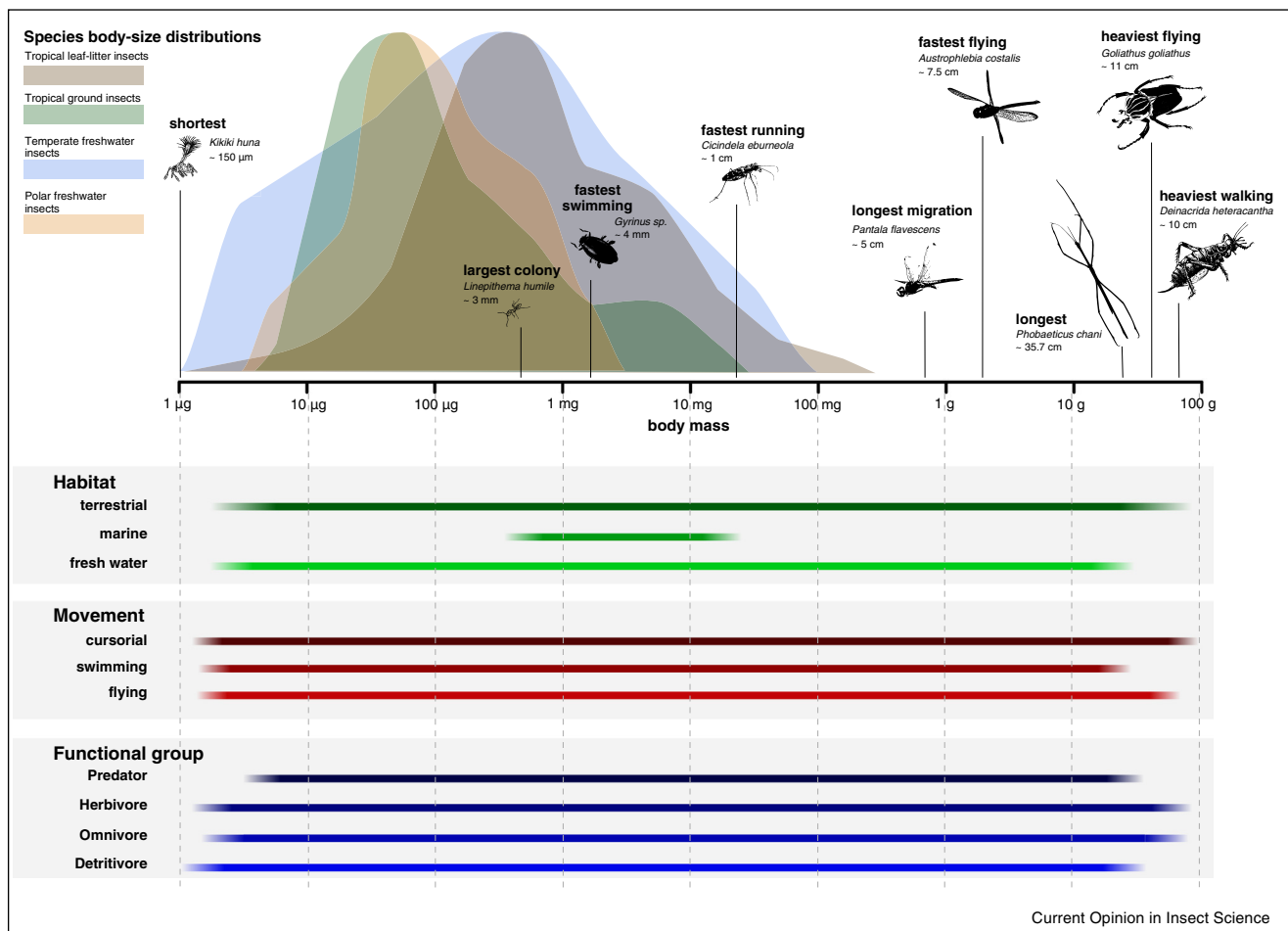
The body size of any organism strongly constrains many aspects of its physiology and ecology [1–5]. In insects, size influences their metabolic rate [6,7], their individual growth rate [83] and stoichiometric properties [8], how fast they move [9–11], how often they encounter prey [12,13] and how many prey they consume [14], and a huge suite of other traits central to their daily lives [1,5,15]. Because size is so important for individuals, patterns in the size distributions of groups of insects have crucial influences on the structure and function of higher levels of biological organization, such as populations, communities, and ecosystems (e.g. by affecting decomposition, primary productivity and carbon cycling; [16,17]). Body size is also easy to measure directly, or at least estimate, while at the same time can be used as a proxy for many other physiological and ecological traits [18]. Thus, a size-based understanding of insect ecology should be both attainable and useful, with significant basic and applied benefits.

To date, studies of body size in ecology have focused primarily on vertebrates [1–3,4] and vascular plants [19,20], although more recent work that focuses on insects (and, more generally, on invertebrates) addresses this

imbalance (e.g. [6,15,21,22,23,24]). The high taxonomic, ecological and functional diversity of insects, and the fact they span roughly nine orders of magnitude in mass (Figure 1) and are common in many of Earth's ecosystems (especially on land and in freshwater), make them an excellent study group to investigate size-related patterns and processes in ecology. To separate our paper from two excellent recent reviews [15,25\*\*] we pay particular attention to how size influences insect movement and behavior, which impacts how insects forage and thus has significant implications for the strength and outcome of species interactions, and especially trophic interactions [12,13\*\*,26,27]. At the same time, quantifying behavior and movement in accurate and precise ways is becoming easier due to the development of novel

automated methods [28\*\*]. A more mechanistic understanding of species interactions should enable linkage of the ecology of individuals to higher levels of ecological organization [25\*\*]. This research area, at the intersection between behavioral (i.e. movement ecology; [29]) and community (e.g. food web ecology; [25\*\*,30]) ecology, is characterized by significant advances in recent years on both empirical and theoretical fronts that is resulting in a deeper understanding of the role of body size in insect ecology. For example, the integration of allometric scaling with visual acuity and environmental drivers has furthered our understanding of the mechanisms that influence prey encounter and consumption rate [12,13\*\*,26]. The historical focus of size-based research on vertebrates and plants means that throughout our

Figure 1



Schematic overview of the ecology of insects in relation to their body mass. Upper panel: Examples for outstanding insect species representing the spread of the group in regard to body size, number of species, habitat, movement and ecological function. Also shown are four example species body-size distributions (transparent colored areas), detailing the number of species of different average body sizes within each community. Each of the four distributions are normalized to equal height on the y-axis: tropical leaf-litter insects (brown,  $n = 548$ ; [81]), tropical ground insects (green,  $n = 228$ ; [79]), temperate freshwater insects (blue,  $n = 25$ ; [82]), polar freshwater insects (orange,  $n = 16$ ; [80]). Lower panel: Estimated spread of body mass for insects within different habitats, movement types and functional groups.

review we draw strongly from literature that is not insect focused, which is justified given the apparent universality of many allometric principles across domains of life [1,4,5,15,25\*\*].

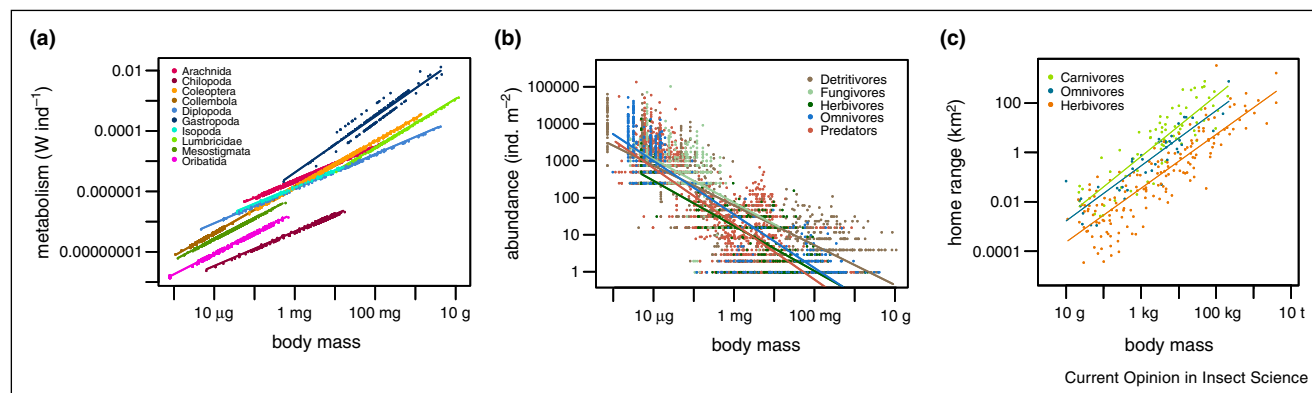
### Key recent developments in the field of allometry

Recent years have seen significant moves forward on a number of research fronts, but undoubtedly some of the most important advancements have come in the development of a predictive theoretical framework about size effects in ecology, which is mechanistically based on well-understood biological and physical mechanisms. Perhaps most impactful has been the Metabolic Theory of Ecology (MTE), which suggests that the power-law relationship between body size and metabolic rate that persists across taxa and ecosystems arises because of the ubiquitous fractal structure of transportation networks within organisms [5,31]. MTE aims to predict the structure and function of higher levels of biological organization (e.g. populations, communities, ecosystems) from the level of an individual organism, with a particular focus on metabolic rate [5,17]. In MTE, individual body size and body temperature are considered key drivers of many ecological processes, via their direct effects on metabolic rate ([5,6]; also see Figure 2a), with subsequent effects on trophic [27,32,33\*\*] and other types of species interactions and thus communities and ecosystems [5,17]. Thought to also be related to the allometry of metabolic rates, size-abundance scaling models characterize the commonly observed pattern of most ecological communities comprising many small and few large organisms ([3,34,35\*]; see Figure 2b). This community-wide pattern has important implications for trophic interactions, as individual consumers are more likely to encounter the more abundant smaller resources they often feed on [36],

a pattern which appears crucial for the stability of invertebrate predator–prey interactions and food webs [14\*\*,37]. The validity and generality of the simple yet powerful MTE remains hotly debated [38,39], and indeed recent analyses of insect data suggest that alternative models might outperform MTE in explaining certain empirical patterns ([7\*,21]; but see [40]). One of these alternative models is the cost of locomotion rooted in biomechanical principles [7\*,41], which stresses the importance of locomotion for insect metabolism, physiology and ecology (see below).

Owing to technological limitations in the past (e.g. size of devices for bio-logging; [42]), available empirical studies of allometric scaling in movement ecology (e.g. migration) were almost exclusively restricted to vertebrates ([43,44,45\*\*]; also see Figure 2c). By contrast, there are numerous studies on the size scaling of insect movement from laboratory-based comparative physiology and morphology (e.g. [46,47]), while more recent studies address insect-specific patterns across larger spatial and temporal scales (e.g. allometric effects on dispersal in butterflies; [48]). Moreover, it appears that for insect movement, and its implications for higher-level ecological processes, the allometry of morphology (and not just total body size) is especially important (e.g. wing size–body size relationships; [49]). To date, our understanding of the energetic implications of these relationships are also unclear. Although small animals require more energy to travel a given distance relative to their body mass [50], more recent work suggests that maximum migration distance should be similar when considered in relation to body length, which does not scale linearly with total mass [45\*\*]. Additionally, the diverse modes of insect movement (e.g. flying, swimming, running; Figure 1) provide a unique opportunity to explore additional size-related

Figure 2



Relationship between body mass and the example traits: metabolic rate (a), abundance (b) and home range (c). Different phylogenetic groups (a) and functional groups (b and c) show variation in their scaling with body mass. Figures reproduced from [35\*] (a and b) and [43,44] (c). Data for (a) and (b) are for 870 species of litter and soil invertebrates from a large-scale biodiversity study in Germany, data for (c) are from 279 mammal species.

constraints on dispersal, with potentially crucial implications for meta-community structure [51<sup>•</sup>]. Most prior studies concentrate on larger scale movement, such as dispersal and migration, while research addressing the scaling of more local traits related to individual behavior and foraging, which, although important for species interactions, is largely absent for insects [52]. Thus, while research on the allometry of insect movement and foraging behavior is occurring (e.g. [42]), more is required to obtain a clearer picture of the mechanistic basis of a phenomenon already well recognized: body size is key in shaping the strength and outcome of species interactions, and especially trophic interactions.

### Body size and trophic interactions

The role of body size has long featured prominently in studies of trophic interactions [24,36,53,54], and integration of energetic considerations into the picture has allowed ecologists to better understand the pivotal role of size for consumer–resource dynamics, and food webs more generally [55–58]. For instance, in a recent study on forest soil invertebrates, Ehnes *et al.* [35<sup>•</sup>] showed that accounting for the efficiency of energy transfer between trophic levels could explain deviations from the basic assumptions of MTE and mass-abundance rules more generally. Likewise, Ott *et al.* [8] recently showed that allometry interacts with the stoichiometry of the basal resource to determine the distribution of biomasses across the food web populations. From this and other related work it is becoming clearer that explaining the outcome and strength of trophic interactions requires information in addition to body size, which may or may not relate to body size in simple ways.

One area that is receiving a lot of current attention is the foraging behavior of consumers, which many authors now see as crucial to trophic interactions [13<sup>••</sup>,27,30,57,59]. For example, the hump-shaped relationship observed between attack rates and body size for a wide range of animals, including terrestrial (e.g. [14<sup>••</sup>]) and aquatic insects (e.g. [12]), may be partly explained by foraging behavior. In their analysis of functional responses and size selectivity of notonectid predators and their daphnid prey, Gergs and Ratte [12] used video tracking experiments to disassemble the attack rates of classical functional responses into encounter rates and success rates. They found that while encounter rates increased with body size following a quadratic relationship, success rates were characterized by a hump-shaped relationship [12]. Encounter rates are assumed to be driven by the consumer's detection ability (related to their foraging behavior) following allometric relationships [60], which have successfully been used to build an allometric vision and motion model of optimal foraging [13<sup>••</sup>,26]. Interestingly, a meta-analysis of vertebrate studies suggests these detection probabilities are driven by temporal perception which, in turn, is related to body size, with smaller

animals showing a higher temporal resolution of the sensory system [61]. Rigorous tests of the allometric relationships of detection probabilities and the relation to temporal perception and foraging decision in insects remain elusive. The hump-shaped relationship in attack rates [14<sup>••</sup>,30] or in capture success [12] might also be driven by the asymmetry between higher maneuverability in small prey and maximum foraging speed in large predators, as has been explored in fish [62]. Again, we are not aware of comparable research on insects. A detailed analysis of these relationships should also concentrate on burst speed and acceleration potential, which are presumably important for trophic interactions [47,63].

In the context of trophic interactions, functional morphology and the intertwined consumer foraging mode have been proposed as one of the main concepts that explains why a trophic interaction occurs between any given predator–prey pair. This implies a match between the 'tools' available for a predator to capture and overcome a particular prey, and the 'tools' available for a prey to evade capture from that particular predator [25<sup>••</sup>,64,65,66<sup>••</sup>]. Integrating these traits into an allometric framework appears to us a useful advancement of current food web models, where a considerable portion of the variation in predator–prey interactions remains unexplained by more simple size-based approaches (examples include [67] for terrestrial predators; [66<sup>••</sup>] for aquatic predators). Prior attempts to connect functional morphology and allometric scaling for movement relationships have focused on dispersal [68] and migration [49], but similar research on trophic interactions is required. For instance, flying performance in dragonflies not only depends on total body size but also wing morphology (i.e. the morpho-allometric relationship between body size and wing size; [49]), with important influences on sexual selection and optimization of different flying tasks [49]. Similarly, functional morphology is key to understanding non-body size related differences in locomotion performance in terrestrial [50] and aquatic [69] insects: where on land the effective length of body appendages responsible for movement accounts for most of the variation [50], the relationship for aquatic movement seems to be more complicated [69]. Hence, given their diverse modes of living and their large range of body size (Figure 1), investigating these relationships in insects would seem useful for further understanding bio-mechanical constraints on foraging behavior [25<sup>••</sup>]. Given each of these considerations, it now seems feasible to extend current scaling frameworks to integrate allometric scaling relationships across levels of organization, from the physiology and morphology of individuals to trophic interactions and ultimately to the energetics of entire communities and ecosystems [65,66<sup>••</sup>].

### Future directions

Globally, insects are an important functional component of terrestrial and freshwater systems, often with strong

economic and cultural importance for humans [70]. By integrating body-size related information such as physiological constraints (as characterized by the MTE — [5,17] — or competing approaches — [7\*,21]), together with body-size relationships for consumer–resource pairs [36] and entire food webs [24,71], ecologists now have a better understanding of ecosystem stability and functioning. Thus, patterns in insect body size distributions, together with intra-specific and inter-specific allometric relationships, are important for a wide range of basic and applied questions. For instance, allometric effects can explain how predator loss in soil-litter systems affects crucial ecosystem functions such as litter decomposition and nutrient cycling [54]. Moreover, intraspecific size distributions apparently have far-reaching consequences at the community level [16,72], but most often these data are not available. Therefore, there is a need for continued development of highly-resolved empirical datasets, such as population body size distributions for multiple interacting species ([23,79]) or body-mass variation across various levels of insect phylogeny [15]. Insect-specific analyses of subsets of existing data bases for species interactions (e.g. [32,33\*\*]) are a logical next step. Future research on individual-level interactions of insects from a diverse range of ecosystems might then shed light on important ecosystem mechanisms, providing a deeper understanding of how crucial ecological functions are organized and maintained. One particularly useful approach appears to be novel automated methods [28\*\*], which should help elucidate the mechanistic link between individual-level, morphologically and physiologically constrained behavior and higher levels of ecological and biological organization.

A generalized version of allometric theory needs to be developed that is able to account for apparent non-size related variation, by incorporating additional behavioral and functional morphological traits. The first steps toward this goal have already been made in quantitative studies of food webs and other ecological networks: for instance, Naisbit *et al.* [73] used a ‘two-dimensional’ approach where phylogenetic relatedness could explain food-web structure better than body size alone. In addition, Eklöf *et al.* [65] showed that the structure of different types of ecological networks are best explained by models that incorporate approximately three to four additional traits (e.g. habitat type, mobility, phenology, phylogenetic information; [65]) together with body size. Here again, functional morphology was explicitly highlighted (e.g. fruit size and bill gape for frugivorous birds; [65]). Additional traits and relationships that should be incorporated into an extended framework of ecological allometry in insects include environmental temperature (e.g. [5,27,32,33\*\*]), the degree of hunger of predators [74] and their experience with handling particular prey [75], the stoichiometry of food resources [76], and even the individual ‘personality’ of predators [77,78\*]. Thus, a full

and mechanistic understanding of insect ecology will only be achieved by approaches that integrate both size and (apparent) non-size effects [25\*\*]. We particularly encourage approaches addressing the link between allometric constraints on behavior with functional morphology and foraging relationships to gain a better understanding of the processes that shape the typical hump-shaped relationship between predator–prey size ratios and capture success [12,14\*\*,30]. Although this topic has been investigated with vertebrates (e.g. [60–62]), a similar integration of such relationships is required for insects and other invertebrates.

Future research at the intersection between insect behavioral and community ecology should therefore embrace, and ultimately integrate, these approaches to establish a new framework that links distinct layers of biological and ecological organization.

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