Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits

Marco Moretti[1]*, André T.C. Dias[2], Francesco de Bello[3,4], Florian Altermatt[5,6], Steven L. Chown[7], Francisco M. Azcárate[8], James R. Bell[9], Bertrand Fournier[10], Michael Hedde[11], Joaquín Hortal[12,13], Sébastien Ibanez[14], Erik Öckinger[15], José Paulo Sousa[16], Jacintha Ellers[17+] and Matty P. Berg[17,18+]

[1] Swiss Federal Research Institute WSL, Biodiversity and Conservation Biology, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
[2] Departamento de Ecologia, Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro (UERJ), Maracanã, Rio de Janeiro, RJ, Brazil.
[3] Institute of Botany, Czech Academy of Sciences, Dukelska 135, 379 82 Třeboň, Czech Republic
[4] Faculty of Sciences, University of South Bohemia, Na Zlate Stoce 1, 370 05 České Budějovice, Czech Republic
[5] Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, 8600 Dübendorf, Switzerland
[6] Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zürich, Switzerland
[7] School of Biological Sciences, Monash University, Clayton VIC 3800, Australia
[8] Terrestrial Ecology Group (TEG), Department of Ecology, Universidad Autónoma de Madrid, C/Darwin 2, 28049 Madrid, Spain
[9] Rothamsted Research, West Common, Harpenden, Hertfordshire, AL5 2JQ, UK
[10] Laboratoire Chrono-Environnement, UMR 6249 CNRS, Université de Bourgogne Franche-Comté, 16 route de Gray, 25030 Besançon Cedex, France
[11] INRA, UMR 1402 EcoSys, RD 10, 78026 Versailles, EU, France
[12] Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales (MNCN-CSIC), C/Jose Gutierrez Abascal 2, 28006 Madrid, Spain
[13] Centre for Ecology, Evolution and Environmental Changes (Ce3C), Faculdade de Ciências da Universidade de Lisboa (FCUL), Ed. C2, Campo Grande, 1749-06 Lisboa, Portugal
[14] Laboratoire d'Ecologie Alpine, CNRS UMR 5553, Université de Savoie, Bâtiment Belledonne Ouest, 73376 Le Bourget-du-Lac, France
[15] Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, 750 07 Uppsala, Sweden
[16] Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, 3000-456 Coimbra, Portugal
[17] Department of Ecological Science, Faculty of Earth and Life Sciences, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands
[18] Conservation Ecology group, Groningen Institute for Evolutionary life sciences, University of Groningen, Postbox 11103, 9700 CC Groningen, The Netherlands

[+] These two authors share the senior authorship; * Corresponding author (marco.moretti@wsl.ch)

Summary

1. Trait-based approaches are increasingly being used to test mechanisms underlying species assemblages and biotic interactions across a wide range of organisms including terrestrial arthropods and to investigate consequences for ecosystem processes. Such an approach relies on the standardized measurement of functional traits that can be applied across taxa and regions. Currently, however, unified methods of trait measurements are lacking for terrestrial arthropods and related macroinvertebrates (terrestrial invertebrates hereafter).

2. Here, we present a comprehensive review and detailed protocol for a set of 29 traits known to be sensitive to global stressors and to affect ecosystem processes and services. We give recommendations how to measure these traits under standardized conditions across various terrestrial invertebrate taxonomic groups.

3. We provide considerations and approaches that apply to almost all traits described, such as the selection of species and individuals needed for the measurements, the importance of intraspecific trait variability, how many populations or communities to sample and over which spatial scales.

4. The approaches outlined here provide a means to improve the reliability and predictive power of functional traits to explain community assembly, species diversity patterns, and ecosystem processes and services within and across taxa and trophic levels, allowing comparison of studies and running meta-analyses across regions and ecosystems.

5. This handbook is a crucial first step towards standardizing trait methodology across the most studied terrestrial invertebrate groups, and the protocols are aimed to balance general applicability and requirements for special cases or particular taxa. Therefore, we envision this handbook as a common platform to which researches can further provide methodological input for additional special cases.

Key-words: species features, species characteristics, physiology, morphology, feeding, behaviour, life-history, functional diversity.

Introduction

Over the last decade strong calls have been made to shift the research focus of community ecology from purely species-based approaches to trait-based ones (among others Lavorel & Garnier 2002; McGill *et al.* 2006; Diaz *et al.* 2007b; Suding *et al.* 2008; Webb *et al.* 2010; Chown 2012; Mouillot *et al.* 2013). Despite early work (e.g. Shelford 1911), this call is driven by an increasing awareness that trait-based approaches can significantly enhance our mechanistic understanding and predictive capabilities of the processes that play a major role in community ecology. Moving from a taxonomic approach to a functional trait approach reduces context dependency and therefore enables generalization across communities and ecosystems that is needed to address macro-ecological questions (McGill *et al.* 2006; Suding *et al.* 2008; Hortal *et al.* 2015; Kunstler *et al.* 2016). For example, traits can help explain the effects of climate change on species distribution and range shift (e.g., Kaustuv *et al.* 2001; Berg *et al.* 2010; Diamond *et al.* 2011), environmental gradients and stressors on the distribution of species and community (dis)assembly (e.g., Dias *et al.* 2013; Astor *et al.* 2014; Woodcock *et al.* 2014), as well as the effect of community composition on ecosystem processes and the provision of ecosystem services across ecological scales (Naeem & Wright 2003; Messier, McGill & Lechowicz 2010; Luck *et al.* 2012; Brittain *et al.* 2013; Deraison *et al.* 2015). Trait-based approaches have recently also been advocated as promising tools also in ecotoxicology and environmental risk assessment of chemical substances (Rubach *et al.* 2011; Van den Brink *et al.* 2013).

Recent developments in trait-based ecology have been led by plant ecologists, as plant traits have become effective predictors of community assembly (Götzenberger *et al.* 2012; HilleRisLambers *et al.* 2012) and ecosystem processes (Lavorel 2013), and are now widely used. The prime utilization of plant functional traits is to identify abiotic and biotic mechanisms that determine species composition, ecosystem processes and service delivery (Lavorel & Garnier 2002; Diaz *et al.* 2007a; Luck *et al.* 2009; de Bello *et al.* 2010; Lavorel *et al.* 2013). Plant ecologists have been able to scale up successfully from individual plant physiological traits to vegetation processes, such as competition and environmental filtering, as well as ecosystem processes such as decomposition, across a wide range of plant communities (Diaz *et al.* 2004; Cornwell *et al.* 2008; Kunstler *et al.*

2016), and link trait variability to global carbon cycle and climate models (Atkin *et al.* 2015). The early success of the plant trait approach has fuelled the discussion about which traits need to be measured and how they should be quantified in a standardized way. The development of large online trait databases in plant ecology, such as LEDA (Kleyer *et al.* 2008) and TRY (Kattge *et al.* 2011), now provide quick access to plant trait values, allowing comparisons even between ecosystems and biomes. Despite potential limitations of using these databases (Cordlandwehr *et al.* 2013), such success in plant ecology has fostered and increasing interest ecologists to adopt a similar trait-based approach in other taxonomic groups (e.g., Poff *et al.* 2006; Vandewalle *et al.* 2010; Aubin *et al.* 2013; Pakeman & Stockan 2014; Pey, Laporte & Hedde 2014; Fournier *et al.* 2015; Schemara *et al.* 2015). Particularly for terrestrial invertebrates, attempts to develop trait frameworks for specific taxa, e.g., Fountain-Jones, Baker & Jordan (2015) for beetles, or to construct trait databases for snails (Falkner *et al.* (2001), Bouget, Brustel & Zagatti (2008) for saproxylic beetles, Speight & Castella (2010) for hoverflies, Bertelsmeier *et al.* (2013) for ants (see also Yates *et al.* 2014), Homburg *et al.* (2014) for carabid beetles, and Pey, Laporte & Hedde (2014) for soil invertebrates), as well as new statistical developments (e.g., Brown *et al.* 2014) have been published.

Invertebrates have crucial roles as consumers of primary producers (e.g., herbivores, fungivores, granivores etc.) and the afterlife products of animals and plants (i.e., detritivores, such as feeding on leaf-litter, dead wood, dung and carrion), they provide a staple food for higher trophic levels (e.g., for predators, parasites and parasitoids) and are recognised as both facilitators of primary production (i.e. pollinators and detritivores) and as ecosystem engineers (e.g., soil bioturbators; see Gagic *et al.* 2015 for an overview). Hence, knowledge of invertebrate traits are key to understanding multi-trophic processes and ecosystem functioning (e.g., Lavorel *et al.* 2013; Schmitz *et al.* 2015). Current terrestrial invertebrate trait databases are often built around a set of basic traits from a mixture of studies and observations, that are obtained without uniform methodology and with little consistency in which traits were chosen for measurements. In addition, functional traits, such as species temperature tolerance and drought resistance, are often missing or inferred from the abiotic conditions at the (micro)habitats where they have been observed and not measured directly on individuals. However, (micro)habitat selection of species and realized niche in general might result from interactions between species rather than physiological and phenological characteristics of single individuals and populations (Colwell & Fuentes 1975; Ellers, Dias & Berg 2010; Araujo *et al.* 2013; Colas *et al.* 2014; He & Bertness 2014), but see also Warren, Giladi & Bradford (2010). The use of such inferred traits as predictors of community and ecosystem processes has been strongly discouraged (Violle *et al.* 2007), advocating for traits to be measured on indivual organisms. The arguments above raise the urgent need for reliable and unified methods to measure functional traits that are directly linked to species performance. A coherent, unified and standardized trait approach for various types of terrestrial invertebrates requires consensus on 1) what the basic set of functional traits would be and, particularly, on 2) how they should be measured. A key element in the advance of plant trait-based approaches has been the provision of a handbook of standardized functional traits that detail the methods and definitions of key traits worldwide (Cornelissen *et al.* 2003), and its recent update with additional traits and measuring techniques (Pérez-Harguindeguy *et al.* 2013). Such an effort is therefore required in other key organisms such as terrestrial invertebrates. The present work aims to provide such incentive to trait-based approaches for this broad and diversified group of species, by describing a set of standardized trait measurements to improve the reliability and general applicability of functional traits.

Overall approach to the handbook

This handbook aims to provide a set of protocols for trait measurements that can be used across a wide range of terrestrial invertebrate species, including the major taxonomic groups of Insecta, Collembola, Aranea, Crustaceae, Myriapoda, Gastropoda and Oligochaeta. We selected the terrestrial environment as a circumscribed habitat that differs in key features from aquatic ones – rate of temperature change, threat of desiccation, very different osmoregulatory challenges, much greater temperature variability on average and over the short term. We chose these groups of organisms because they are similar enough in lifestyle to apply our protocols to. The handbook does not include specific methods for measuring traits of nematodes, parasites and (semi-)aquatic invertebrates, although some of the protocols may be used for these groups too.

We recognise that the wide variety of life forms encompassed by the present handbook makes it a challenging undertaking. In general, invertebrate traits, overall, may incorporate greater complexity than plant traits, because animals can respond to environmental changes by movement and behaviour. Therefore, the trait protocols contain recommendations for adjustments to accommodate the biology of particular taxonomic groups, while maintaining comparability and standardization across taxa.

The handbook is meant as a first step to advance the trait-based approach to groups other than plants and vertebrates and to stimulate discussion about additional traits that should be included in the handbook for terrestrial invertebrates. We foresee that this set of traits might be expanded in the future as the use of the functional approach becomes increasingly used among animal ecologists. Moreover, the trait protocols are designed for standardized measurement of traits to facilitate a widespread use and to allow high-throughput phenotyping to enable measurements on large numbers of species. For this reason, some of the most advanced technological methods that are currently used by specialized research groups only and for few specific taxonomic groups are not part of the standardized methods, but included as special cases in the protocols. We would like to emphasize that the handbook's main purpose is to maximize comparability of measurements across a wide range of taxa. Below, we first provide an overview of the criteria and concepts used for selecting the set of traits, subsequently we describe the standard format of the protocols, followed by several general recommendations. The protocols themselves are provided as electronic Supporting Information.

Trait selection

We reviewed the literature on ecology of terrestrial invertebrates, and selected the 29 traits (see Table 1) for which we found clear evidence that they directly link organism performance with environmental conditions or ecosystem processes. These traits have been then further discussed among a group of specialist scientists working on the ecology, ecophysiology, and evolutionary aspects of predominantly terrestrial invertebrate fauna at different trophic levels with the aim to standardize the methods for their unambiguous use in any terrestrial biome and for the majority of its constituents.

Overall, the selected set of traits largely covers the primary functions related to species performance, assembly processes, and interactions between trophic levels at various spatial scales from plots to landscapes and even biomes. For this first step in generalizing traits across taxonomic groups we excluded traits that are specific to single groups (e.g., pollen transport mode in bees, web construction strategy in spiders, or chemical and physical defenses in ants or some caterpillars) and cannot be standardized across taxa. Selected traits can be ~~separated into~~ considered either response traits (i.e., determining the response of the species to an environmental change or to an interaction with another organism from the same or different trophic level) or effect traits (i.e. contributing) to the effect of the species on an ecosystem function or the interaction with the another trophic level, or both (Lavorel & Garnier 2002; Naeem & Wright 2003; Sunding & Goldstein 2008; Lavorel *et al.* 2013). We focus on several traits which, based on the existing literature, are among the most widely used or are in urgent need of standardized measurement protocols that can be applied across taxa. From the user perspective, trait selection is often one of the crucial aspects in trait-based approaches and it has to be based clearly bearing the research question being asked (Rosado *et al.* 2013; Shipley *et al.* 2016). We do refer to the known functionality of traits considered in our protocols.

Most of the selected traits are quantitative and directly measurable on an individual under standardized conditions; others are categorical (e.g., activity time and feeding guild) or ordinal (e.g., ontogeny and respiration system). Broadly, the selected traits can be grouped into five categories, i.e., morphology, feeding, life history, physiology, and behaviour. *Morphological traits* such as eye morphology, body pigmentation or body size are important features of an organism's interaction with the abiotic and biotic environment. For example, body size across different taxonomic groups is a predictor of multiple ecological processes, such as decomposition and mineralization by soil macro-detritivores, pollination by bees or water regulation by earthworms (de Bello *et al.* 2010), and strongly correlated with an individual's metabolic rate (Chown *et al.* 2007). Body size also scales with many other life history traits (Ellers & Jervis 2003) and determines the structure and function of ecological networks (Peters 1983; Brown *et al.* 2004; Woodward *et al.* 2005). *Feeding traits* are related to the trophic position of a species and describe aspects of the morphology and behaviour associated with their diet. Feeding related traits can therefore be important for understanding niche partitioning, trophic interactions and the way the structure of ecological networks is shaped (Stang *et al.* 2009; Ibanez 2012; Ibanez *et al.* 2013).

Life history traits describe the age schedule of reproduction of an organism, including key reproductive aspects such as age at maturity, clutch size, voltinism, and life span (Stearns 1992). These traits have strong links to fitness and are expected to be among the most sensitive to environmental stress, making them useful to assess the vulnerability of species to global change. For instance, egg size varies enormously between species (Fox & Czesak 2000) and affects hatching success (Fischer *et al.* 2006) and resistance to desiccation (Fischer *et al.* 2006) and heat (Liefting *et al.* 2010). Moreover, trade-offs exist between reproductive traits and dispersal (Guerra 2011), leading to a reduced reproductive investment in some insects with strong range expansion under the influence of global warming (Hughes, Hill & Dytham 2003).

Physiological traits refer to features that allow species to tolerate variations in abiotic conditions (resistance adaptations), as well as biochemical modifications that adjust the rate of metabolic function (capacity adaptations) in response to environmental changes (Cossins & Bowler 1987; Somero 1992). Physiological tolerance traits, such as heat tolerance and desiccation resistance have been successfully applied in predicting species distribution patterns along temperature and humidity gradients (Dias *et al.* 2013), while growth rate can determine an individuals' susceptibility to predation (Denno *et al.* 2002; Coley, Bateman & Kursar 2006) and temperature fluctuations (Fordyce & Shapiro 2003). Further, physiological tolerances can be affected by changes in diet (Verdu *et al.* 2010).

Finally, *Behavioural traits* enable flexible, rapid responses to environmental change without any associated changes to physiological or morphological phenotypes. Traits such as activity time, aggregation, and locomotion enable organisms to seek out preferred microhabitats and to avoid (a)biotic stress. Behavioural strategies can also increase tolerance to abiotic stresses, for instance through adopting flight strategies that maximize heat dissipation (Verdu, Alba-Tercedor & Jimenez-Manrique 2012) or by choosing specific microhabitats to achieve nutritional homeostasis (Clissold, Coggan & Simpson 2013) or escape adverse climatic conditions. Yet in soil fauna species, stratification in soil interacts with other traits, such as physiological traits, thus modifying the individual response to changes in environmental conditions (Cloudsley-Thompson 1962) and vulnerability to extreme temperature events (van Dooremalen *et al.* 2012).

The handbook protocols

The trait protocols are described using a standard format aimed to facilitate comparisons among traits The protocols are provided as Supporting Information to this study. Each protocol includes four main sections. The section *Definition and relevance* provides a formal definition and a short, non-exhaustive justification why that particular trait is of ecological significance based on its role in responding to stressors and/or effecting trophic interactions or ecosystem processes. This section also describes the main approaches to measure a particular trait. The section *What and how to measure* describes the standardized method, and provides the units of expression and, if applicable, mathematical formulas for trait value calculations. The section *Additional notes* contains, if available, alternative techniques, often more expensive and challenging, and mainly used by more specialized research groups to answer deeper questions. This section may also list modifications of the methods for specific taxonomic groups and draws attention to potential caveats and improvements. Finally, the *Reference*s list a number of key papers which are cited in the protocol.

Standardization of measurements and acclimation of animals

Organisms respond to a multitude of external environmental factors, leading to differences in trait values due to trait plasticity, learning and shifts in physiological status. As a consequence, trait values may depend on the immediate conditions an organism is subjected to at the place or time of collection. To achieve standardized trait measurements it is necessary to provide the comparable conditions for all individuals measured, which for many traits requires an acclimation period in order to minimize the effect of local conditions (Cornelissen *et al.* 2003). By doing this, the trait variability within species will more tightly reflect genetic rather than environmental effect and information about intraspecific trait variability can become valuable (see below). Therefore, the handbook starts off with a standardization protocol that describes recommendations for pre-treating and acclimating animals to obtain comparable values within and among species for all taxonomic groups. Here, the importance of static conditions relative to fluctuating ones (e.g. Colinet *et al*. 2015), which reflect the natural environment more closely, are discussed. The matter is not a straightforward one (Chown & Gaston 2016) because the introduction of variable conditions in a standard protocol setting implies that assessments, and subsequent comparisons, have to be made across regimes that differ in mean values, and variation that is described by amplitude, frequency and predictability of a condition (see Angilletta *et al*. 2006; Chown & Terblanche 2007).

For traits which are expressed in terms of survival time as the unit of measurement, such as inundation resistance, all individuals should have the same nutritional status at the start of the measurements and should either be fully fed or subjected to a short starvation period to empty their gut prior to trait measurements. When measuring feeding traits (e.g., food preference, ingestion rate) it is necessary that all individuals are acquainted with the food items used during the feeding assays. For traits that are strongly temperature-dependent such as metabolic rate, food ingestion rate and locomotion speed, thermal acclimation is absolutely necessary, although the acclimation time depends on the organisms and specific life cycles, as well as on the trait and ontogenetic stage of interest. As trait plasticity can occur during an organism's ontogeny (e.g. Wilson & Franklin 2002), it might be sometimes necessary to raise animals under controlled conditions (controlled environmental rooms) and measure traits in individuals born into these rooms. Obviously, in cases where the research interest is focused on the actual survival time when animals are exposed to drought in their habitat, the actual diet composition in the field, or the dispersal distance under natural conditions, then standardized measurements will not need to be imposed, except perhaps for serving as a baseline to measure the extent by which field conditions depart from basal adaptations.

Selection of specimens and number of individuals per species

A key consideration is selecting the appropriate specimens for trait measurements. Aiming to compare standardized trait measurements across studies and taxa of any developmental stage and sex, we recommend selecting healthy, well-shaped, and fully-developed individuals of the ontogenetic stage of interest, without any signs of damage and diseases, an approach already suggested in plant-trait analyses (Cornelissen *et al.* 2003). The use of interception trapping devices, such as pitfall traps, windowpane traps and Malaise traps to collect species for trait measurements should be regarded with caution as the quality of the captured individuals depends on construction, location, time of day, season or year, weather, and trap clearance frequency (Gibb & Oseto 2006), and, importantly, they might be selective for specimen with certain traits. We recommend therefore that the sampling methods should be reported in detail and that additional information on trapping efficiency should be provided together with the trait measurements.

When laboratory strains are used for measurements, care should be taken as laboratory adaptation may cause spurious changes in life history and physiological traits of species (Sgrò & Partridge 2001; Griffiths, Schiffer & Hoffmann 2005). The type of culturing method, the size of the stock population and the length of the period of laboratory culture are all factors that determine the magnitude of selection response in laboratory population, and therefore these factors need to be reported meticulously with the trait measurements.

Sample size is a general issue in trait-based approaches and has already been covered in other publications, although mainly on plants (e.g., Pakeman & Quested 2007; Bolnick *et al.* 2011; de Bello *et al.* 2011; Fu *et al.* 2013; Pérez-Harguindeguy *et al.* 2013). If one would like to capture the full spatiotemporal variability of a species trait mean, a proportional number of individuals should be measured from different populations, seasons, communities, and ecosystems (Pakeman & Quested 2007; de Bello *et al.* 2011; Violle *et al.* 2012). This number will further increase if other sources of intraspecific variation will be included, e.g. polymorphism, sexual dimorphism and ontogenetic stages (Yang & Rudolf 2010; Violle *et al.* 2012), which are all particularly important among invertebrates. In general, the minimal number of individuals to be measured for a given species will depend on the variation of the trait values. The higher the variation, e.g., in case of behavioural traits, the higher the numbers of individuals to be measured for reliable estimates of the species mean trait value.

Future perspectives

This handbook is a first step towards standardizing trait methodology across some of the most well-investigated terrestrial invertebrate groups. We are aware that its protocols do not cover all special cases and may miss information for particular taxa. Below we highlight three fields that we hope will be developed further with the aid of this handbook and offer a perspective on these fields of trait research.

Incorporating intraspecific trait variability

Evidence is increasing that intraspecific trait variability plays a significant role in demography and community assembly, and has (Bolnick *et al.* 2011; de Bello *et al.* 2011; Violle *et al.* 2012; Siefert *et al.* 2015). Within-species variability may originate from spatial variability in trait values within a species range, or may be due to genetic or environmental variation within a population at a single site. Information on both types of variability is extremely valuable, e.g. for understanding the mechanisms underlying community assembly or as input for models on functional consequences of global drivers (Gaston, Chown & Evans 2008; Yang & Rudolf 2010). Until now the lack of standardized measurements for invertebrate traits, as well as the tiny sample size for many traits, has prohibited a clear indication of the trait variability beyond the single species level. We believe that the use of the standardized protocols can overcome this gap and we recommend not to report only species trait means for the traits measured, but also measures such a standard deviation (Carmona *et al.* 2016).

Definition and validation of effect traits

Quantifying community functional trait structure such as the variation in response traits, the diversity and redundancy among species sharing similar effect traits, and the overlap between response and effect traits is important for enhancing predictability of ecosystem functioning under environmental change (Folke, Holling & Perrings 1996; Elmquist *et al.* 2003; Mori, Furukawa & Sasaki 2013). While our knowledge on response traits of terrestrial invertebrates is relatively good, information on the extent to which response traits and effect traits can be linked within taxa, either via trait correlations or trait trade-offs, is still largely lacking. Even less is known about response-to-effect models across trophic levels (Schmitz 2008; Lavorel *et al.* 2013; Moretti *et al.* 2013; Pakeman & Stockan 2014; Deraison *et al.* 2015), although the degree of overlap between the two types of traits will determine our ability to predict changes in key ecosystem processes under variable environmental conditions.

The current definition of response and effect traits in terrestrial invertebrates is based on literature and expert knowledge, but validation based on controlled experiments is urgently needed.

Construction of a trait database for terrestrial invertebrates

The benefits of standardized trait measurements to the research community can be amplified if this information is compiled in a communal database. Following the successful example of the worldwide TRY initiative (Kattge *et al*. 2011), we propose that increased access to trait information collected with standardized protocols will promote the interest to use this data. For many research questions, traits obtained from trait databases can be used as a first step to test hypotheses (Cordlandwehr *et al.* 2013) and for analyses at broad spatial scales (Hortal *et al.* 2015). In plant ecology this has been a very successful approach, sometimes leading to additional trait measurements at different spatial scales (de Bello *et al.* 2009) or with a stronger focus on intraspecific trait variability (Bolnick *et al.* 2011). However, the construction and maintenance of such a large database is a major undertaking that likely requires a dedicated staff and long-term funding. We hope that an enthusiastic and regular use of this first handbook of protocols for standardized measurement of terrestrial invertebrate functional traits will encourage researchers and funding agencies alike to taking this crucial long term option.

References

Angilletta, M.J., Bennett, A.F., Guderley, H., Navas, C.A., Seebacher, F. & Wilson, R.S. (2006) Coadaptation: a unifying principle in evolutionary thermal biology. *Physiological and Biochemical Zoology*, **79**, 282-294.

Araujo, M.B., Ferri-Yanez, F., Bozinovic, F., Marquet, P.A., Valladares, F. & Chown, S.L. (2013) Heat freezes niche evolution. *Ecology Letters,* **16,** 1206-1219.

Astor, T., Strengbom, J., Berg, M.P., Lenoir, L., Marteinsdottir, B. & Bengtsson, J. (2014) Underdispersion and overdispersion of traits in terrestrial snail communities on islands. *Ecol Evol,* **4,** 2090-2102.

Atkin, O.K., Bloomfield, K.J., Reich, P.B., Tjoelker, M.G., Asner, G.P., Bonal, D. *et al.* (2015) Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. *New Phytologist,* **206,** 614-636.

Aubin, I., Venier, L., Pearce, J. & Moretti, M. (2013) Can a trait-based multi-taxa approach improve our assessment of forest management impact on biodiversity? *Biodiversity and Conservation,* **22,** 2957-2975.

Berg, M.P., Kiers, E.T., Driessen, G., van der Heijden, M.G.A., Kooi, B.W., Kuenen, F.J.A. *et al.* (2010) Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology*, **16**, 587-598.

Bertelsmeier, C., Luque, G.M., Confais, A. & Courchamp, F. (2013) Ant Profiler – A database of ecological characteristics of ants (Hymenoptera: Formicidae). *Myrmecological News,* **18,** 73-76.

Bolnick, D.I., Amarasekare, P., Araujo, M.S., Burger, R., Levine, J.M., Novak, M. *et al.* (2011) Why intraspecific trait variation matters in community ecology. *Trends Ecol Evol,* **26,** 183-192.

Bouget, C., Brustel, H. & Zagatti, P. (2008) The french information system on saproxylic beetle ecology (frisbee): an ecological and taxonomical database to help with the assessment of forest conservation status. *Revue Écologie (Terre Vie),* **10,** 33-36.

Brittain, C., Williams, N., Kremen, C. & Klein, A.-M. (2013) Synergistic effects of non-Apis bees and honey bees for pollination services. *Proceedings of the Royal Society B-Biological Sciences,* **280,** 20122767.

Brown, J.H., Gillooly, J.F., Allen, A.P., van Savage, M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology,* **85,** 1771-1789.

Brown, A.M., Warton, D.I., Andrew, N.R., Binns, M., Cassis, G., Gibb, H., 2014. The fourth-corner solution – using predictive models to understand how species traits interact with the environment. Methods in Ecology and Evolution 5, 344-352.

Carmona, C.P., de Bello, F., Mason, N.W.H. & Leps, J. (2016) Traits Without Borders: Integrating Functional Diversity Across Scales. *Trends in Ecology & Evolution,* **31,** 382-394.

Chown, S.L. (2012) Trait-based approaches to conservation physiology: forecasting environmental change risks from the bottom up. *Philosophical Transactions of the Royal Society B-Biological Sciences,* **367,** 1615-1627.

Chown, S.L. & Gaston, K.J. (2016) Macrophysiology – progress and prospects. *Functional Ecology,* **30**, 330-344.

Chown, S.L., Marais, E., Terblanche, J.S., Klok, C.J., Lighton, J.R.B. & Blackburn, T.M. (2007) Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. *Functional Ecology*, **21**, 282-290.

Chown, S.L. & Terblanche, J.S. (2007) Physiological diversity in insects: ecological and evolutionary contexts. *Advances in Insect Physiology*, **33**, 50-152.

Clissold, F.J., Coggan, N. & Simpson, S.J. (2013) Insect herbivores can choose microclimates to achieve nutritional homeostasis. *Journal of Experimental Biology,* **216,** 2089-2096.

Cloudsley-Thompson, J.L. (1962) Microclimate and the distribution of terrestrial arthropods. *Annual Review of Ecology,* **7,** 199-222.

Colas, F., Vigneron, A., Felten, V. & Devin, S. (2014) The contribution of a niche-based approach to ecological risk assessment: Using macroinvertebrate species under multiple stressors. *Environ Pollut,* **185,** 24-34.

Coley, P.D., Bateman, M.L. & Kursar, T.A. (2006) The effects of plant quality on caterpillar growth and defense against natural enemies. *Oikos,* **115,** 219-228.

Colinet, H., Sinclair, B.J., Vernon, P. & renault, D. (2015) Insects in fluctuating thermal environments. *Annual Review of Entomology*, **60**, 123-140.

Colwell, R.K. & Fuentes, E.R. (1975) *Experimental studies of the niche*.

Cordlandwehr, V., Meredith, R.L., Ozinga, W.A., Bekker, R.M., van Groenendael, J.M. & Bakker, J.P. (2013) Do plant traits retrieved from a database accurately predict on-site measurements? *Journal of Ecology,* **101,** 662-670.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E. *et al.* (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany,* **51,** 335-380.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O. *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters,* **11,** 1065-1071.

Cossins, A.R. & Bowler, K. (1987) *Temperature Biology of Animals*. Chapman and Hall, London.

de Bello, F., Lavorel, S., Albert, C.H., Thuiller, W., Grigulis, K., Dolezal, J. *et al.* (2011) Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods in Ecology and Evolution,* **2,** 163-174.

de Bello, F., Lavorel, S., Diaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D. *et al.* (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation,* **19,** 2873-2893.

de Bello, F., Price, J.N., Münkemüller, T., Liira, J., Zobel, M., Thuiller, W. *et al.* (2012) Functional species pool framework to test for biotic effects on community assembly. *Ecology,* **93,** 2263-2273.

de Bello, F., Thuiller, W., Leps, J., Choler, P., Clément, J.-C., Macek, P. *et al.* (2009) Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. *Journal of Vegetation Science,* **20,** 475-486.

Denno, R.F., Gratton, C., Peterson, M.A., Langellotto, G.A., Finke, D.L. & Huberty, A.F. (2002) Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology,* **83,** 1443-1458.

Deraison, H., Badenhausser, I., Loeuille, N., Scherber, C. & Gross, N. (2015) Functional trait diversity across trophic levels determines herbivore impact on plant community biomass. *Ecology Letters,* **18,** 1346-1355.

Diamond, S.E., Frame, A.M., Martin, R.A. & Buckley R.B. (2011) Species' traits predict phenological responses to climate change in butterflies. *Ecology*, **92,** 1005-1012.

Dias, A.T., Krab, E.J., Marien, J., Zimmer, M., Cornelissen, J.H., Ellers, J. *et al.* (2013) Traits underpinning desiccation resistance explain distribution patterns of terrestrial isopods. *Oecologia,* **172,** 667-677.

Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A. *et al.* (2004) The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science,* **15,** 295-304.

Diaz, S., Lavorel, S., de Bello, F., Quetier, F., Grigulis, K. & Robson, T.M. (2007a) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America,* **104,** 20684-20689.

Diaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G. *et al.* (2007b) Plant trait responses to grazing - a global synthesis. *Global Change Biology,* **13,** 313-341.

Ellers, J., Dias, A.T.C. & Berg, M.P. (2010) Interaction milieu explains performance in species in simple food webs analog an environment gradient. *The Open Ecology Journal,* **3,** 12-21.

Ellers, J. & Jervis, M. (2003) Body size and the timing of egg production in parasitoid wasps. *Oikos,* **102,** 164-172.

Elmquist, T., Folke, C., Nystrom, M., Garry, P., Bengtsson, J., Walker, B. & Norber, J. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment,* **1,** 488-494.

Falkner, G., Obrdlik, P., Castella, E. & Speight, M.C.D. (2001) *Shelled Gastropoda of Western Europe*. Friedrich-Held-Gesellschaft, München.

Fischer, K., Bot, A.N.M., Brakefield, P.M. & Zwaan, B.J. (2006) Do mothers producing large offspring have to sacrifice fecundity? *Journal of Evolutionary Biology,* **19,** 380-391.

Folke, C., Holling, C.S. & Perrings, C. (1996) Biological diversity, ecosystems, and the human scale. *Ecological Applications,* **6,** 1018-1024.

Fountain-Jones, N.M., Baker, S.C. & Jordan, G.J. (2015) Moving beyond the guild concept: developing a practical functional trait framework for terrestrial beetles. *Ecological Entomology,* **40,** 1-13.

Fournier, B., Gillet, F., Le Bayon, R.-C., Mitchell, E.A.D. & Moretti, M. (2015) Functional responses of multitaxa communities to disturbance and stress gradients in a restored floodplain. *Journal of Applied Ecology,* **52,** 1364-1373.

Fox, C.W. & Czesak, M.E. (2000) Evolutionary ecology of progeny size in arthropods. *Annu Rev Entomol,* **45,** 341-369.

Fu, H., Yuan, G.X., Zhong, J.Y., Cao, T., Ni, L.Y. & Xie, P. (2013) Environmental and Ontogenetic Effects on Intraspecific Trait Variation of a Macrophyte Species across Five Ecological Scales. *Plos One,* **8**.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C. *et al.* (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B-Biological Sciences,* **282,** 20142620.

Gaston, K.J., Chown, S.L. & Evans, K.L. (2008) Ecogeographic rules: elements of a synthesis. *Journal of Biogeography*, **35**, 483-500.

Gibb, T. & Oseto, C.Y. (2006) *Arthropod Collection and Identification - Laboratory and Field Techniques*. Elsevier Academic Press, New York.

Götzenberger, L., de Bello, F., Brathen, K.A., Davison, J., Dubuis, A., Guisan, A. *et al.* (2012) Ecological assembly rules in plant communities--approaches, patterns and prospects. *Biological Reviews*, **87,** 111-127.

Griffiths, J.A., Schiffer, M. & Hoffmann, A.A. (2005) Clinal variation and laboratory adaptation in the rainforest species Drosophila birchii for stress resistance, wing size, wing shape and development time. *Journal of Evolutionary Biology,* **18,** 213-222.

Guerra, P.A. (2011) Evaluating the life-history trade-off between dispersal capability and reproduction in wing dimorphic insects: a meta-analysis. *Biological Reviews,* **86,** 813-835.

He, Q. & Bertness, M.D. (2014) Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology,* **95,** 1437-1443.

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. & Mayfield, M.M. (2012) Rethinking Community Assembly through the Lens of Coexistence Theory. *Annual Review of Ecology, Evolution, and Systematics, Vol 43,* **43,** 227-248.

Homburg, K., Homburg, N., Schäfer, F., Schuldt, A., Assmann, T., Dytham, C. & Ewers, R. (2014) Carabids.org - a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conservation and Diversity,* **7,** 195-205.

Hortal, J., de Bello, F., Diniz, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015) Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **46,** 523-549.

Hughes, C.L., Hill, J.K. & Dytham, C. (2003) Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries. *Proceedings of the Royal Society B-Biological Sciences,* **270,** S147-S150.

Ibanez, S. (2012) Optimizing size thresholds in a plant-pollinator interaction web: towards a mechanistic understanding of ecological networks. *Oecologia,* **170,** 233-242.

Ibanez, S., Lavorel, S., Puijalon, S. & Moretti, M. (2013) Herbivory mediated by coupling between biomechanical traits of plants and grasshoppers. *Functional Ecology,* **27,** 479-489.

Kattge, J., Diaz, S., Lavorel, S., Prentice, C., Leadley, P., Boenisch, G. M. *et al.* (2011) TRY - a global database of plant traits. *Global Change Biology,* **17,** 2905-2935.

Kaustuv, R, Jablonski, D. & Valentine, J.W. (2001) Climate change, species range limits and body size in marine bivalves. *Ecology Letters*, **4,** 366-370.

Kleyer, M., Bekker, R.M., Knevel, I.V., Bakker, J.P., Thompson, K., Sonnenschein, M. *et al.* (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology,* **96,** 1266-1274.

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C. *et al.* (2016) Plant functional traits have globally consistent effects on competition. *Nature,* **529,** 204-U174.

Lavorel, S. (2013) Plant functional effects on ecosystem services. *Journal of Ecology,* **101,** 4-8.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology,* **16,** 545–556.

Lavorel, S., Storkey, J., Bardgett, R.D., de Bello, F., Berg, M.P., Le Roux, X. *et al.* (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.

Liefting, M., Weerenbeck, M., van Dooremalen, C. & Ellers, J. (2010) Temperature-induced plasticity in egg size and resistance of eggs to temperature stress in a soil arthropod. *Functional Ecology,* **24,** 1291-1298.

Luck, G.W., Harrington, R., Harrison, P.A., Kremen, C., Berry, P.M., Bugter, R. *et al.* (2009) Quantifying the Contribution of Organisms to the Provision of Ecosystem Services. *Bioscience,* **59,** 223-235.

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.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol,* **21,** 178-185.

Messier, J., McGill, B.J. & Lechowicz, M.J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters,* **13,** 838-848.

Moretti, M., de Bello, F., Ibanez, S., Fontana, S., Pezzatti, G.B., Dziock, F. *et al.* (2013) Linking traits between plants and invertebrate herbivores to track functional effects of land-use changes. *Journal of Vegetation Science,* **24,** 949-962.

Mori, A.S., Furukawa, T. & Sasaki, T. (2013) Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews,* **88,** 349-364.

Mouillot, D., Graham, N.A., Villeger, S., Mason, N.W. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends Ecol Evol,* **28,** 167-177.

Naeem, S. & Wright, J.P. (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters,* **6,** 567-579.

Pakeman, R.J. & Quested, H.M. (2007) Sampling plant functional traits: What proportion of the species need to be measured? *Applied Vegetation Science,* **10,** 91-96.

Pakeman, R.J. & Stockan, J.A. (2014) Drivers of carabid functional diversity: abiotic environment, plant functional traits, or plant functional diversity? *Ecology,* **95,** 1213-1224.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. *et al.* (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany,* **61,** 167.

Peters, R.H. (1983) *The ecological implications of body size*. Cambridge University Pres, Cambridge.

Pey, B., Laporte, B. & Hedde, M. (2014) BETSI database tutorial. pp. 33.

Poff, N.L., Olden, J.D., Vieira, N. K., Finn, D.S., Simmons, M.P. & Kondratieff, B.C. (2006) Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, **25**, 730-755.

Rubach, M.N., Ashauer, R., Buchwalter, D.B., De lange, H.J., Hamer, M., Preuss, T.G. *et al.* (2011) Framework for Traits-Based Assessment in Ecotoxicology. *Integrated Environmental Assessment and Management,* **7,** 172-186.

Rosado, B.H.P., Dias, A.T.C. & de Mattos, E.A. (2013) Going back to basics: importance of ecophysiology when choosing functional traits for studying communities and ecosystems. *Natureza & Conservação*, **11**, 1-8.

Schmera, D., Podani, J., Heino, J., Erős, T., & Poff, N.L. (2015) A proposed unified terminology of species traits in stream ecology. *Freshwater Science*, **34**, 823-830.

Schmitz, O.J. (2008) Effects of predator hunting mode on grassland ecosystem function. *Science,* **319,** 952-954.

Schmitz, O.J., Buchkowski, R.W., Burghardt, K.T. & Donihue, C.M. (2015) Functional Traits and Trait-Mediated Interactions: Connecting Community-Level Interactions with Ecosystem Functioning. *Advances in Ecological Research* (eds G.W. Samraat Pawar & I.D. Anthony), pp. 319-343. Academic Press.

Shelford, V.E. (1911) Physiological animal geography. *Journal of Morphology*, **22**, 551-618.

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.

Sgro, C.M. & Partridge, L. (2001) Laboratory adaptation of life history in Drosophila. *American Naturalist,* **158,** 657-658.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A. *et al.* (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters,* **18,** 1406-1419.

Somero, G.N. (1992) Biochemical ecology of deep-sea animals. *Experientia,* **48,** 537-543.

Speight, M.C.D. & Castella, E. (2010) StN Database: content and glossary of terms. *Syrph the Net, the database of European Syrphidae* (eds M.C.D. Speight, E. Castella, J.-P. Sarthou & C. Monteil), pp. 83. Syrph the Net publications, Dublin.

Stang, M., Klinkhamer, P.G., Waser, N.M., Stang, I. & van der Meijden, E. (2009) Size-specific interaction patterns and size matching in a plant-pollinator interaction web. *Ann Bot,* **103,** 1459-1469.

Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.

Suding, K.N. & Goldstein, L.J. (2008) Testing the Holy Grail framework: using functional traits to predict ecosystem change. *New Phytologist,* **180,** 559-562.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Díaz, S., Garnier, E. *et al.* (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology,* **14,** 1125-1140.

Van den Brink, P.J., Baird, D.J., Baveco, H. & Focks, A. (2013) The use of traits-based approaches and eco(toxico)logical models to advance the ecological risk assessment framework for chemicals. *Integrated Environmental Assessment and Management,* **9,** E47-E57.

van Dooremalen, C., Gerritsen, L., Cornelissen, B., van der Steen, J.J.M., van Langevelde, F. & Blacquiere, T. (2012) Winter Survival of Individual Honey Bees and Honey Bee Colonies Depends on Level of Varroa destructor Infestation. *Plos One,* 7, e36285.

Vandewalle, M., de Bello, F., Berg, M.P., Bolger, T., Doledec, S., Dubs, F. *et al.* (2010) Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation,* **19,** 2921-2947.

Verdu, J.R., Alba-Tercedor, J. & Jimenez-Manrique, M. (2012) Evidence of Different Thermoregulatory Mechanisms between Two Sympatric Scarabaeus Species Using Infrared Thermography and Micro-Computer Tomography. *Plos One,* **7,** e33914.

Verdu, J.R., Casas, J.L., Lobo, J.M. & Numa, C. (2010) Dung Beetles Eat Acorns to Increase Their Ovarian Development and Thermal Tolerance. *Plos One,* **5,** e10114.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution,* **27,** 244-252.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. *et al.* (2007) Let the concept of trait be functional! *Oikos,* **116,** 882-892.

Warren, R.J., II, Giladi, I. & Bradford, M.A. (2010) Ant-mediated seed dispersal does not facilitate niche expansion. *Journal of Ecology,* **98,** 1178-1185.

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.

Wilson, R.S. & Franklin, C.E. (2002) Testing the beneficial acclimation hypothesis. *Trends in Ecology and Evolution*, **17**, 66-70.

Woodcock, B.A., Harrower, C., Redhead, J., Edwards, M., Vanbergen, A.J., Heard, M.S. *et al.* (2014) National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key UK arable crops. *Journal of Applied Ecology,* **51,** 142-151.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. *et al.* (2005) Body size in ecological networks. *Trends in Ecology & Evolution,* **20,** 402-409.

Yang, L.H. & Rudolf, V.H.W. (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters,* **13,** 1-10.

Yates, M.L., Andrew, N.R., Binns, M. & Gibb, H. (2014). Morphological traits: predictable responses to macrohabitats across a 300 km scale. *PeerJ* **2,** e271.

Table 1 – List of the terrestrial invertebrate traits selected for the handbook and considered to be key in responding to the environment and/or effecting ecosystem processes and services at various scales from local plots, to landscapes and biomes.

Trait type **Trait**	**Definition**	**Comment**
Morphology		
Body size	Size of the body. It includes body length, body width, body mass, and body volume	Environmental conditions affect body size which will influence amount and composition of resources used
Eye morphology	Form of the eye. It includes: eye number, eye size, eye sight	Eye morphology can be filtered by environmental conditions which will reflect prey and/or predator recognition
Respiration system	Structures developed to perform gas exchange	Type of respiration mode directly affect drought tolerance and desiccation resistance
Hairiness	Degree of hair coverage. It includes: hair length and hair density	Abiotic condition and biotic interactions (pollination) affect hairiness providing fitness and performance
Colour	Body coloration. It includes: colour, intensity, contrast	Abiotic condition and biotic interactions (e.g. predation) affect pigmentation providing fitness and performance
Feeding		
Feeding guild	Food type, upon which species feed. It informs about “who eats what or whom”	Feeding guild is a good surrogate for trophic level and position in the food web. It determines the quality of resources, which influences a species growth, reproduction and survival
Ingestion rate	Quantity of food consumed in a given period	The rate of food ingested by an organism reflects its nutritional and energetic requirements and is related to species responses to food quality

Biting force	Biomechanical force exerted on food items by the tip of the mouth-parts, claws or fore legs	Biting force mainly determines the effect on trophic network interactions and thus on ecosystem function
Life history		
Ontogeny	Developmental history. It includes type and number of developmental stages	Response to environmental stressors and effects on the ecosystem can change significantly across an organism's life history. Changes in environmental conditions can affect ontogeny and ecosystem processes
Clutch size	Number of eggs or juveniles produced in one reproductive event	Clutch size respond significantly to environmental conditions which affect number of offspring and their impact on the ecosystems
Egg size	Size dimension or mass of an egg	Resistance to environmental and particularly climatic conditions increase with egg size, which indirectly determines impact on the ecosystem via changes in population sizes
Life span	Amount of time an adult individual lives, from emergence from last instar until death	Stressors can heavily affect life span which is reflected in different ecosystem functions
Age at maturity	Age at first reproductive event	Time of first reproductive event can be changed under environmental stress, with consequences for population size and ecosystem processes
Parity	The number of times a females lays eggs or gives birth	The spreading of reproductive events over a life time has fitness consequences that are related to the trade-off between current and future reproduction
Reproduction mode	Mode by which new offspring are produced (sexual or asexual)	Mode of reproduction can be changed under environmental stress, with consequences for population sizes and ecosystem processes
Voltinism	The number of generations an organism completes in a single year.	Voltinism is under genetic and environmental control, being mostly influenced by the photoperiod, the local climatic conditions.
Physiology		

Resting metabolic rate	Amount of energy expended by an organism at rest	Metabolic rate is related to several organism features such as behaviour, longevity and reproduction output and its reaction norm with temperature can indicate how organisms differ in their response to environmental changes
Relative growth rate	Increasing in mass of an organism per unit of time	Relative growth rate is related to other several life history traits, such as body size and age at maturity. Therefore, growth rate can influence different fitness components such as fecundity and survival
Desiccation resistance	Ability to withstand dry conditions	Physiological capacity to resist dry conditions is related to species distribution along water availability gradients and to species response to changes in water availability
Inundation resistance	Ability of terrestrial organisms to survive under water	Flooding and increased frequency and intensity of extreme precipitation can impose strong restrictions on survival
Salinity resistance	Ability to withstand conditions of high salinity	Ability to withstand conditions of high salinity determines species survival under high salt stress and will influence growth and reproduction via trade-offs
Temperature tolerance	Ability to survive at any temperature. It includes: hot and cold	Toleration of hot and cold temperatures determines species survival under stress and will influence growth and reproduction via trade-offs
pH resistance	Ability to withstand acidic or alkaline conditions	Ability to withstand acidic or alkaline conditions determines species survival under acidity stress and will influence growth and reproduction via trade-offs
Behaviour		
Activity time	Activity period of a species within 24h	Environmental conditions, e.g. climatic conditions, determine the activity time. This can affect ecosystem function through asynchrony, e.g. spatiotemporal mismatch in biotic interactions
Aggregation	Clustering of individuals	Clustering of individual reduces microclimatic stress, especially overcoming cold and drought and can locally result in enhanced ecosystem process rates via high population sizes

Dispersal mode	The form of self-directed movements an animal uses to move from one place to another	Dispersal mode influences access to new habitat, resources and suitable environments, mates, and shelters, and opportunities to escape adverse environmental conditions
Locomotion speed	The pace of self-propelled movement of an organism	Habitat conditions and biotic interactions influence locomotion speed which reflect behaviours critical for survival, including efficient use of resources, foraging, predator avoidance, fitness and survival
Sociality	Degree of interactive behaviour with other members of its species to the point of having a recognizable and distinct society	Disturbance and land use changes are expected to affect sociality. High levels of sociality are expected to have a bigger impact on ecosystem function
Annual activity time	Period in an organism's life cycle when growth, development, and physical activity are temporarily stopped	Offers the possibility to overcome unfavourable environmental conditions in a resting stage