

CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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Reconciling trait based perspectives along a trait-integration continuum

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Abstract. Trait based ecology has developed fast in the last decades, aiming to both explain mechanisms of community assembly, and predict patterns in nature, such as the effects of biodiversity shifts on key ecosystem processes. This body of work has stimulated the development of several conceptual frameworks and analytical methods, as well as the production of trait databases covering a growing number of taxa and organizational levels (from individuals to guilds). However, this breeding ground of novel concepts and tools currently lacks a general and coherent framework, under which functional traits can help ecologists organize their research aims, and serve as the common currency to unify several scientific disciplines. Specifically, we see a need to bridge the gaps between community ecology, ecosystem ecology, and evolutionary biology, in order to address the most pressing environmental issues of our time. To achieve this integration goal, we define a trait-integration continuum, which reconciles alternative trait definitions and approaches in ecology. This continuum outlines a coherent progression of biological scales, along which traits interact and hierarchically integrate from genetic information, to whole organism fitness-related traits, to trait syndromes and functional groups. Our conceptual scheme proposes that lower-level trait integration is closer to the inference of ecoevolutionary mechanisms determining population and community properties, whereas higher-level trait integration is most suited to the prediction of ecosystem processes. Within these two extremes, trait integration varies on a continuous scale, which relates directly to the inductive-deductive loop that should characterize the scientific method. With our proposed framework, we aim to facilitate scientists in contextualising their research based on the trait-integration levels that matter most to their specific goals. Explicitly acknowledging the existence of a trait-integration continuum is a promising way for framing the appropriate questions, thus obtaining reliable answers and results that are comparable across studies and disciplines.

Key words: *biological scales; community assembly mechanisms; ecosystem processes; functional trait interactions; inference; interdisciplinarity; performance; prediction.*

INTRODUCTION

The composition of biological communities is drastically affected by human-induced land-use changes, species invasions, and acceleration of species extinctions

(Vitousek et al. 1997, Chapin et al. 2000). These biodiversity shifts likely cause potentially irreversible changes to ecosystem processes and services (Hooper et al. 2005), such as biomass production, carbon storage, and ecosystem resilience. Although evidence has clearly

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shown that the notion of species diversity is at the core of the research addressing the simultaneous maintenance of multiple ecosystem processes across space (Soliveres et al. 2016) and time (Allan et al. 2011, Isbell et al. 2011), attention is progressively moving towards functional traits (Cernansky 2017).

Functional traits, the phenotypic features of organisms that affect their fitness (Violle et al. 2007), on the one hand determine the organisms' adaptation to the environment (response) and, on the other hand, affect biotic interactions and drive ecosystem processes through biomechanical and metabolic activities (effects). By improving the predictability of such relationships, functional traits' ecology also offers more possibilities for generalization in the face of the blurring diversity of species- and site-specific responses, as well as of the interactions among organisms (Levine 2016). Therefore, considering the functional aspect of biodiversity improves our understanding of important questions that are at the core of current ecological research (Garnier et al. 2015).

Trait based ecological tools and concepts have been developing fast in the last decades, particularly along both conceptual and quantitative directions (McGill et al. 2006, Violle et al. 2007, Litchman and Klausmeier 2008, Bolnick et al. 2011, Lavorel et al. 2013). Such an effort has resulted in a rich panel of approaches that encompasses a range of trait types, ecological scales, and applications. Though enriching, the vast variety of options available in trait based ecology could pose difficulties in deciding which and how many traits are necessary to answer specific ecological questions and to integrate results across studies. To apply trait based ecology effectively it is thus important to harmonize the multitude of concepts and approaches. Here we propose to consider traits as units that interact within a coherent progression of biological scales, and that merge along a continuum of integration levels, ranging from genes to populations, communities, and ecological networks. This approach facilitates scientists in contextualizing research questions placed on the continuum spanning from explaining mechanisms to predicting patterns, by choosing the trait-integration level that is most suited to their research goals. In the following sections, we present the rationale for this approach, the concept of trait-integration continuum, and examples of how it can help frame the appropriate questions to obtain reliable answers.

THE NEED FOR A GUIDING CONCEPT IN TRAIT BASED ECOLOGY

A growing demand for elucidating species assembly rules and biodiversity effects on ecosystem processes has boosted the search for functional measures of organisms that comprehensively and pertinently represent similarities and differences across temporal, spatial, and biological scales (Hillebrand and Matthiessen 2009, Carroll et al. 2011). The emerging paradigm in trait based

ecology is to characterize organisms' similarities and differences by means of multiple traits (e.g., Kraft et al. 2015, Lefcheck et al. 2015). Accordingly, through the combination of modern genomic tools, high-throughput metabolomic, phenomic analyses, and technical advances in general, it is now possible—relatively easily and cheaply—to identify and measure a myriad of traits in practically any system and on a large number of individuals, species, or groups. In response, several conceptual and quantitative approaches have been proposed to address the multivariate nature of an organism's phenotype, or of a niche, and the type of traits that can be considered (e.g., Villéger et al. 2008, Carmona et al. 2016, Fontana et al. 2016). Therefore, although novel data sets of functional traits become increasingly available, uncertainty in the choice of methods and concepts to link responses and effects may also increase, especially because of interactions among organisms and their environment, which are inherently scale dependent, and characterized by high data dimensionality and complexity (Agrawal 2020).

At each hierarchical level of biological complexity, from genes to ecosystems, different research questions require different approaches and levels of data integration (Osnas et al. 2018, Dias et al. 2020). For example, if we are interested in ecophysiological processes, traits measured at the level of a single organ, or even cell, could become a priority. On the contrary, whole-body or performance traits, resulting from the integration of multiple traits, are probably more important when analyzing population dynamics or community assembly. This calls for a concept that helps contextualize research questions over the landscape defined by traits and their interactions, and unify methodological approaches on the same theoretical foundation. We propose an approach that allows a more harmonic consolidation of trait based concepts and disciplines, such as ecology, evolution and molecular biology.

THE TRAIT-INTEGRATION CONTINUUM

Perhaps the most critical point for a broad application of trait based approaches is to define what researchers commonly consider to be a functional trait, and to characterize how different traits and definitions can be combined into a holistic framework. Violle et al. (2007) provided an already broad and highly inclusive definition of the term "functional trait" by summarizing different previous concepts. Particularly, they defined traits as functional only when they impact the organism's fitness directly, or indirectly, via their effects on growth, reproduction, and survival. Such a definition fits well with the Darwinian view of traits being collections of features that show variation at the population level, have variable effects on fitness and are heritable (Gould and Lewontin 1979, Godfrey-Smith 2009). Violle et al. (2007) went further in their treatise and proposed that changes within individuals' traits may influence

processes at higher organizational levels, such as communities and ecosystems. Hence, they provided an integrative framework for trait based ecology. The key element of their framework, which is the expansion of the original “performance paradigm” (Arnold 1983), is that multiple traits interact with each other to define the performance of an organism under different abiotic and biotic conditions.

Although Violle et al. (2007) specify that traits are morphological, physiological, or phenological features measurable at the individual level (from the cell to the whole organism’s level), very often a broader definition of an organism’s phenotype can be applied to traits that are measured at different levels of biological organization, for example, at the genomic and transcriptomic levels (i.e., within cells). It is thus possible to expand the framework proposed by Violle et al. (2007) by further refining the hierarchy concept, with different types of traits interacting with each other across increasing levels of complexity (Fig. 1). This is akin to the concept of trait integration proposed by Marks (2007), where individual traits combine into an increasingly complex level of integration, to determine organisms’ fitness and ultimately ecological processes. Such a concept allows to effectively complete the framework by Violle et al. (2007), by adding trait interactions along a continuum of multiple biological scales, ranging hierarchically from genetic information to the whole organism’s performance and beyond, and including ecological and evolutionary dynamics.

We represent this conceptual integration continuum of hierarchically interacting traits in Fig. 1. At each level of this continuum, traits can have direct, interactive, and indirect effects (of different strengths: solid vs. dotted lines). Such an integration approach could be exemplified as follows: genes integrate into metabolic pathways, whose interactions make phenotypes, which determine trait syndromes, and dictate population dynamics through interaction with the environment, and community composition (e.g., Griffiths et al. 2018). All these steps ultimately result in the formulation of functional groups that define ecosystem properties (Agrawal and Fishbein 2006, McLaren and Turkington 2010, Raffard et al. 2017). We note that the relationships between different trait-integration levels can be driven by a variety of mechanisms. For example, cell- or organ-level traits interact with each other through the physiology and metabolism of the whole organism to determine its performance in a given environment (Marks 2007, Violle et al. 2007). Higher trait-integration levels (i.e., population- and community-level traits) are then determined by biotic interactions between individual organisms within and across species (Violle et al. 2007). As reported by Li et al. (2019), we expect positive or negative trait correlations (including trade-offs) to emerge at intermediate to high integration levels (Agrawal 2020). This hierarchical structure, particularly in view of whole organisms’ performance, allows different levels of analyses, and an integration of different disciplines addressing

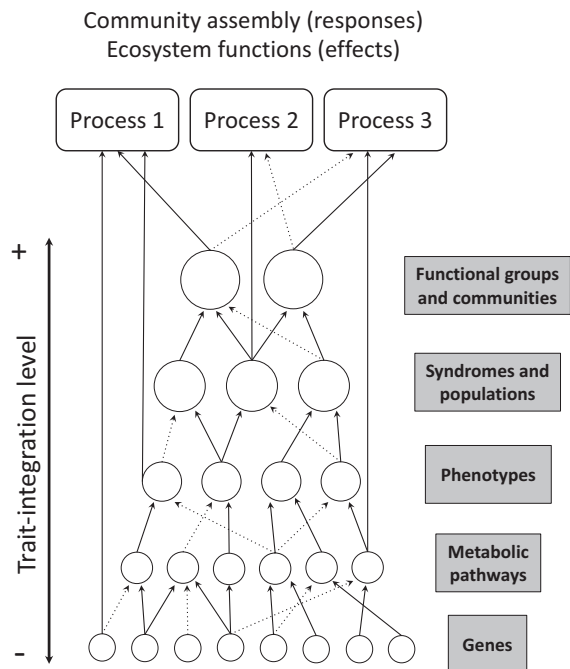


FIG. 1. Schematic diagram illustrating the continuum of a hierarchical network of trait interactions, which move across biological scales (i.e., increasingly complex levels of biological organization, see boxes on the right side). High trait integration is closer to the prediction of processes (e.g., species sorting or primary production), whereas low trait integration allows the inference of underlying mechanisms. Arrows depict direct and indirect effects of traits (circles) on subsequent levels of integration: solid vs. dotted lines symbolize different strength of effects. Note that arrows going down the hierarchy of trait integration (feedback from ecology to evolution) also exist (Pelletier et al. 2009), but are not represented here for simplicity. The same is true for arrows bypassing some levels of integration without affecting processes directly. Inspired by Marks (2007) and Violle et al. (2007).

the causes and consequences of trait variability at each hierarchical level. Our conceptual scheme suggests that high trait integration is closer to the prediction of ecosystem processes (including community assembly), whereas at low levels of integration traits are better suited to explain ecoevolutionary mechanisms determining the observed patterns.

For example, a gene can be directly involved in the appearance of a phenotypic trait, interact with other genes by modulating their expression and phenotypic consequences, and/or indirectly affect some other traits through allometric relationships. Traits at the lowest end of the integration continuum are directly linked to genes and gene expression pathways (e.g., hormone production; Fig. 1). In this context, a combination of genetic information causing physiological responses will determine how given phenotypic attributes are manifested and will affect the performance of an organism. A simple example of this is *Thalassemia*, where inherited genetic information is translated into different hemoglobins’

production, with health consequences, but also generating resistance to Malaria.

In contrast, many traits can be considered as highly integrated because of their intrinsic dependence and synergy with other traits, which can be evident both at the intra- and interspecific level (Laughlin and Messier 2015, Messier et al. 2017). This nonindependency among traits can arise from metabolic constraints (i.e., body size is related to many other traits, in accordance with the metabolic theory of ecology; Brown et al. 2004), or from a direct genetic linkage between traits (Bateson et al. 1905, Morgan 1910, Lobo and Shaw 2008). Alternatively, traits are at a high integration level because they are mathematically derived from other underlying traits (e.g., specific leaf area in plants), or represent easier-to-measure proxies for traits that are more directly related to a given mechanism (e.g., mandible size for mandible strength in insects). Finally, traits can be integrated into broad emergent properties, or trait syndromes, which by definition consist of combinations of multiple traits acting in concert in response to environmental stimuli or constraints (e.g., drought tolerance in plants is mediated by simultaneously changing abscisic acid production, leaf stomatal conductance, root water uptake, the concentration of solutes in the cell membranes, and so on; Fig. 1).

The sum or interaction of all individual trait responses have consequences (effects) that propagate to higher biological scales (populations, communities, and ecosystems; Clark 2010, Violle et al. 2012, Wright et al. 2016). By representing the fundamental unit of response to selective processes, the multidimensional genotype (and by extension, the phenotype) of an individual organism determines its survival, growth, and reproductive success in a given abiotic and biotic environment. We note that, in certain cases, single genes, phenotypes, or syndromes can have high predictive power all the way up directly on ecosystem processes, bypassing the integration with other traits (Hendry et al. 2017): these are depicted as direct solid arrows to processes in Fig. 1. We suggest that these are cases in which physiological responses have significant and direct effects on ecosystem processes and services without necessarily changing ecological interactions. For instance, variation in the pool of soil bacterial genes responsible for the assemblage of nitrogen into different compounds can have profound effects at the whole ecosystem level, dictating nutrient cycling and ecosystem productivity (Braker et al. 2000, Kuypers et al. 2018). Similarly, the presence of nitrogen-fixing genes in cyanobacteria allows the persistence and productivity of the entire phytoplankton community (and the pelagic food web) in oligotrophic environments (Zehr and Kudela 2011). Evolution of tolerance or resistance towards chemical warfare, such as the insurgence of antibiotic resistance in bacteria, or tolerance to pesticides in pests, are often mediated by single genes or pathways and have profound effects on organisms, populations, and entire ecosystems (Hendry et al. 2017).

The trait-integration network can be more or less complex, depending on the organism of study. Although relatively direct links between genes and ecosystem processes exist also in trees (Schweitzer et al. 2004), for example, we expect fewer levels in the trait hierarchy in unicellular organisms compared to multicellular. In a vascular plant's organ, such as a leaf or seed, there are many different types of specialized cells interacting, which creates the possibility of alternative leaf designs that have similar performance (Pistón et al. 2019). Different specialized plant organs then interact to influence performance at the whole plant level, creating more possibilities of alternative designs that reduce the correlation between traits and performance. In contrast, single-cell or colonial autotrophs, like phytoplankton, lack some of those levels of complexity, with a more direct route from genes to fitness and ecological processes. These differences in overall complexity of the trait hierarchy may explain why trait based approaches appear to explain more ecological variation in studies of phytoplankton than in studies of vascular plants (e.g., Acevedo-Trejos et al. 2018, van der Plas et al. 2020). Placing research questions on our proposed integration hierarchy, whose configuration can be tailored to the organisms of interest based on pre-existing knowledge, can provide context for such comparisons in trait based ecology.

ACKNOWLEDGING AN INTEGRATION CONTINUUM IN TRAIT BASED ECOLOGY

Historically, ecologists have predominantly focused on a restricted number of traits, limited to single biological scales (mainly species and functional groups), rather than considering a broader continuum (as shown in Fig. 1). For example, plant ecologists have dedicated a great deal of effort to generate standardized, broad-range, and easy-to-measure functional traits, such as specific leaf area, which can be interpreted as a proxy for photosynthetic potential (lower level of integration), or relative growth rate (higher level of integration). Although this approach has proven essential to back up trait based approaches in ecology, acknowledging the existence of continuous and intermediate levels of trait integration is necessary to foster the connection with other research fields focusing, for example, on trait heritability, plasticity, or the tolerance of organisms and populations to changing environmental conditions. This limitation may explain why community and ecosystem ecology, and evolutionary biology, have developed into largely independent research fields (Loreau 2010), leading to an apparent dichotomy between the inference of mechanisms at low levels of organization on one side, and the prediction of ecological and evolutionary patterns at high levels of trait integration on the other side.

The investigation of community assembly drivers and the inference of associated mechanisms have represented for decades a major cornerstone in ecological research

(e.g., Hutchinson 1959, Cody and Diamond 1975, Chesson 2000). Community assembly mechanisms produce patterns detectable at various biological scales (Weiher and Keddy 1995). However, they are more straightforwardly explained by trait variation, which has been measured mostly at the level of species or functional groups (MacArthur and Levins 1967). We know that species coexistence and community composition are determined by the interplay of several driving forces, including dispersal, environmental filtering, competition, niche and fitness differences, facilitation, trophic interactions, pathogenesis, and demographic stochasticity (Chesson 2000, Adler et al. 2007, Vellend 2010). These mechanisms arguably invoke multiple trait dimensions, and may depend upon either highly or lowly integrated functional traits, depending on the specific environmental selection factor. One example is sexual selection-driven color diversification in cichlid fishes in African Great Lakes: while being driven by changes in a relatively simple genetic architecture, when in correspondence with varying ecological opportunity, color diversification can predict whether adaptive radiations will occur (Seehausen and Schluter 2004, Santos and Salzburger 2012, Wagner et al. 2012). Similarly, sexual dichromatism in canaries, having large impact on their fitness, is determined by a single enzyme-encoding gene (Gazda et al. 2020). On the other hand, broad abiotic environmental filtering may select for combinations of traits that have high level of integration (Kraft et al. 2015).

Traits also represent the main mediators of the positive biodiversity effects on key ecosystem processes, such as biomass production and nutrient cycling, and their stability through time (Hooper et al. 2005, Reiss et al. 2009). Indeed, community trait diversity measured using highly integrative indices was found to outcompete taxonomy-based metrics in predicting ecosystem functioning (e.g., Gagic et al. 2015, Fontana et al. 2018). This is not surprising, as both selection and complementarity effects (e.g., Tilman 1997, Loreau and Hector 2001) ultimately emerge from trait differences. It is therefore crucial to understand which traits and integration levels confer the highest fitness given the ecological context, trigger dominance and high productivity, and favor complementary resource acquisition strategies, ultimately determining differences among individuals and species.

The importance of different and continuous trait-integration levels is supported by overwhelming empirical evidence. Population-level traits, such as parameters of the functions that describe net growth rate over an environmental gradient, including the optimum and range of temperature response curves, or maximum growth rate and half saturation constant for resource uptake (Litchman and Klausmeier 2008), are determined by multiple interacting pathways. The distribution of these traits within and across communities is a key predictor of community composition across environmental gradients, such as climate warming (Thomas

et al. 2012, Antão et al. 2020, Trisos et al. 2020). Community assembly mechanisms can be successfully explained by traits determining temperature tolerance and competition for nutrients and light, for example in phytoplankton (Edwards et al. 2012, Litchman et al. 2012, Fontana et al. 2019).

In plants, when trying to infer mechanisms, emphasis has been put on traits thought to be directly linked to resource acquisition and responses to environmental gradients (Cornwell and Ackerly 2009, Enquist et al. 2015). In dragonflies, physiological traits, such as the expression of few metabolic enzymes, were demonstrated to determine behavioral differences in the presence of distinct predators, and thus successfully explain community composition within a multitrophic context (Start et al. 2018). On the other hand, highly integrative measures of trait variation have been shown to be good predictors of ecosystem functioning (e.g., Griffin et al. 2009). This is the case, for example, of the number of functional groups in the early grassland biodiversity and ecosystem functioning experiment by Tilman et al. (1997) or, more recently, overall community trait diversity measures (e.g., Petchey et al. 2004, Fontana et al. 2018) and body size variation (Enquist et al. 1998, Acevedo-Trejos et al. 2018).

Size and shape of organisms, which are highly integrated phenotypic traits, link the principal axes of resource uptake, metabolic rates and trophic interactions in many ecosystems (Brown et al. 2004, White et al. 2007). In phytoplankton, large cells have low surface-to-volume ratio and are less efficient than small cells in nutrient uptake, and are therefore at a disadvantage under low nutrient conditions. In contrast, having large cells or colonies is a defensive trait, allowing organisms to be less susceptible to being grazed, for example due to gape limitations in herbivores (Pomati et al. 2020). This trade-off between fast resource uptake and defense against grazing is at the basis of the ecological causes of phytoplankton biomass accumulation, that is, algal blooms (Cloern 2018). Harmful algal bloom events are, on the other hand, characterized by an additional array of defence traits, known as algal toxins, which are mediated by single genes or metabolic pathways (low integration level) and have profound and long-lasting ecosystem effects (Neilan et al. 2008, Paerl and Otten 2013, Matthews et al. 2020).

The examples above suggest that the choice of traits should depend on the research hypothesis and the ecological process of interest (Brousseau et al. 2018). Both must be defined explicitly and in as much detail as possible to understand which trait (combinations) and level of integration (individual, population, community, ecosystem) are most appropriate (Fig. 1). At the same time, we note that the position along the trait-integration continuum, and therefore the ability to infer mechanisms or predict patterns, also depends on the analytical method chosen to study trait variation, as each approach deals differently with data aggregation

and dimensionality reduction. A comprehensive tutorial on how to map the appropriate analyses into the trait-integration continuum goes far beyond the scope of the present paper. However, it is clear that several existing analytical methods generally aim at increasing trait integration by reducing data dimensionality (e.g., trait diversity indices, as well as principal component analysis or radial plots for representing trait syndromes; Defossez et al. 2018). We note that the choice of the appropriate method does not really depend on the integration level (as virtually all existing methods can be applied at different levels of trait integration), but rather on the type of relationship that exists between a trait and the next level of integration. For example, if the traits under investigation are involved in nonadditive interactions, and non-linear effects are expected, regression trees or boosted regression trees could be applied (Pistón et al. 2019). On the contrary, complex trade-offs among traits could be investigated by means of principal component analysis (PCA). The performance of different methods (e.g., boosted regression trees vs. PCA) can also be compared to understand the prevailing type of relationship among traits in a given data set.

It is the combination of trait selection, biological scale, and methodological approach that determines the ability to infer mechanisms or predict patterns. For example, despite integrating several trait dimensions into one single number, trait diversity indices still have the potential to shed light on community assembly mechanisms, if traits are carefully selected to represent ecological interactions and measured at the individual level (Fontana et al. 2019). On the contrary, highly integrated trait syndromes, such as the leaf economic spectrum (Wright et al. 2004) at high taxonomic levels (genera or families) and global scales, might not be suited to the inference of assembly mechanisms in local communities (Messier et al. 2017, Anderegg et al. 2018). This is the case even though the single trait axes of the leaf economic spectrum arguably govern fundamental trade-offs in energy allocation (Shipley et al. 2006). This apparent mismatch is not particularly surprising, though, as trait associations at different scales are likely to emerge from distinct evolutionary processes (Agrawal 2020).

BENEFITS AND PERSPECTIVES OF THE TRAIT-INTEGRATION CONCEPT

Acknowledging the existence of a continuum of traits with different integration levels, which reflects their interdependency, allows approaching the two important research topics of prediction of patterns and inference of mechanisms, by including the whole range of ecological processes giving rise to similarities and differences among organisms (Fig. 2). Here we do not explicitly develop the conceptual and analytical framework to integrate ecoevolutionary processes across biological scales. We recognize, however, that this is still a significant research gap that should be filled, and would bring

an additional perspective in the field of trait based ecology.

Our proposed concept, linked to ecoevolutionary dynamics by responses and effects that are mediated by traits, can help guide research efforts. For instance, the evolutionary importance of beak size and claw sharpness for foraging habits in Darwin finches, long hypothesized by Darwin (1859), was confirmed when measuring the foraging-related traits in finches placed in sympatry vs. allopatry on the Galapagos islands (Grant and Grant 2006). Concerning plants, the ecological significance of volatile and nonvolatile secondary metabolites in wild tobacco (*Nicotiana attenuata*) growing in the Sonoran Desert has been demonstrated by sequentially silencing several genes related to secondary metabolites production, and later measuring their ecological effects by comparing mutant plants with their respective wild types in field common garden experiments (Kessler and Baldwin 2001, 2002). Unfortunately, such type of comprehensive research is still largely lacking in the trait based ecology agenda. We thus advocate for the ample use of approaches ranging from pattern based to mechanism based, which can be used iteratively to refine predictions of the “adaptive” functions of traits, and then validate them under field conditions (Fig. 2A). We note that exploring novel traits, that is, those not routinely measured in ecological studies, is a fundamental step in this iterative process. The need to go beyond conventional trait lists by increasing the variety of traits under investigation is particularly urgent whenever inference or prediction do not yield satisfactory results. At the same time, the novel traits need to be measured and described in a standardized way in order to allow for comparisons across species, gradients, and biomes (Moretti et al. 2017).

The vast amount of information generated by current –omics tools, for example, through next-generation DNA sequencing, spatial modeling, or high-throughput metabolomics, is spawning into a conundrum of how to use these data effectively in order to answer ecological questions. For instance, high-throughput assays of functionally important genes have been already proposed as a promising way to understand mechanisms of adaptation and community assembly in ecological studies (Whitham et al. 2006). For this, –omics on model organisms such as *Arabidopsis thaliana* can also be used to understand how complex trait interactions determine plant adaptation in natural populations (Bergelson and Roux 2010). The integration of untargeted metabolomics analyses with classic functional trait measurements has been recently used to infer complex responses, which include physical and chemical changes of plant communities in response to warming and the concomitant higher herbivore pressure (Descombes et al. 2020). However, how untargeted metabolomics, consisting of hundreds, if not thousands of molecular features, can be simultaneously analyzed with the relatively few classically measured functional

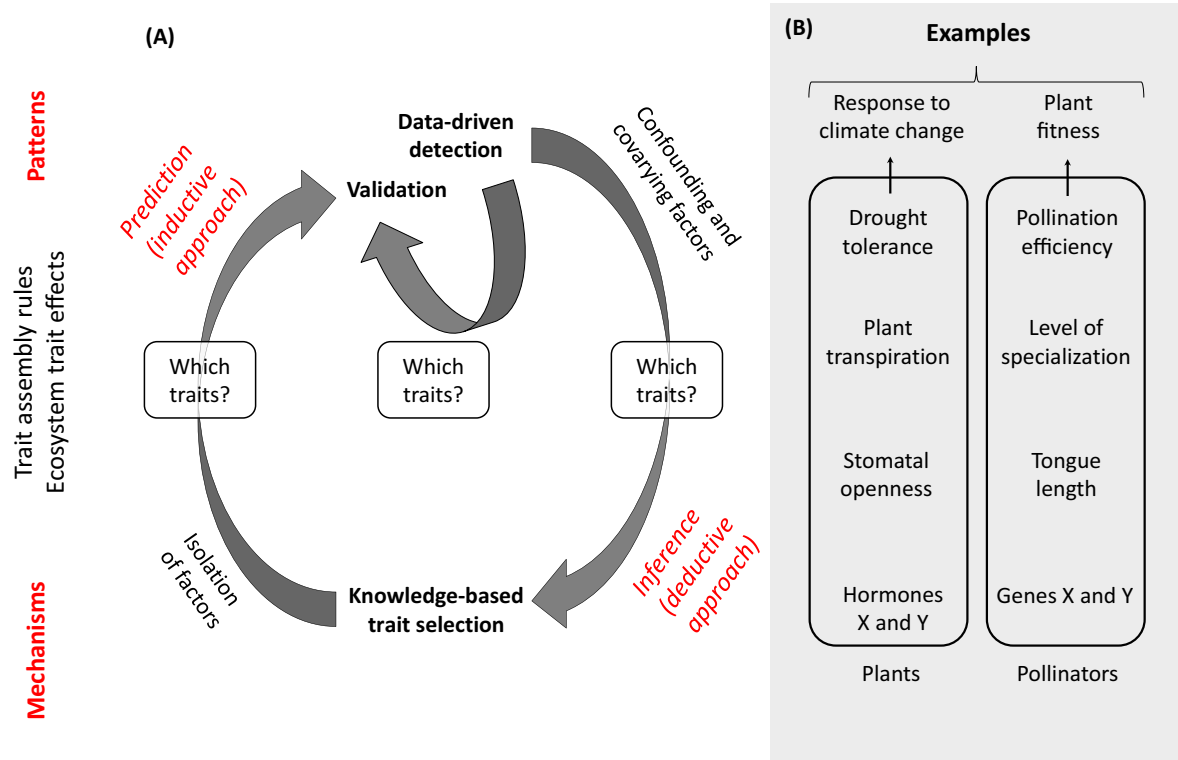


FIG. 2. (A) The trait-integration concept (within a continuum of trait-integration levels as in Fig. 1) can be mapped onto a scheme representing the interconnected research aims of inference and prediction. The observation of patterns serves the *prediction* of processes or the inductive formulation of hypotheses (upper part), which allow the deductive *inference* of mechanisms that can be tested experimentally by limiting as much as possible confounding and covarying factors (bottom part). The whole process can be repeated to refine the hypotheses iteratively, and in trait based ecology each step always involves the choice of the most appropriate traits to consider. (B) Accordingly, we report some examples of traits from different taxonomic groups along the trait-integration network.

traits, is one of the upcoming challenges in functional ecology research (Sedio 2017).

By combining the different levels of organization of life with classic trait based analyses of species interactions with their environment, scientists can harmonize their research goals and approaches. The appropriate level of trait integration must be chosen according to the degree of mechanistic vs. pattern-oriented aims and questions. An example of this approach could be described as follows. Let's imagine a researcher investigating the functional role of phenolic compounds (e.g., tannins, flavonoids, lignins) in ligneous plants growing along an elevation gradient. A pattern based approach highlights that some phenolic compounds increase, while others decrease with elevation. Planting genetic variants for phenolics' production of these plants at different elevations, and measuring their fitness, will address the direct adaptive role of the molecules, which can be mediated by abiotic factors (climate) or biotic factors (herbivory or pathogen attack). Interestingly, however, the bulk degree of degradation of these molecules impacts on the build-up of soil organic matter (i.e., an ecosystem property). Therefore, using the trait-integration continuum concept

as proposed here, allows moving beyond the common practice of assessing the relative importance of a trait to serve as response (e.g., evolutionary adaptation), or generate an effect (e.g., ecosystem function) in nature. Such an approach can ultimately be used to harmonize a full array of crucial questions in ecology, and for addressing the most urgent environmental issues of our time.

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LITERATURE CITED

- Acevedo-Trejos, E., E. Mara \tilde{n} on, and A. Merico. 2018. Phytoplankton size diversity and ecosystem function relationships across oceanic regions. *Proceedings of the Royal Society B* 285:20180621.
- Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. *Ecology Letters* 10:95–104.
- Agrawal, A. A. 2020. A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology. *Ecology* 101:e02924.

- Agrawal, A. A., and M. Fishbein. 2006. Plant defense syndromes. *Ecology* 87:S132–S149.
- Allan, E., et al. 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proceedings of the National Academy of Sciences of the United States of America* 108:17034–17039.
- Anderegg, L. D. L., et al. 2018. Within-species patterns challenge our understanding of the leaf economics spectrum. *Ecology Letters* 21:734–744.
- Antão, L. H., et al. 2020. Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nature Ecology and Evolution* 4:927–933.
- Arnold, S. J. 1983. Morphology, performance and fitness. *American Zoologist* 23:347–361.
- Bateson, W., E. R. Saunders, and R. C. Punnett. 1905. Reports to the Evolution Committee of the Royal Society. Report II. Experimental studies in the physiology of heredity. Harrison & Sons, London, UK.
- Bergelson, J., and F. Roux. 2010. Towards identifying genes underlying ecologically relevant traits in *Arabidopsis thaliana*. *Nature Reviews Genetics* 11:867–879.
- Bolnick, D. I., et al. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* 26:183–192.
- Braker, G., J. Zhou, L. Wu, A. H. Devol, and J. M. Tiedje. 2000. Nitrite reductase genes (*nirK* and *nirS*) as functional markers to investigate diversity of denitrifying bacteria in Pacific Northwest marine sediment communities. *Applied and Environment Microbiology* 66:2096–2104.
- Brousseau, P. M., D. Gravel, and I. T. Handa. 2018. On the development of a predictive functional trait approach for studying terrestrial arthropods. *Journal of Animal Ecology* 87:1209–1220.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Carmona, C. P., F. de Bello, N. W. H. Mason, and J. Lepš. 2016. Traits without borders: integrating functional diversity across scales. *Trends in Ecology and Evolution* 31:382–394.
- Carroll, I. T., B. J. Cardinale, and R. M. Nisbet. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology* 92:1157–1165.
- Cernansky, R. 2017. The biodiversity revolution. *Nature* 546:22–24.
- Chapin, F. S. III, et al. 2000. Consequences of changing biodiversity. *Nature* 405:234–242.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- Clark, J. S. 2010. Individuals and the variation needed for high species diversity in forest trees. *Science* 327:1129–1132.
- Cloern, J. E. 2018. Why large cells dominate estuarine phytoplankton. *Limnology and Oceanography* 63:392–409.
- Cody, M. L., and J. M. Diamond. 1975. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.
- Cornwell, W. K., and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79:109–126.
- Darwin, C. 1859. On the origin of species. John Murray, London, UK.
- Defosse, E., L. Pellissier, and S. Rasmann. 2018. The unfolding of plant growth form–defence syndromes along elevation gradients. *Ecology Letters* 21:609–618.
- Descombes, P., C. Pitteloud, G. Glauser, E. Defosse, A. Kerunteuil, P.-M. Allard, S. Rasmann, and L. Pellissier. 2020. Novel trophic interactions under climate change promote alpine plant coexistence. *Science* 370:1469–1473.
- Dias, A. T. C., B. H. P. Rosado, F. de Bello, N. Pistón, and E. A. De Mattos. 2020. Alternative plant designs: consequences for community assembly and ecosystem functioning. *Annals of Botany* 125:391–398.
- Edwards, K. F., E. Litchman, and C. A. Klausmeier. 2012. Functional traits explain phytoplankton community structure and seasonal dynamics in a marine ecosystem. *Ecology Letters* 16:56–63.
- Enquist, B. J., J. H. Brown, and G. B. West. 1998. Allometric scaling of plant energetics and population density. *Nature* 395:163–165.
- Enquist, B. J., et al. 2015. Scaling from traits to ecosystems: Developing a general trait driver theory via integrating trait-based and metabolic scaling theories. *Advances in Ecological Research* 52:249–318.
- Fontana, S., O. L. Petchey, and F. Pomati. 2016. Individual-level trait diversity concepts and indices to comprehensively describe community change in multidimensional trait space. *Functional Ecology* 30:808–818.
- Fontana, S., M. K. Thomas, M. Moldoveanu, P. Spaak, and F. Pomati. 2018. Individual-level trait diversity predicts phytoplankton community properties better than species richness or evenness. *ISME Journal* 12:356–366.
- Fontana, S., M. K. Thomas, M. Reyes, and F. Pomati. 2019. Light limitation increases multidimensional trait evenness in phytoplankton populations. *ISME Journal* 13:1159–1167.
- Gagic, V., et al. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B* 282:20142620.
- Garnier, E., M.-L. Navas, and K. Grigulis. 2015. Plant functional diversity. Oxford University Press, Oxford, UK.
- Gazda, M. A., et al. 2020. A genetic mechanism for sexual dichromatism in birds. *Science* 368:1270–1274.
- Godfrey-Smith, P. 2009. Darwinian populations and natural selection. Oxford University Press, Oxford, UK.
- Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society B* 205:581–598.
- Grant, P. R., and B. R. Grant. 2006. Evolution of character displacement in Darwin's finches. *Science* 313:224–226.
- Griffin, J. N., V. Mendez, A. F. Johnson, S. R. Jenkins, and A. Foggo. 2009. Functional diversity predicts overyielding effect of species combination on primary productivity. *Oikos* 118:37–44.
- Griffiths, J. I., O. L. Petchey, F. Pennekamp, and D. Z. Childs. 2018. Linking intraspecific trait variation to community abundance dynamics improves ecological predictability by revealing a growth–defence trade-off. *Functional Ecology* 32:496–508.
- Hendry, A. P., K. M. Gotanda, and E. I. Svensson. 2017. Human influences on evolution, and the ecological and societal consequences. *Philosophical Transactions of the Royal Society B* 372:20160028.
- Hillebrand, H., and B. Matthiessen. 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters* 12:1405–1419.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? *American Naturalist* 93:145–159.
- Isbell, F., et al. 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477:199–202.
- Kessler, A., and I. T. Baldwin. 2001. Defensive function of herbivore-induced plant volatile emissions in nature. *Science* 291:2141–2144.

- Kessler, A., and I. T. Baldwin. 2002. Plant responses to insect herbivory: the emerging molecular analysis. *Annual Review of Plant Biology* 53:299–328.
- Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences of the United States of America* 112:797–802.
- Kuypers, M. M. M., H. K. Marchant, and B. Kartal. 2018. The microbial nitrogen-cycling network. *Nature Reviews Microbiology* 16:263–276.
- Laughlin, D. C., and J. Messier. 2015. Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends in Ecology and Evolution* 30:487–496.
- Lavorel, S., 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.
- Lefcheck, J. S., et al. 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nature Communications* 6:6936.
- Levine, J. M. 2016. A trail map for trait-based studies. *Nature* 529:163–164.
- Li, Y., D. A. Petrov, and G. Sherlock. 2019. Single nucleotide mapping of trait space reveals Pareto fronts that constrain adaptation. *Nature Ecology and Evolution* 3:1539–1551.
- Litchman, E., K. Edwards, C. A. Klausmeier, and M. K. Thomas. 2012. Phytoplankton niches, traits and eco-evolutionary responses to global environmental change. *Marine Ecology Progress Series* 470:235–248.
- Litchman, E., and C. A. Klausmeier. 2008. Trait-based community ecology of phytoplankton. *Annual Review of Ecology and Systematics* 39:615–639.
- Lobo, I., and K. Shaw. 2008. Discovery and types of genetic linkage. *Nature Education* 1:139.
- Loreau, M. 2010. Linking biodiversity and ecosystems: towards a unifying ecological theory. *Philosophical Transactions of the Royal Society of London B* 365:49–60.
- Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76.
- MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377–385.
- Marks, C. O. 2007. The causes of variation in tree seedling traits: the roles of environmental selection versus chance. *Evolution* 61:455–469.
- Matthews, B., et al. 2020. On biological evolution and environmental solutions. *Science of the Total Environment* 724:138194.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21:178–185.
- McLaren, J. R., and R. Turkington. 2010. Ecosystem properties determined by plant functional group identity. *Journal of Ecology* 98:459–469.
- Messier, J., M. J. Lechowicz, B. J. McGill, C. Violle, and B. J. Enquist. 2017. Interspecific integration of trait dimensions at local scales: the plant phenotype as an integrated network. *Journal of Ecology* 105:1775–1790.
- Moretti, M., et al. 2017. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology* 31:558–567.
- Morgan, T. H. 1910. Sex-limited inheritance in *Drosophila*. *Science* 132:120–122.
- Neilan, B. A., et al. 2008. The genetics and genomics of cyanobacterial toxicity. *Advances in Experimental Medicine and Biology* 619:417–452.
- Osnas, J. L. D., et al. 2018. Divergent drivers of leaf trait variation within species, among species, and among functional groups. *Proceedings of the National Academy of Sciences of the United States of America* 115:5480–5485.
- Paerl, H. W., and T. G. Otten. 2013. Harmful cyanobacterial blooms: causes, consequences, and controls. *Microbial Ecology* 65:995–1010.
- Pelletier, F., D. Garant, and A. P. Hendry. 2009. Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society of London B* 364:1483–1489.
- Petchey, O. L., A. Hector, and K. J. Gaston. 2004. How do different measures of functional diversity perform? *Ecology* 85:847–857.
- Pistón, N., et al. 2019. Multidimensional ecological analyses demonstrate how interactions between functional traits shape fitness and life history strategies. *Journal of Ecology* 107:2317–2328.
- Pomati, F., J. B. Shurin, K. H. Andersen, C. Tellenbach, and A. D. Barton. 2020. Interacting temperature, nutrients and zooplankton grazing control phytoplankton size-abundance relationships in eight Swiss lakes. *Frontiers in Microbiology* 10:1–17.
- Raffard, A., A. Lecerf, J. Cote, M. Buoro, R. Lassus, and J. Cucherousset. 2017. The functional syndrome: linking individual trait variability to ecosystem functioning. *Proceedings of the Royal Society B* 284:20171893.
- Reiss, J., J. R. Bridle, J. M. Montoya, and G. Woodward. 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution* 24:505–514.
- Santos, M. E., and W. Salzburger. 2012. How cichlids diversify. *Science* 338:619–621.
- Schweitzer, J. A., et al. 2004. Genetically based trait in a dominant tree affects ecosystem processes. *Ecology Letters* 7:127–134.
- Sedio, B. E. 2017. Recent breakthroughs in metabolomics promise to reveal the cryptic chemical traits that mediate plant community composition, character evolution and lineage diversification. *New Phytologist* 214:952–958.
- Seehausen, O., and D. Schluter. 2004. Male-male competition and nuptial-colour displacement as a diversifying force in Lake Victoria cichlid fishes. *Proceedings of the Royal Society B* 271:1345–1353.
- Shipley, B., M. J. Lechowicz, I. Wright, and P. B. Reich. 2006. Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology* 87:535–541.
- Soliveres, S., et al. 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature* 536:456–459.
- Start, D., S. McCauley, and B. Gilbert. 2018. Physiology underlies the assembly of ecological communities. *Proceedings of the National Academy of Sciences of the United States of America* 115:6016–6021.
- Thomas, M. K., C. T. Kremer, C. A. Klausmeier, and E. A. Litchman. 2012. A global pattern of thermal adaptation in marine phytoplankton. *Science* 338:1085–1088.
- Tilman, D. 1997. Distinguishing between the effects of species diversity and species composition. *Oikos* 80:185.
- Tilman, D., et al. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302.
- Trisos, C. H., C. Merow, and A. L. Pigot. 2020. The projected timing of abrupt ecological disruption from climate change. *Nature* 580:496–501.
- van der Plas, F., et al. 2020. Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning. *Nature Ecology and Evolution* 4:1602–1611.
- Vellend, M. 2010. Conceptual synthesis in community ecology. *Quarterly Review of Biology* 85:183–206.

- Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301.
- Violle, C., et al. 2007. Let the concept of trait be functional! *Oikos* 116:882–892.
- Violle, C., et al. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution* 27:244–252.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystems. *Science* 277:494–499.
- Wagner, C. E., L. J. Harmon, and O. Seehausen. 2012. Ecological opportunity and sexual selection together predict adaptive radiation. *Nature* 487:366–369.
- Weiher, E., and P. A. Keddy. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos* 74:159–164.
- White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution* 22:323–330.
- Whitham, T. G., et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics* 7:510–523.
- Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.
- Wright, J. P., G. M. Ames, and R. M. Mitchell. 2016. The more things change, the more they stay the same? When is trait variability important for stability of ecosystem function in a changing environment. *Philosophical Transactions of the Royal Society B* 371:20150272.
- Zehr, J. P., and R. M. Kudela. 2011. Nitrogen cycle of the open ocean: from genes to ecosystems. *Annual Review of Marine Science* 3:197–225.