

SUPPLEMENTARY INFORMATION

A database of 2,476 publications related to trait-based approaches was extracted from a search on Web of Science (TS=(functional trait OR trait-based) AND TS=(aquatic OR marine OR ocean OR coastal OR deep-sea OR pelagic OR benthic OR fresh water OR lake OR river OR limnology)) AND DOCUMENT TYPES: (Article) – on 11.29.2018). Publications were classified into 8 main scientific fields grouped from their Web of Science research areas. A similar search on Web of Science of all freshwater and marine ecology articles was carried out and the percentage of articles related to trait-based approaches computed over time. These informations have been illustrated in Figure S2.

The network (Figure S1) was created using ©VOSviewer version 1.6.8 (van Eck and Waltman 2010). To create the network, data were cleaned using a thesaurus file, merging keywords into more general terms and homogenizing them (removing plurals, merging synonyms). For example “trait plasticity”, “trait evolution”, “trait ecology”, “trait adaptation”, “quantitative trait”, “biological trait approach” are closely related terms and were merged into “trait”. This step is important to increase the overlap between publications. The analysis method relied upon an incidence matrix of 13,337 keywords, appearing in at least 26 publications. Based on this threshold, 100 top-keywords of the highest co-occurrence were identified. A network was built based on co-occurrence calculations (i.e. nodes correspond to keywords, edges correspond to the strength of the links between keywords) and for its representation the diameter of the corresponding circle was plotted as proportional to their total occurrence in the 2,476 publications. The association strength method (also called proximity index, for computation see van Eck and Waltman 2009) was used to normalize the strength of the links between keywords. There were 3 clusters (blue, orange and purple), identified as minimizing the distance between nodes (for the weighted and parameterized variant of modularity-based

clustering method used for bibliographic networks, see Waltman et al. 2010), with a minimum size defined as 20 keywords for easier interpretation.

Trait-based modeling

Trait-based ecological models can simulate functional traits as a continuum of trait values according to particular trade-offs (Follows and Dutkiewicz 2011). In such models, the numerical analog of an “individual” is the numerical entity defined by a unique vector of parameters that constitute its numerical traits. These models then simulate the response of individual phenotypic plasticity to environmental forcing and frequently rely on optimization for maximizing individual fitness (Smith et al. 2011). When parameters can vary to represent genotypic variability, these models can also be used to model trait adaptation and evolution (such as temperature optimum trait of phytoplankton growth, e.g. Grimaud et al. 2015). Most of these trait-based models focused on protists, as it may be easier to describe in a mechanistic way the functional traits and associated trade-offs of unicellular organisms (Merico et al. 2009; Follows and Dutkiewicz 2011). However, trait-based models were also developed for multicellular organisms such as copepods (Prowe et al. 2019) or even fish (e.g. Andersen et al. 2016). In these models, the traits that are the most commonly simulated are morphological and/or physiological traits, in particular traits that relate to size and allometric relationships (e.g. Hartvig et al. 2011; Acevedo-Trejos et al. 2015; Andersen et al. 2016; Blanchard et al. 2017) and/or to resource acquisition, including assimilation rates (e.g. Fiksen et al. 2013) or light-harvesting vs nutrient-harvesting investment for protists (with usually a focus on pigment-related traits, e.g. (Litchman et al. 2007; Hickman et al. 2010) or more recently on mixotrophy (e.g. Chakraborty et al. 2017; Leles et al. 2018). Some models have also focused on modeling life history traits, such as copepod dormancy (Maps et al. 2014) or bivalve fecundity and age at maturity (Sarà et al. 2013). Another type of trait-based model relies on traits to define

functional groups whose dynamics are explicitly simulated, such as the Plankton Ecology Group (PEG) models (Sommer et al. 1986, 2012) or the Plankton Functional Type (PFT) models (Le Quere et al. 2005; Hood et al. 2006). In these models, traits are usually fixed parameters (e.g. size, nutrient assimilation rates, trophic regime) that are used in a mechanistic approach of ecological and physiological processes relying on trade-offs between the fundamental functions of the organisms (e.g. Smith et al. 2014). Functional types based on size, feeding modes and ecosystem engineering (bioturbation) have also been used for modeling benthic fauna (e.g. Chardy and Dauvin 1992; Rosenberg 2001; Alexandridis et al. 2017). Dynamic Energy Budget (DEB) models (Nisbet et al. 2000) could also be seen as trait-based models that rely on the DEB theory (Kooijman and Kooijman 2000) and its trade-offs among energy allocation. Several models actually borrow from both approaches by defining, for example, a few groups of organisms for which life-cycle strategies or peculiar trade-offs are hardwired, while allometric relationships to the size master trait allow for inter-individual or inter-specific variability within the functional groups (e.g. Ward et al. 2012). Finally, statistical trait-based models (involving statistical relationships rather than differential equations based on mechanistic assumptions) have also been developed, for instance for relating functional traits to body trace metal concentrations in freshwater invertebrates (Peter et al. 2018) .

Trait-based models were used for simulating the distribution of traits at the community scale (Andersen and Beyer 2006), emergent trait biogeography (Follows et al. 2007; Record et al. 2013), size spectrum (e.g. Andersen et al. 2016), competition among species and/or seasonal dynamics (Merico et al. 2009; Terseleer et al. 2014; Leblanc et al. 2018), impact of traits on biogeochemical cycles (Stamieszkin et al. 2015; Coles et al. 2017), or impact of human pressures such as fishing on trait and trophic structure (Andersen and Pedersen, 2010). Trait-based models can also be used for estimating unknown traits, for instance from phylogeny (Bruggeman 2011) or for estimating the inter- and intra-specific variability of traits (Maps et

al. 2014). A description of some examples of trait-based models developed in marine ecology can be found in Kiørboe et al. (2018), with a special focus on optimality-based resource acquisition in unicellular plankton and size-based trophic dynamics of fish communities. To our knowledge, mechanistic trait-based models developed for benthic organisms remain relatively scarce (e.g. Sarà et al. 2013) and have considered size, ecosystem engineering, adult motility, fecundity and dispersal. A few statistical trait-based models have also been developed for these organisms (e.g. Peter et al. 2018).

With the exception of a few studies (e.g. Maps et al. 2014; Banas and Campbell 2016), the intra-specific variability of the traits is poorly or not taken into account, mainly because of the lack of empirical information on this variability. A first perspective for trait-based modeling could then be to tackle this question of inter-individual variation of traits and its impact on ecosystem structure and functioning. Trait-based models can for instance be used to quantify the impact of environmental changes on the intra- and inter-specific variability of functional traits (e.g. inter-individual variability of lipid content and inter-specific variability of size of Arctic copepods in the Barents Sea, Renaud et al. 2018). A second perspective would be the development of a new generation of trait-based models using -omics data (Mock et al. 2016; Stec et al. 2017; Coles et al. 2017). Metatranscriptomic data could for instance be used to identify physiological traits of phytoplankton, combined to a mechanistic model of the phytoplankton cell, and used to construct a trait-based global marine ecosystem model (Mock et al. 2016). Emergent communities of marine microbes (from bacteria to phytoplankton) have also been predicted by directly simulating their metagenomes and metatranscriptomes (Coles et al. 2017). Such models could then be used for estimating functional trait plasticity across ecosystems. The idea of improving ecosystem models using -omics is not new (Hood et al. 2006), but functional trait-based approaches could constitute the common framework needed

for modellers, observers, molecular biologists, and ecologists working in limnology and oceanography.

SUPPLEMENTARY TABLE**Suppl. Table 1: Main definitions related to traits and commonly used in trait-based**

studies. Examples are given in grey. For clarity and consistency in trait-based aquatic ecology, we recommend the use of the definitions indicated in bold (cf Table 1 in the main manuscript).

Term	Definitions	References	Examples
Trait	Any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization.	(Violle et al. 2007)	
	A well-defined, measurable property of organisms, usually measured at the individual level and used comparatively across species.	(McGill et al. 2006)	
Functional trait	Any trait that impacts fitness indirectly via its effects on growth, reproduction and survival.	(Violle et al. 2007)	
	Morphological, biochemical, physiological, structural, phenological, or behavioral characteristics that are expressed in phenotypes of individual organisms and are considered relevant to the response of such organisms to the environment and/or their effects on ecosystem properties.	(Díaz et al. 2013)	
	Characteristics of an organism that are considered relevant to its response to the environment and/or its effects on ecosystem functioning.	(Díaz and Cabido 2001)	
	Components of an organism's phenotype that influence ecosystem level processes.	(Petchey and Gaston 2006)	
	Any trait that strongly influences organismal performance.	(McGill et al. 2006)	
	Any trait directly influencing organismal performance.	(Mouillot et al. 2013)	
Performance trait	Any functional trait directly influencing organismal performance	(Violle et al. 2007)	Somatic biomass, reproductive output, such as offspring biomass or number, and survival.

Effect trait	Traits that determine effects of [organisms] on ecosystem functions.	(Lavorel and Garnier 2002)	
	Traits that are usually relevant at the ecosystem level	(Hébert et al. 2017)	Respiration, excretion, clearance rate.
	Any trait which reflects the effects of [an organism] on environmental conditions, community or ecosystem properties.	(Violle et al. 2007)	
Response trait	Any trait whose value varies in response to changes in environmental conditions	(Violle et al. 2007)	
	Traits associated with the response of [organisms] to environmental factors such as resources and disturbances.	(Lavorel and Garnier 2002)	
	Traits that are usually most relevant at the community level	(Hébert et al. 2017)	Behavior-related traits.
Realized trait	Trait actually measured <i>in situ</i> or in the laboratory	(Reu et al. 2011)	
Potential trait	Trait described from the literature, usually at the species level, and ideally covering a large variety of environmental conditions.	(Reu et al. 2011)	
Biological traits	Traits that describe the biological attributes of the species.	(Mondy and Usseglio-Polatera 2014)	For instance, for freshwater invertebrates: size, life span, number of reproductive cycle per year, type of aquatic stages, reproduction strategy, and dispersal strategy, resistance forms, respiration mode, locomotion or substratum relation, and feeding mode.
Ecological traits	Traits that refer to habitat or environmental requirements.	(Beauchard et al. 2017)	
	Traits that describe the species-habitat relationships.	(Mondy and Usseglio-Polatera 2014)	For instance for freshwater invertebrates: altitudinal, substratum, temperature and salinity

			preferences, or acidification tolerance.
Demographic traits	Traits that are relevant at the population level	(Hébert et al. 2017)	Generation time.
Life history traits	Traits referring to life history , such as the type of reproduction (sexual versus asexual) or the ability to form resting stages.	(Litchman and Klausmeier 2008)	
	Traits that are relevant at the individual level	(Hébert et al. 2017)	Fitness-related traits.
Morphological trait	Traits related to the morphology of organisms,	(Litchman and Klausmeier 2008)	Cell size, cell shape.
Physiological trait	Traits related to the physiology of organisms,	(Litchman and Klausmeier 2008)	Nutrient acquisition, response to light.
Behavioral trait	Traits related to the behavior of organisms,	(Litchman and Klausmeier 2008)	Motility.

SUPPLEMENTARY FIGURES

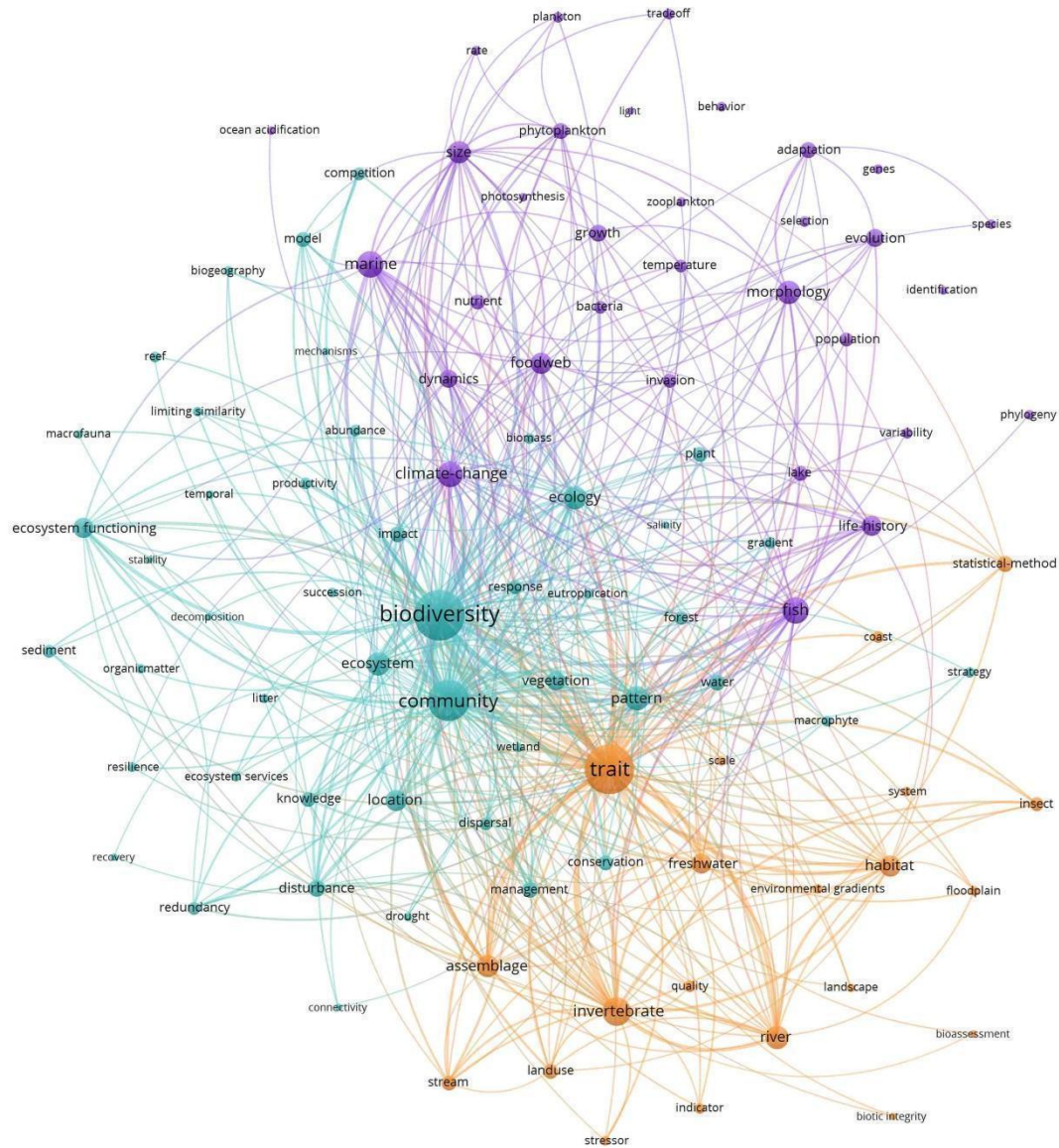


Figure S1: Bibliographic network representing the database of publications on trait-based approaches. Three clusters of co-occurring keywords were identified within this network. The first (in orange) and the second (in purple) clusters mainly refer to two different ecosystems. The “freshwater”, “river” and “stream” ecosystems drive the first cluster as well as “invertebrate” organisms, while the second cluster refers to “marine” ecosystems with “fish”, “zooplankton” and “phytoplankton” organisms. These clusters highlight different

ecological questions either linked to “indicators” and “land-use” (cluster 1 in orange) or to “food webs” and “climate-change” (cluster 2 in purple). The third cluster (in blue) is mainly associated with theoretical ecology, grouping “biodiversity”, “community”, “ecology”, “ecological functioning” and “pattern” showing numerous links rather evenly distributed between freshwater and marine ecosystem studies. This third cluster also refers to “sediment” or “organic matter”, two components transcending both limnology and oceanography.

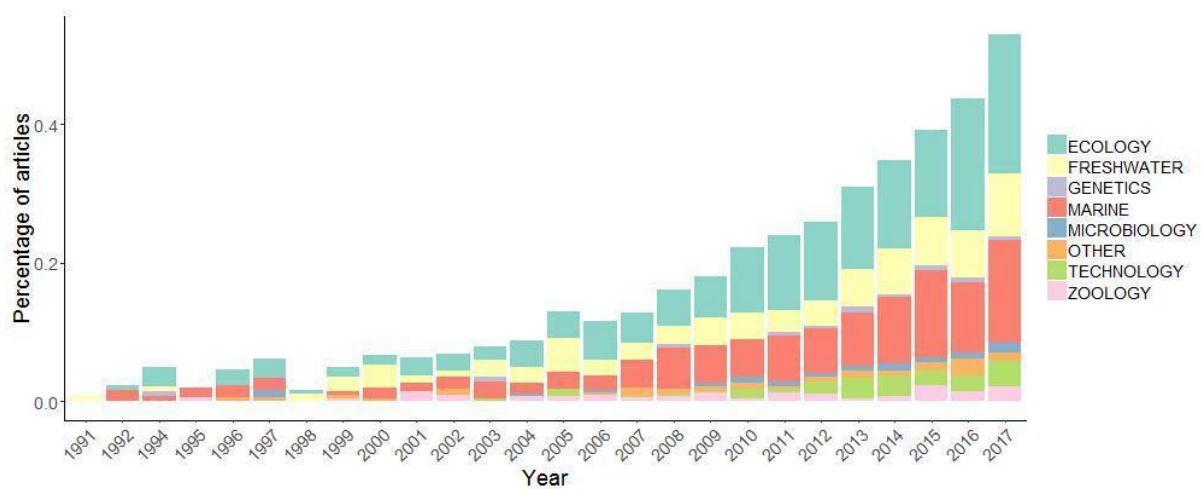


Figure S2: The percentage of publications relative to all the ones published in freshwater and marine ecology showing an increase over time, based on a literature survey (described in Supplementary Information). This percentage has increased over time, reaching about 0.5% in 2017. More recently, these two terms began to appear in the Web of Science research fields identified as: “genetics”, “microbiology” and “technology” (Figure S1).

Supplementary references (not cited in the main manuscript):

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