Trait-based modelling in ecology: lessons from two decades of research

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Abstract

Trait-based approaches are an alternative to species-based approaches for functionally linking individual organisms with community structure and dynamics. In the trait-based approach, the focus is on the traits, the physiological, morphological, or life-history characteristics, of organisms rather than their species. Although used in ecological research for several decades, this approach only emerged in ecological modelling about twenty years ago. We review this rise of trait-based models and trace the occasional transfer of trait-based modelling concepts between terrestrial plant ecology, animal and microbial ecology, and aquatic ecology. Trait-based models have a variety of purposes, such as predicting changes in species distribution patterns under climate and land-use change, planning and assessing conservation management, or studying invasion processes. In modelling, trait-based approaches can reduce technical challenges such as computational limitations, scaling problems, and data scarcity. However, we note inconsistencies in the current usage of terms in trait-based approaches and these inconsistencies must be resolved if trait-based concepts are to be easily exchanged between disciplines. Specifically, future trait-based models may further benefit from incorporating intraspecific trait variability and addressing more complex species interactions. We also recommend expanding the combination of trait-based approaches with individual-based modelling to simplify the parameterization of models, to capture plant-plant interactions at the individual level, and to explain community dynamics under global change.

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Introduction

Understanding community structure and dynamics is a key element of modern ecology, especially in the light of global change (Harte and Shaw, 1995; Knapp, 2002). This understanding was traditionally mediated by species-based approaches. More recently, such approaches were complemented by approaches based on traits. Trait-based approaches are popular, because they allow the direct connection of organism performance to its functions and to the functions of higher levels of organization such as populations, communities and ecosystems. While trait-based approaches are now firmly established in empirical research (Violle et al., 2007; Suding and Goldstein, 2008), they were only introduced to modelling about twenty years ago. Given that modelling is important for understanding community structure and dynamics, trait-based modelling can reduce some of the challenges faced by species-based modelling. For example, species-based models are usually complex, difficult to parameterize and often produce outcomes that cannot be generalized to other species. Trait-based models often require less parameterization effort than species-based models, facilitate scaling-up, and produce more generalizable results. Here, we review the rise of trait-based models over the past twenty years, highlight their main fields of application and point out avenues for future trait-based modelling.

Traits arose from the concept of plant functional groups and these groups were the first published classification of organisms according to function instead of taxonomy (Raunkiaer, 1934; Grime, 1974). The next wave of interest into functional groups was led by the desire to predict community and ecosystem responses to environmental change (Diaz and Cabido, 1997; Lavorel et al., 1997; Chapin et al., 2000). The focus then shifted from functional groups to functional traits and thus from species grouped because they use similar strategies to the similar characteristics underlying those strategies (Yanzheng Yang et al., 2015). Distinct aspects of strategies were reflected in sets of correlated traits that were defined as trait dimensions (Westoby et al., 2002). This shift from a species-based approach to a trait-based approach is described as the ‘Holy Grail of Ecology’ (Lavorel and Garnier, 2002). This approach involves the use of plant functional traits, rather than species identities, to generalize complex community dynamics and to predict the effects of environmental changes (Suding and Goldstein, 2008).

Functional traits not only help derive individual strategies (Wright et al., 2004), but also to connect them to functions at organizational levels higher than those of the species such as the community or ecosystem level. There are four requirements for a trait (Lavorel et al. 2007). It should be connected with a function. It should be relatively easy to observe and quantify. It should be possible to measure it in a standardized way across a wide range of species and environmental settings. And it should have a consistent ranking. Trait-based ecology is further based on the assumption that trade-offs and constraints have shaped phenotypic variation in different trait dimensions (Messier et al., 2017).

Sets of plant traits that reliably represent the processes of growth, survival, and reproduction (Violle et al., 2007) make it possible to facilitate and generalize empirical and modelling studies. Therefore, researchers attempted to define a universal set of traits. Pachepsky et al. (2001) identified twelve critical traits that affected resource uptake, the area over which resource is captured, the internal allocation of resources between structure, storage and reproduction, time of reproduction, number of progeny produced, dispersal of progeny, and survival. Other researchers used smaller numbers of traits. The leaf economics spectrum, for example contains only six (Wright et al., 2004). Díaz et al. (2015) also used six traits but not those of the leaf economics spectrum, and several researchers even used a set with as few as three traits (Westoby, 1998; Westoby et al., 2002; Wright et al., 2004; Chave et al., 2009; Garnier and Navas, 2012). Thus, rather than applying a universal trait set, modern use of the concept implies a selection of a small set of critical functional traits specific to the needs of a specific study and dependent on the specific organisms for which strategies are being described.

Using trait-based approaches overcomes some of the well-known problems of species-based approaches. In trait-based approaches, for example, it is possible to directly connect community functions such as production to environmental changes via functional traits. Moreover, the trait-based approach is an intuitive approach for addressing evolutionary processes because evolution selects organisms in a community according to their function and not their taxonomy. Trait-based approaches are, furthermore, more suitable than species-based approaches for generalizations across species as they are not tied to taxonomy. In addition, trait data are, in most cases, more readily available than species data due to the rapid expansion of trait databases. Trait databases are especially well developed for plants (Kleyer et al., 2008; Kattge et al., 2011).

Although current trait-based approaches have several benefits, they also have some shortcomings not present in species-based approaches. One of these is the choice of appropriate functional traits and their trade-offs with other traits given that a great diversity of traits are available (Funk et al., 2017). Furthermore, traits differ intraspecifically but these differences are often neglected (Violle et al., 2012; Bolnick et al., 2011). Existing trait databases are usually of limited use when it comes to species interactions, intraspecific trait variation and variable environmental settings (Funk et al., 2017). In addition, the theoretical assumptions of trait-based studies are not always supported by experimental data (Suding and Goldstein, 2008). These shortcomings can be overcome by closer cooperation between empirical and theoretical researchers and by the development of standards for trait data collection (e.g. Garnier and Shipley, 2001; Pérez-Harguindeguy et al., 2013).

In the most recent 20 years trait-based approaches have entered ecological modelling. The main advantage of modelling over empirical approaches is that it allows the comparison of several scenarios with different sets of assumptions, so conducting virtual experiments. This makes possible the systematic exploration of the outcomes under each set of assumptions and the elucidation of the mechanisms underlying the patterns observed. Using models therefore avoids the costs and risks of real-world experiments. In principal, trait-based models consist of combinations of functional traits that respond to environmental changes (response traits) and affect community and ecosystem properties (effect traits) (Fig. 1). Implementing trait-based approaches for modelling may also help overcome the high data demand of species-based models (Garrard et al., 2013; Weiss et al., 2014), simply due to the fact that traits usually represent more than one species. For the same reason, trait-based modelling may also reduce computing times. Moreover, using traits in modelling can facilitate scaling of physiological processes to global scales (Shipley, Vile, & Garnier, 2006; Lamarque et al., 2014) because traits can function as a common currency across scales in these models.

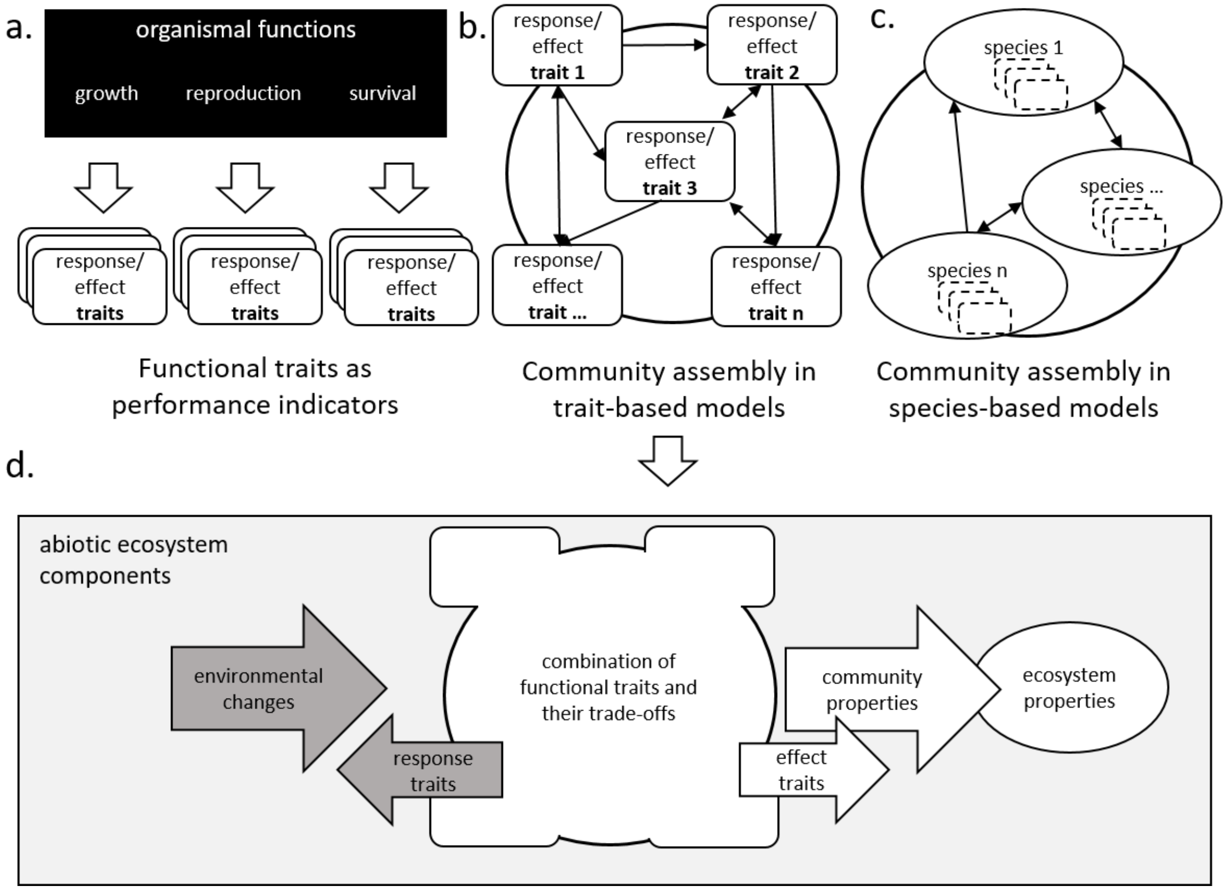

Fig. 1. Conceptual overview of trait-based models compared to species-based models. Functional response and effect traits (rounded rectangles) are performance indicators that are related to organismal functions (a). Trait-based models represent community (circle) assembly by interacting functional response and effect traits (b). Species-based models represent community assembly by interacting species that may implicitly contain traits (c). Trait-based models can be divided into models that use functional traits only as static inputs (white elements in d) that affect community and ecosystem properties and models that use functional traits both as inputs and dynamic outputs (white and grey elements in d). Response traits change dynamically depending on changing environmental conditions.

Given the advantages of trait-based approaches, it is still surprising that their incorporation into the tool-kit of ecological modelling has been slow and that they are applied in proportionally fewer cases of modelling than of empirical work. In this paper, our aim is to systematically review applications of trait-based models in ecology. More specifically, we 1) discuss definitions and terminology of trait-based approaches, 2) evaluate how trait-based models are used in different disciplines, and 3) identify avenues for the future implementation of trait-based models, including cross-discipline exchange. The trait-based modelling applications in this review contribute to identifying principles that underlie spatiotemporal community dynamics, exploring species distributions, investigating species interactions, scaling ecosystem processes from individual traits to ecosystem functioning, explaining the consequences of climate and land-use changes for community dynamics, and also supporting conservation and invasion studies.

Methods

This paper is based on a systematic literature review. We searched for papers using a topic search on the “Web of Science Core collection”. We first used the search term “trait-base*” AND model* and in a second search “traitbase*” AND model*. The first search yielded 772 papers all of which turned out to postdate 1978. The second search added 4 papers, which were from the period 2010-2018. We excluded all papers from obviously irrelevant fields, such as psychology, medicine, engineering, business, management, history, industrial relations, linguistics, education, nutrition, and biotechnology (Supplementary Material. Tab. 2). After this filtering of both searches, we retained 623 papers that focused on ecology and related biological sciences. These ecological and biological publications were the most recent among all the papers we found (Fig. 2). In addition to the publications found during this systematic literature search, we also included papers discovered by the snowball principle, i.e. the papers cited in papers already selected. We also included additional publications recommended by experts in the field. We finalized our research by selecting only those papers from our compilation that directly addressed concrete trait-based models. We excluded pure genetics, toxicology, climate and evolution studies, because we wanted to focus on ecological studies. We did not consider studies that focused on statistical analysis of empirical data, but we did include statistical models if the focus was on the model such as in species distribution modelling. Our focus was on primary modelling papers, so that we only referred to secondary modelling papers that discuss, use, extend or review previously published models when they introduce a new trait-based perspective. We did not consider editorial material or technical software descriptions. This procedure yielded 188 papers (Supplementary Material. Tab. 1, Fig. 2).

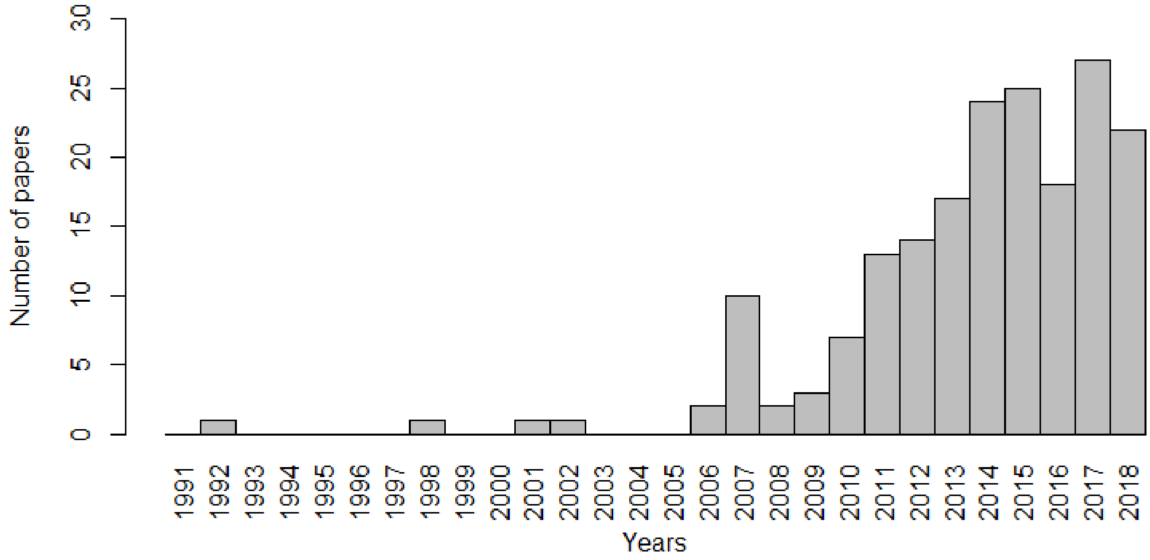

Fig 2. Papers on trait-based models included in the final list of the reviewed model (Supplementary Material. Tab. 1).

Glossary

Functional traits well-defined morpho-physio-phenological characteristics of individual organisms that relate to the patterns of growth, reproduction, and survival of the species (McGill et al., 2006; Violle et al., 2007), and that evolved in response to abiotic environmental conditions and interactions with other species (Reich et al., 2003; Clark et al., 2012).

Hard traits those directly related to important physiological processes that define the growth, reproduction and survival of an organism. Hard traits are usually hard to measure, and therefore in practice they are identified and measured on the basis of surrogate **soft traits** (Hodgson et al., 1999) that are correlated with hard traits but are more easily or cheaply measured.

Response traits determine how a species reacts to a disturbance or a change in abiotic or biotic processes in its environment (Lavorel et al., 1997; Lavorel and Garnier, 2002).

Effect traits determine how a species influences ecosystem properties (Lavorel et al., 1997; Lavorel and Garnier, 2002). Effect traits alter abiotic and biotic processes corresponding to a wide range of ecosystem functions (Eviner and Chapin III, 2003).

Plant functional types (PFT) Groups of species with presumably similar roles in ecosystem functioning (Lavorel et al., 1997). They are considered as an important ecological framework for describing the mechanisms underlying vegetation responses (McIntyre et al., 1995; Pausas, 1999).

Community-weighted mean (CWM) traits Quantification and use of aggregated trait attributes of the community as a measure of diversity that does not take species into account. To calculate a community aggregated trait value, relative abundances of species and their trait values are used (Violle et al., 2007; Funk et al., 2016).

Intraspecific trait variability (variation) is the difference in the values of functional traits within one species that results from the development and adaptation of species to environmental change (Albert et al., 2011; Schirpke et al., 2017). There are two sources for this variation. One is heritable differences between individuals and the other phenotypic plasticity in trait values across different environmental conditions (Moran et al., 2016).

Conceptual models models that are not implemented in equations or programming code. In practice, they are usually a graphical representation of causal relationships (or flows) between factors or processes.

Statistical models descriptive mathematical models of relationships between variables based on assumptions about the data sampled. They represent a set of probability distributions on the sample space (Cox et al., 1979).

Equation-based models mathematical models that are formulated as a set of ordinary differential equations, partial differential equations, or integro-differential equations. They can be solved analytically or numerically. These models are sometimes also called **mechanistic models**, **physiological models** or **process-based models**, although each of these terms is also used for non-equation-based models. For instance, process-based models are based on a theoretical understanding of the relevant ecological processes. They are built on explicit assumptions about how a system works, and these models are especially well-designed to predict the effects of global change (Cuddington et al., 2013). **Dynamic Global Vegetation Models** (DGVMs) and **Earth System Models** (ESM) also fall in this category.

Individual-based models (or **agent-based models**) explicitly consider individual organisms as objects with characteristics (traits) that influence interactions with other individuals and the environment (Grimm and Railsback, 2005). They adopt a bottom-up approach where population-level behavior emerges from these individual interactions (DeAngelis and Grimm, 2014). Individual-based models are usually not based on equations, but on rules implemented in programming code. Individual-based models are highly suitable for spatially explicit implementations (Grimm et al., 2005), often combined with a **grid-based modelling** approach.

Types and scales of trait-based models

We classified the papers discovered in our systematic search according to model type and target scale. For model type, we distinguished between conceptual models, statistical models, equation-based models, individual-based models, and their combinations (see Glossary and Supplementary Material. Tab. 1). Statistical models occurred in 26% of the reviewed papers and equation-based models in 60-61%. Together they were the most common types in trait-based modelling. Conceptual models are probably more common than was reflected in the papers we examined

(5% of the reviewed papers) because they often precede a mathematical or code-based model formulation. Individual-based models represented 16% of the reviewed papers.

Trait-based models address questions at local to landscape and global scales (Supplementary Material. Tab. 1) and at the organizational level of individuals, species, populations, communities, and ecosystems. Where the models targeted the ecosystem level, they were implemented as equation-based models. This is probably due to the fact that ecosystem-level models focus on matter or energy fluxes and individual-based models are not suitable for modelling fluxes. However, models at the species, population or community level do not usually consider fluxes but use organisms as their inputs. This is typical of individual-based models but all other model types are also used at species, population, and community levels. Models of processes at the level of individual organisms or their organs were either implemented as statistical models of plant growth or, when emphasizing physiological mechanisms, as equation-based models.

Overall, different model types benefit in different ways from the integration of traits depending on the target scale of the question addressed by the model. In the following sections, we present studies that illustrate the potential benefits of using trait-based modelling for various scales and model types to study plants and animals in terrestrial and aquatic ecosystems, microbial organisms, and soil decomposers.

1. Trait-based modelling of plants in terrestrial ecosystems

Trait-based approaches were originally developed and discussed for plants in terrestrial ecosystems. This focus on plant sciences was mirrored in the trait-based modelling studies. Fifty percent of all studies in this review addressed terrestrial vegetation (note that we discuss the two studies on fungi in our review as part of this section). The aims of trait-based vegetation models were diverse. They covered investigations of plant growth and interactions, species distributions, plant invasiveness, community assembly and dynamics, biodiversity hypotheses, ecosystem services, and global vegetation patterns and dynamics (Fig. 3).

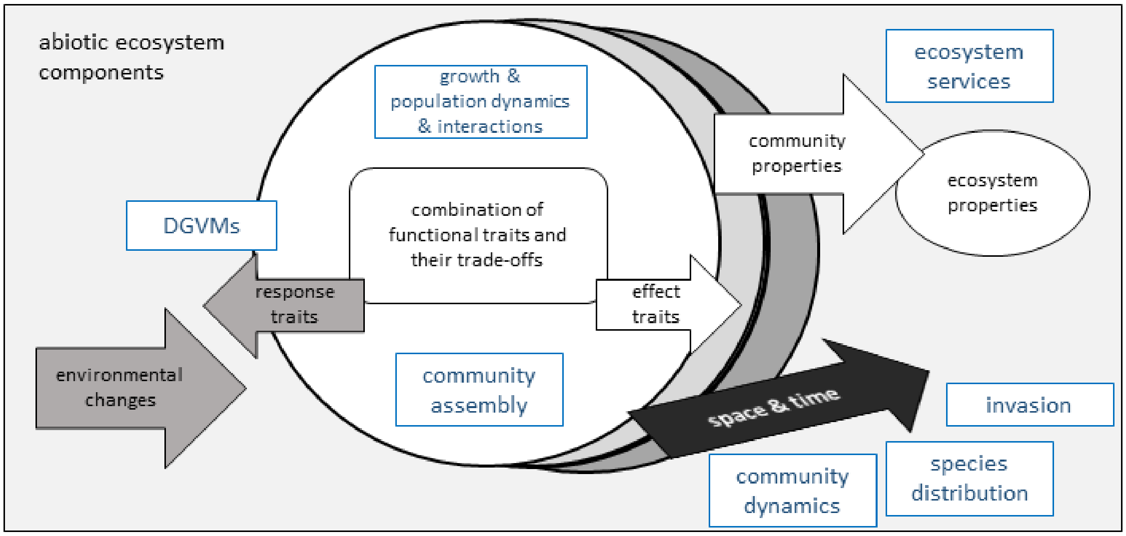

Fig. 3. Overview of the models of plants in terrestrial ecosystems based on their main purposes and research questions (rectangles with blue edges). Large circles represent community development in space and time (see Fig. 1 for further explanation).

1.1.Trait-based models on plant growth, population dynamics, and interactions

Plant growth, population dynamics, and interactions were modelled with a range of model types, including statistical, equation-based and individual-based models (Supplementary Material. Tab. 1). The influence of traits on the growth of individual plants or plant organs was most commonly addressed using statistical models. These statistical models were either non-linear regression models (Chavana-Bryant et al., 2017), Bayesian approaches, or both (Hérault et al., 2011; Aubry-Kientz et al., 2015; Thomas and Vesk, 2017a; Thomas and Vesk, 2017b). Equation-based approaches focused on mechanisms such as carbon and biomass fluxes within and across plants (Enquist et al., 2007; Sterck and Schieving, 2011), water uptake (Fort et al., 2017) or on the physiological processes producing salt tolerance (Paleari et al., 2017).

Both models on plant population dynamics in our review were equation-based models. One study investigated the influence of considering whole life cycles in fitness assessments (Adler et al., 2014), and the other one studied the population dynamics and viability of a primrose (and a lizard) population (Jaffré and Le Galliard, 2016). Comparing the results from the equation-based integral projection model with those from an analogous individual-based model, Jaffré and Le Galliard (2016) highlighted the importance of constructing individual-based models when very small populations are investigated. Our review confirms the conclusion of Salguero-Gómez et al. (2018) that trait-based approaches are still underrepresented in studies of population dynamics. However, note that such combinations of trait-based and demographic approaches are more common for aquatic organisms (Vindenes et al., 2014; O'Farrell et al., 2015) or terrestrial mammals (Santini et al., 2016; Jaffré and Le Galliard, 2016; van Benthem et al., 2017) than for plants.

Interactions such as competition have mainly been studied with equation- and individual-based models or their combination. Using dynamic process-based models, Ali et al. (2013) and Ali et al. (2015) contrasted two alternative competition theories and demonstrated how elevated carbon dioxide concentration influences plant competition and, consequently, community composition in an ecosystem. In a combined equation- and individual-based approach, Fyllas et al. (2014) simulated ecosystem fluxes based on two axes: the leaf economics spectrum (Wright et al., 2004) and tree architecture spectrums (Chave et al., 2005; Mori et al., 2010). Individual-based models are particularly useful for representing plant interactions because it is the individual level at which interactions are initiated. For example, Taubert et al. (2012) used them to investigate biofuel production in grasslands of temperate regions. In this model, above- and below-ground plant functional traits were used to characterize how successful plants were in taking up resources and competing with neighbors.

Based on these examples and the nature of the models, we suggest that different kinds of models have different efficiencies in the sense of producing good results without requiring large amounts of data. Statistical models are most efficient for describing the relationship between traits and plant growth but equation-based models are most efficient for describing mechanisms, simple interactions, or ecosystem fluxes. Individual-based models are the best choice, however, for complex trait-based interactions. This is because individuals are the nexus of trait-based interactions.

1.2.Trait-based models on species distributions

Although trait-based modelling was often applied as an alternative to species-based approaches, a number of trait-based modelling papers were devoted to questions related to species distribution. For example, a combination of species distribution models and trait-based approaches was explicitly recommended to estimate the impact of climate change on species (Willis et al., 2015).

The great majority of the studies on species distribution modelling combined a trait-based approach with statistical modelling, often by using a Bayesian approach (Supplementary Material. Tab. 1). For example, Powney et al. (2014) showed that predictions of trait-based species distribution models were best for broad-scale changes in regions with similar land-cover composition. In another example, a new application of time-to-detection modelling was able to detect multiple species as a function of plant morphological and phenological traits (Garrard et al., 2013). The model by Rosenfield and Müller (2017) estimated the relative abundances of species that meet the values of functional traits found in a target ecosystem.

Trait-based models provide some advantages when predicting local community assembly, especially where environmental filtering and niche differentiation shape communities. Among the algorithms used in the papers on trait-based models, Maxent (e.g. Shipley et al., 2011; Sonnier et al., 2010) and the Traitspace model (e.g. Laughlin et al., 2012; Laughlin et al., 2015; Laughlin and Joshi, 2015) were used for trait-based environmental filtering. These algorithms predict low probabilities for any species whose trait distribution fails to pass through the environmental filter (Laughlin and Laughlin, 2013). The Maxent model and the Traitspace model differ in their ability to predict the relative abundance of species from a regional species pool (Laughlin and Laughlin, 2013). Maxent predictions are degraded when high intraspecific variability is included (Merow et al., 2011). The importance of intraspecific variation in functional traits was underlined by Violle et al. (2012); Read et al. (2017) who found that intraspecific variability compensated for the effects of interspecific variation along a climatic gradient. Moreover, trait-based models are not only inaccurate when intraspecific variability is ignored but also when environmental changes are rapid. Therefore, when the environment changes rapidly, trait-based models become inaccurate because the traits measured were selected for by a previous, different, environment (Welsh et al., 2016). A statistical approach uniting trait-based and species distribution models was also applied to model the distribution of wood-inhabiting fungi (Abrego et al., 2017).Finally, the only equation-based model in this section was a model that incorporated plant physiology to predict tree distributions along resource gradients (Sterck et al., 2014).

Thus, trait-based approaches are useful for modelling species distributions. Current efforts in trait-based species distribution modelling focus on moving from mean trait values to intraspecific trait variability, e.g. by implementing a Bayesian framework (Laughlin et al., 2012).

1.3.Trait-based models of community assembly

Community assembly results from species sorting by environmental filters and biotic interactions. Until now, trait-based models of community assembly used mainly statistical modelling and equation-based approaches to capture this process (Supplementary Material. Table 1). We further found one individual-based model [(Pachepsky et al., 2007) based on a model by Bown et al. (2007) mentioned in section 1.1. Trait-based models on plant growth, population dynamics, and interactions], and three conceptual models (Bhaskar et al., 2014; Crowther et al., 2014; Losapio and Schöb, 2017), including one on fungal community assembly (Crowther et al., 2014). The group of models of community assembly partially overlapped with models of species distribution and was thus already partly discussed in section 1.2.Trait-based models on species distributions. Three groups of studies emerged: First, a large group of publications where the intention was to identify traits that affect community assembly; second, a group of four papers studying intraspecific trait variability (Pachepsky et al., 2007; Laughlin et al., 2012; Yang et al., 2015; Schliep et al., 2018) ; and, third, another group of three papers where traits were used as response traits to distinguish between biotic and abiotic filtering (Bhaskar et al., 2014; Chauvet et al., 2017) and to assess effects of environmental change (Losapio and Schöb, 2017).

The majority of the models reviewed in the current section were in the first group that aimed to distinguish traits that influence species abundance, richness and functional diversity. One case study, for instance, indicated that seed production and dispersion traits are important for regional species abundance (Marteinsdóttir, 2014). In another case study, a trait-based model incorporated both neutral theory and niche theory to identify whether, and which, plant traits determine community assembly and biodiversity patterns, including plant species richness and abundance, across environments (Shipley et al., 2006). To unify classic coexistence theory and evolutionary biology with recent trait-based approaches, Laughlin et al. (2012) incorporated intraspecific trait variation into a set of trait-based community assembly models. These models generate species abundances to test theories about which traits, which trait values, and which species assemblages are most effective for achieving a specified functional diversity. Larson and Funk (2016) advocated for including regeneration traits in a model of community assembly. A few statistical trait-based models in the first group aimed at quantifying the relationship between environmental gradients and individual-level traits or community-weighted mean traits to describe environmental filters (Laughlin et al. 2015). The common assumption of such models was that traits are unimodally distributed and centered on an optimal trait value in any given environment. In contrast, an extended Traitspace model (Laughlin et al., 2015) adopting a hierarchical Bayesian approach (Laughlin et al., 2012) captured multimodal trait distributions. Improving the Traitspace model in this way increases the power of trait-based predictions of species abundances. The power increase arises because the prediction of species abundance distributions then reflects the true functional diversity of a community. These community assembly models were also used to test the mass ratio hypothesis (Laughlin, 2011; Laughlin, 2014) and to refine restoration objectives, either by manipulating abundances of species already existing in the system or by adding species from warmer climates to the local species pool (Laughlin et al., 2017). Similar to models on species distribution, the MaxEnt algorithm is also used for models of community assembly to predict the effect of trait-based environmental filtering on the species pool, for example, in forest community assembly (Laughlin et al., 2011) or using the community assembly via trait selection approach (CATS) (Laliberté et al., 2012; Frenette-Dussault et al., 2013).

Equation-based models in the first group tended more towards theoretical questions: For example, they investigated the multidimensional nature of species coexistence based on traits (Kraft et al., 2015), they implemented biophysical principles to test niche vs neutral processes (Sterck et al., 2011); or they showed that self-limitation promotes rarity (Yenni et al., 2012).

Thus, it is possible to use trait-based community assembly models for tackling questions of fundamental and applied ecology. To be optimally effective, more of such models should incorporate multimodal trait distributions and intraspecific trait variability.

1.4.Trait-based models of community dynamics

Trait-based modelling can be helpful for explaining not only static community assembly but also the temporal and spatial dynamics of communities. We found twice as many equation-based models of community dynamics as individual-based models (Supplementary Material. Tab. 1). The equation-based approaches included basic and applied research. Among the basic research, two studies investigated vegetation dynamics at the landscape level (Falster et al., 2011; Quétier et al., 2011), one study quantified environmental filtering and immigration rates of new species (Jabot, 2010), and one study assessed plant community stability considering litter decomposition (Miki and Kondoh, 2002). Among the more applied research, three studies included the effect of environmental change: Moor (2017) studied the relationship between dispersal and species diversity along a climate warming gradient; Savage et al. (2007) investigated overyielding and other responses to environmental change; and Tanaka (2012) advanced Savage et al.'s (2007) study by considering interspecific competition and trait covariance structure. One further equation-based model with an applied question was developed to compare the effect of different cropping systems on weed traits (Colbach et al., 2014).

The individual-based models in this section targeted effects of regional processes on grasslands (Weiss et al., 2014), as well as the processes of grazing and disturbances. The effects of grazing on a grassland community were investigated in two individual- and trait-based models (May et al., 2009; Weiss and Jeltsch, 2015). The results of these models indicated that trait size symmetry of competition is central for community dynamics. This indication arose from the model only generating the patterns predicted by the grazing reversal hypothesis under specific conditions. These conditions were the explicit inclusion in the model of shoot and root competition, and the assumptions that plants with larger aboveground parts were superior competitors and belowground competition was consistently symmetrical. A similar functional group scheme based on four key traits representing typical species responses to disturbance was used in an individual-based model that led to the conclusion that the competition-colonization trade-off is insufficient to predict community dynamics (Seifan et al., 2012; Seifan et al., 2013). Thus, trait-based approaches have great potential in community dynamics modelling. This is especially true where it is important to include spatial interactions because these are often mediated by traits.

1.5.Trait-based dynamic global vegetation models (DGVMs)

Beyond the community and ecosystem levels mentioned in previous sections, global vegetation classification is possible with DGVMs. More specifically, DGVMS advance understanding of the distribution of plant functional types across spatial scales (Prentice et al., 2004). DGVMs are used as precursors of, or parts of, earth system models in which they represent energy, carbon and water fluxes (Scheiter et al., 2013; Drewniak and Gonzalez-Meler, 2017). Dynamic vegetation classification is enabled by calculating separately ecosystem fluxes and plant functional type occurrences both of which can be based on traits. DGVMs are mainly or entirely equation-based models because this form allows them to adequately represent ecophysiological processes (Supplementary Material. Tab. 1). More recent DGVMs have added individual-based components to account for individual variation (Scheiter et al., 2013).

Most DGVMs were used to investigate vegetation responses to current climate and climate change (e.g. Verheijen et al., 2013; Sakschewski et al., 2015). Walker et al. (2017) applied the Sheffield DGVM (Woodward and Lomas 2004) to compare the predictive power of four trait-scaling hypotheses on the distribution of global maximum rate of carboxylation. The four hypotheses used were those on plant functional type, nutrient limitation, environmental filtering, and plant plasticity. The result of this comparison showed that nutrient limitation was the most probable driver of global maximum rate of carboxylation distributions. DGVMs are criticized for being insufficient realistic. This insufficiency arises because they use plant functional types with constant attributes and do not represent competitive interactions (Scheiter et al., 2013). This criticism led to a stronger focus on traits and to the addition of individual-based modules (Harper et al., 2016). The Jena Diversity-DGVM incorporates 15 traits with several functional trade-offs that defined plant growth strategies (Pavlick et al., 2012). These functional properties of the vegetation were derived, unlike in standard DGVMs, from mechanistic trait filtering via environmental selection. The Jena Diversity-DGVM also demonstrated its advantages over bioclimatic approaches (Reu et al., 2010; Reu et al., 2011). Instead of plant functional types, the adaptive DGVM of Scheiter and Higgins (2009) and Scheiter et al. (2013) was based on traits. The novelty of this adaptive DGVM lay in the process-based and adaptive modules for phenology, carbon allocation and fire within an individual-based framework. This allowed the vegetation component in the model to adapt to changing environmental conditions and disturbances. Such adaption is not possible in models based on static functional types.

As our review demonstrates, DGVMs provide a good example of the shift from plant functional types towards functional traits (Yang et al., 2015) (e.g. compare Smith et al. (2001) and Holzwarth et al. (2015)). Moreover, individual-based modelling is increasingly applied to represent individual interactions and foster the dynamic nature of DGVMs.

1.6.Trait-based models of plant invasions

Trait-based modelling was frequently used to study invasion (Supplementary Material. Tab. 1). The frequency of this use probably arises because it is a common goal of invasion biology to identify traits that can be used to predict future invaders. This goal was particularly common among statistical models (Otfinowski et al., 2007; Herron et al., 2007; Küster et al., 2008). The individual-based models of plant invasion focused on understanding the invasion process incorporating, for instance, disturbance (Higgins and Richardson, 1998), or herbivory (Radny and Meyer, 2018). These models have different regional and taxonomic foci including pine trees in the southern hemisphere (Higgins and Richardson, 1998), exotic plants in North America (Otfinowski et al., 2007; Herron et al., 2007), invasion success in Germany (Küster et al., 2008), and establishment success as the combined effect of functional traits and biotic pressures (Radny and Meyer, 2018).

However, these models have yet to yield a universal set of traits that characterize potentially invasive species. Future trait-based invasion models should address all the processes and interactions relevant to the system being studied. This might be facilitated by individual-based modelling approaches.

1.7.Trait-based models of ecosystem services

Ecosystem service models are usually built with a management goal. Thus, they benefit from including plant functional traits because functional traits are aggregate measures that can more easily be targeted by ecosystem management than species. Most models in this section were statistical models (Supplementary Material. Tab. 1), often in the form of generalized linear models (Diaz et al., 2007; Lavorel et al., 2011), whereas three models were equation-based. According to Lavorel et al. (2011), ecosystem properties were better captured by models including spatial variation in environmental variables and plant traits than by land-use models. Variation across the landscape in the community-weighted mean of four traits and their functional divergence were modelled with generalized linear models (Lavorel et al., 2011). Compared to remote sensing, this trait-based statistical modelling approach better reflected the process of land use that underlay ecosystem properties (Homolova et al., 2014). Another model investigated the influence of plant and microbial functional traits on grassland ecosystem services (Grigulis et al., 2013). Based on Lavorel et al. (2011) and Grigulis et al. (2013), future ecosystem services were estimated for three socio-economic scenarios (Schirpke et al., 2017). The approach demonstrated that ecosystem services were potentially highly resilient. In two other semimechanistic models, functional traits facilitated the scaling-up of well-understood functional trade-offs from the organismal to the ecosystem level (Lamarque et al., 2014).

Equation-based models of ecosystem services ranged from assessing the sensitivity of ecosystem services to land-use change (Quétier et al., 2007), determining the vulnerability of pollination services (Astegiano et al., 2015), and evaluating the management of mown subalpine grasslands (Lochon et al., 2018).

Based on the examples in this section, trait-based models demonstrate great potential for solving applied questions in ecosystem studies as well as for those involving scaling.

1.8.Trait-based models on interactions between plants and other organisms

A few trait-based models did not focus purely on vegetation and interactions among plants but also included the interactions of plants with other groups of organisms. These models were partly conceptual and partly equation-based (Supplementary Material. Tab. 1). For example, the effects of biodiversity on multispecies interactions and cross-trophic functions were described in a trait-based bottom-up framework (Lavorel et al., 2013). This conceptual model was linked to a statistical structural equation model which demonstrated that high functional and interaction diversity of animal mutualists promoted the provisioning and stability of ecosystem functions. In another case study, avian body size was identified as an important response trait related to the susceptibility of avian seed dispersers to disturbance by humans (Schleuning et al., 2015). A conceptual model (Pöyry et al. 2017) reconstructed how the effects of soil eutrophication cascade to higher trophic levels across a range of plant-herbivore interactions. The model was evaluated based on butterfly and moth data. The authors suggested that a major future trend will be the increased dominance of insect species that are large, dispersive dietary generalists over those preferring oligotrophic environments. These conceptual models await further testing by being converted into equation- or code-based models and the empirical testing of the predictions of these models.

There were also four equation-based models in this section addressing nutrient competition in an earth system model (Zhu et al., 2016), trade-offs of defensive plant traits in plant-herbivore interactions (Mortensen et al., 2018), plant-soil feedback mediated by litter and microorganisms (Ke et al., 2015), and three-way interactions between a plant, a herbivore and a beneficial microbe in the context of biological invasions (Jack et al., 2017).

2. Trait-based modelling of animals in terrestrial ecosystems

Animals are underrepresented among papers on the trait-based modelling of terrestrial ecosystems, whereas trait-based models of marine ecosystems which included animals abounded. There are about three times as many marine as terrestrial papers including animals in our review (see section 3. Trait-based modelling in aquatic ecosystems). The reason for the imbalance may lie in there being many different behaviours, feeding strategies and morphologies among terrestrial animals (Scherer et al., 2016), making it hard to define common functional traits. Nevertheless, 23 papers covered trait-based modelling of animals in terrestrial ecosystems. There were twice as many equation-based models as individual-based models and almost as many statistical models as equation-based ones (Supplementary Material. Tab. 1). As the following studies show, these models cover a broad range of topics, including population dynamics and survival analysis, predator-prey and host-pathogen interactions, species distributions, and community assembly.

Population dynamics was more frequently investigated in trait-based modelling studies of animals than plants in terrestrial ecosystems. We included here pure population dynamics studies, but also other studies at the population level, namely time-to-detection studies, survival analysis, vulnerability analysis, home range determination, and a study of eco-evolutionary dynamics. For example, the effect of functional traits on the population dynamics of mites was studied with equation-based integral projection models (Smallegange and Ens, 2018), drawing on the dynamic energy budget theory better known from aquatic studies (see section 3. Trait-based modelling in aquatic ecosystems). According to an individual-based model, the population dynamics of meerkats depend on intraspecific variation in body mass (Ozgul et al., 2014). In a similar but equation-based model trait-demography relationships were studied to identify the mechanism underlying population fluctuations (van Benthem et al., 2017). Trait-based models of population dynamics investigated the responses of populations to environmental changes (Santini et al., 2016) and to perturbations (Ozgul et al., 2012). Using an approach similar to that of the time-to-detection studies mentioned in section 1.2 (Trait-based models of species distributions), Schlossberg et al. (2018) modelled detectability for ten mammal species. This model was based on species traits such as body mass, mean herd size and color and employed a statistical approach based on conditional likelihoods. An example of a trait-based survival model was the prediction of bat survival based on reproductive, feeding, and demographic traits such as age, sex, and type of foraging (Lentini et al., 2015). A trait-based vulnerability index was applied to subarctic and arctic breeding birds in a statistical model constructed around MaxEnt and CATs (Hof et al., 2017). We found three further individual-based models: Scherer et al. (2016) explored the response of bird functional types to climate and land-use change; Buchmann et al. (2011) used the methodology to predict the home range and the spatial body mass distribution of species in terrestrial mammal communities in fragmented landscapes; And, for a theoretical study of eco-evolutionary dynamics, Pontarp and Wiens (2017) simulated the evolutionary radiation of a clade across several habitats with differing environmental conditions.

Predator-prey interactions were considered from a functional perspective relatively early on in the history of trait-based approaches, i.e. when generalist and specialist functional types were introduced into modelling (Hanski et al., 1991). Functional traits are a much more recent characteristic of predator-prey modelling studies, e.g. in a general additive model of beetle predation with eight predator traits and four prey traits (Brousseau et al., 2018).The novelty of these models is that the combination of functional traits and phylogeny overcome the limitations of purely descriptive approaches. Where predator-prey interactions are combined into a food web model, body size is often the central trait. This was the case in an allometric trophic network model that explicitly featured intra- and interspecific interference including predator-prey interactions in beetles and spiders (Laubmeier et al., 2018). Pathogen-host interactions resemble predator-prey interactions in many ways as demonstrated by the interactions of amphibian species and their fungal pathogens. In this case, the interactions were modelled with a statistical approach investigating the predictive power of traits related to phylogenetic history, habitat use, and life history traits (Gervasi et al., 2017). Individual- and trait-based movement models are very powerful when it comes to scaling-up across several levels of organization. This feature was exploited in an individual-based model that scaled up from individual movement and behavior to metacommunity structure (Hirt et al., 2018).

Species distributions and species niches were modelled for the cane toad with a statistical approach (Kearney et al., 2008; Kolbe et al., 2010) and for endotherms (Porter and Kearney, 2009) and ants (Diamond et al., 2012) with an equation-based approach. For the endotherms and the ants, biophysical principles were used to link variation in functional traits with environmental data to predict thermal niches (Porter and Kearney, 2009; Diamond et al., 2012).

Community assembly and dynamics were studied with equation-based models which, for example, accounted for spatial variation in community structure with a multi-region multi-species occupancy model (Tenan et al., 2017), investigated irreversible changes in community structure in a consumer-resource model (Haney and Siepielski, 2018); and used trait-mediated interactions to analyze invasiveness and invasibility of ecological networks (Hui et al., 2016). The need to include such process-based components in community assembly models was emphasized by Pontarp and Petchey (2016).

The models in this section show a great diversity of applications for the trait-based modelling of animals in terrestrial ecosystems. However, each topic is represented by one or very few studies. This indicates that there is scope for more applications in these and related fields, regardless of model type.

3. Trait-based modelling of aquatic ecosystems

According to Litchman and Klausmeier (2008), the trait-based approach was first used for modelling aquatic ecosystems in a model of a phytoplankton community by Ramon Margalef (Margalef, 1978). Nevertheless, Follows and Dutkiewicz (2011), in their analysis of the state of the art of marine ecosystems, concluded that trait-based approaches were just then (i.e. in 2011) starting to be used in marine ecosystem models. The conflict between these two statements demonstrates different understandings of what a trait-based model is.

In addition to the research papers, we also found that reviews on trait-based approaches for studying aquatic ecosystems are not uncommon. Therefore, we shortly summarize the most important reviews here. Litchman et al. (2010) reviewed trait-based approaches applied to phytoplankton and revealed a new trend – to look at a trait and the phylogenetic structure of communities simultaneously. This trend, in combination with adaptive trait models, makes it possible to predict trait evolution. In another review on trait-based approaches for studying phytoplankton, Bonachela et al. (2016) showed that it is also possible to successfully use trait-based models to identify and compare possible survival strategies described by a set of functional traits. These models typically include trade-offs between traits such as cell-size and resource allocation.

In the following sections, we first review aquatic trait-based models including those for fish and then those focusing on plankton. There are few trait-based modelling studies of other aquatic realms, which are briefly covered in this paragraph, e.g. studies of bivalve species distribution models (Montalto et al., 2015), inland freshwater communities (Gardner et al., 2014), coral reefs (Edmunds et al., 2014; Madin et al., 2014), a pelagic microbial mixotrophic food web (Castellani et al., 2013), marine benthic communities (Alexandridis et al., 2017), diatoms in peatlands

(Hagerthey et al., 2012) or trace metal concentrations in invertebrates (Hug Peter et al., 2018). Traits were usually the inputs for models but in one case were outputs (Rinaldi et al. 2014). In that paper, mechanistic functional trait models were used to predict life history traits such as body size and fecundity of shellfish in lagoons. The fact that traits were used both as inputs and outputs for models emphasizes the difference between effect traits and response traits (Fig. 1), two concepts introduced earlier to terrestrial ecological theory (Lavorel and Garnier, 2002).

3.1.Trait-based models including fish

Trait-based modelling is widely applied to modelling fish communities. Of those models, the overwhelming majority were equation-based models (Supplementary Material. Tab. 1). There were only four individual-based models (Brochier et al., 2013; Houle et al., 2013; O'Farrell et al., 2015; Huebert et al., 2018), one statistical model (Howeth et al., 2016) and one statistical and conceptual model (Bennett et al., 2016) that generalized the trilateral life history model by Winemiller and Rose (1992). This prevalence of equation-based models may be due to the fact that aquatic ecosystems are more homogeneous than terrestrial ecosystems and therefore lend themselves more naturally to the continuous character of most equation-based models.

Size appears to be the main structuring trait in aquatic ecosystems because size influences the most important organism processes, such as foraging, growth, and reproduction. For example, fish fall into different trophic levels when young than when old. Because size usually correlates with age, trophic level in fish is linked to body size. Size structure prevails up to the community level in marine ecosystems. This fact prompted the formulation of the community size spectrum (Guiet et al., 2016b). The regularity of the community size-spectrum is expressed in the constancy of total ecosystem biomass within "logarithmically equal body size intervals" (Guiet et al., 2016b). Thus, community size-spectrum models represent the ecosystem using two parameters – the slope and the intercept of the community size-spectrum. This type of model mechanistically addresses the role of species diversity via the introduction of the trait size (Hartvig et al., 2011; Maury and Poggiale, 2013; Guiet et al., 2016a). In these models, community dynamics emerge from individual interactions. Trait-based size-spectrum models were developed with a range of goals, including to study the benefit to fish of the reproductive strategy of producing many small eggs or to analyze coexistence between species and link it to maturation sizes and predator-prey size ratios (Hartvig and Andersen, 2013). Trait-based size-spectrum models also demonstrate the impact of fishing on species composition (Shephard et al., 2012), i.e. that fishing out larger individuals shifts the size spectrum towards the dominance of smaller species.

Originally, Andersen and Beyer (2006) introduced a size- and trait-based model to estimate fishing effects at the ecosystem level. In this model, every individual was characterized by two features: body size and asymptotic body size. This model was later expanded (Houle et al., 2013; Zhang et al., 2013; Jacobsen et al., 2014; Jennings and Collingridge, 2015).The asymptotic body size was defined as a main trait because it is the basis for applying life history theory to estimate size at maturity and reproductive output (Jennings and Collingridge, 2015). The indirect influence of fishing on community structure was revealed by an extended version of the initial model considering entire life histories and individual energy budgets (Kolding et al., 2016). Another size- and trait-based model included individual interactions in the form of competition and predation and individual processes such as encounters, growth, mortality and reproduction (Jacobsen et al., 2014). A similar model was developed by Andersen and Pedersen (2010) and Andersen and Rice (2010). In this model, all basic processes at the community level emerged directly or indirectly from individual-level processes. To answer the question how to maximize fishing yield under a certain conservation constraint, Andersen et al. (2015) suggested a conceptual size- and trait-based model. An adaptation and a dynamic version of the model of a theoretical ‘fish community’ (Pope et al., 2006), based on classical multi-species fishery models and community size spectrum models, was reconsidered by Andersen and Pedersen (2010) and Andersen et al. (2015) in the framework of a trait-based approach. A similar model to describe population structure based on the size of the organisms was presented by Hartvig et al. (2011) and Hartvig and Andersen (2013). This model was a product of the synthesis between traditional unstructured food webs, allometric body size scaling, trait-based modelling, and physiologically structured modelling (Hartvig et al., 2011). These approaches were further developed into more complex food web models that showed that climate change effects are highly unpredictable (Zhang et al., 2014; Zhang et al., 2017). Using Approximate Bayesian Computation in their food web model, Melián et al. 2014 highlighted the importance of accounting for intraspecific variability when investigating species coexistence. Such combinations of traditional approaches with novel modelling techniques provides a promising new approach to the study of size-structured food webs.

Other examples, which we briefly describe in this section, covered the topics of marine biodiversity exploitation, marine community modelling including seal species (Houle et al., 2016), adaptive behavioral responses, fish-mesozooplankton interactions, fish-jellyfish interactions and freshwater fish modelling. Marine biodiversity exploitation was studied with an object-oriented individual-based model (Brochier et al., 2013). This model incorporated four main categories of life history depending on which part of the life cycle fish spent in the estuary studied. To reduce the computing power needed, Brochier et al. (2013) used a super-individual approach (Scheffer et al., 1995) with one individual representing a fish school. They also created 15 groups of ecologically similar model species, each representing a group of real species (Ecoutin et al., 2010). Each group contained one or more super-individuals with similar trophic position and ecological traits. Persistent spatial interactions and cascading behavioral interactions were revealed in a marine ecosystem model with detailed size structure and life cycles of mesozooplankton and fish (Castellani et al., 2013). This model became a step towards a mechanistic and adaptive representation of the upper trophic levels in ecosystem models. In this model the main trait was size at maturation. Based on a traditional ocean ecosystem model including chemistry, phytoplankton, micro- and mesozooplankton (Schrum et al., 2006), a new model version replaced the compound group of mesozooplankton by a developmental stage- and species-specific matrix and introduced fish feeding on mesozooplankton (Castellani et al., 2013). A general mechanistic food web model of fish-jellyfish competitive interactions was based on the feeding traits of fish and jellyfish populations (Schnedler-Meyer et al., 2016). The model also incorporated, in addition to feeding traits, elemental composition, allometric scaling of vital rates, locomotion, and life-history traits. The model predicted fish dominance at low primary production and a shift towards jellyfish with increasing productivity, turbidity and fishing.

A few freshwater studies included one on the simulation and screening of freshwater fish invasion which were tackled with the help of trait-based statistical models that used classification trees (Howeth et al. 2016). Another example investigated temperature-dependent colonization and extinction rates of darter fish in a body size-centered dynamic occupancy model (Shea et al., 2015). Stochastic integral projection models were not only used for plants and terrestrial animals, but also in a trait-based modelling study of pike in a freshwater ecosystem (Vindenes et al., 2014).

On the basis of these publications, we believe there is no question that the long and successful history of trait-based modelling including fish centered on size spectrums will continue. Future applications are likely to further improve model predictions by following the increasing number of examples where traits other than size are also included in the models.

3.2.Trait-based models focusing on plankton

As with fish, it is also possible to explicitly model plankton in a trait-based way (Follows et al., 2007; Litchman et al., 2007; Bruggeman and Kooijman, 2007; Kiørboe, 2011). The models used are predominantly equation-based models, as they were for those including fish discussed in the previous section (Supplementary Material. Tab. 1). Similarly, the models considered size as the main functional trait. Only two models were supplemented with individual-based modules (Clark et al., 2013; Pastor et al., 2018), two adopted a statistical approach (Litchman et al., 2007; Terseleer et al., 2014), and one a conceptual approach (Glibert, 2016). The great majority of these models targeted the ecosystem level. This focus on ecosystems is possibly also one of the reasons for the domination of equation-based approaches because such approaches are particularly well suited to capture ecosystem fluxes.

The marine ecosystem model by Follows et al. (2007) became a starting point for the development of a number of trait-based models in microbial ecology and plankton research. This is probably because it successfully reproduced the observed global distributions and community structure of the phytoplankton. The model included a diverse phytoplankton community that was described by a set of physiological traits defined by field and laboratory data with related trade-offs.

Phytoplankton cell size, and especially the drivers of small cell size, were addressed with a trait-based model of cellular resource allocation (Clark et al., 2013). This model considered a three-way trade-off between cell size, nutrient and light affinity, and growth rate. It was developed as a combination of a classic nutrient-phytoplankton-zooplankton model and ‘cost-benefit’ models. The trait-based approach was supported by individual-based modelling such that individual life histories gave rise to the evolutionary dynamics of the whole system. This bottom-up approach allowed missing ecosystem processes to be derived from model data. Where many individuals are similar, as in the general case of plankton and the specific case of this model (Clark et al., 2013), super-individuals can be created that represent groups of individuals with similar traits. As in other super-individual applications (e.g. Brochier et al., 2013 in section 3.1. Trait-based models including fish), this approach reduces computing power requirements. Plankton cell size and the mechanisms underlying observed biogeographical difference in cell size were also studied by Acevedo-Trejos et al. (2015) and Acevedo-Trejos et al. (2018). Their models considered trade-offs between cell size and nutrient uptake, zooplankton grazing, and phytoplankton sinking. Macroscopic system properties such as total biomass, mean trait values, and trait variance were studied with a continuous trait-based phytoplankton model (Chen and Smith, 2018). This model was developed as a sub-module of a larger model the goal of which was to simulate ocean dynamics. The model produced realistic patterns of phytoplankton mean size and size diversity. Co-evolution of traits with respect to chromatic and temperature adaptation was studied with a trait-based ecosystem model (Hickman et al., 2010). Trait-based models with adaptive traits were compared to trait-group resolving models in a study of phytoplankton communities in partially mixed water columns (Peeters and Straile, 2018).

Disease transmission in multi-host communities was the focus of a multi-generational plankton-based model that considered epidemiological traits such as foraging or exposure rate, conversion efficiency, susceptibility, virulence and spore yield (Strauss et al., 2015). This model succeeded in improving the mechanistic and predictive clarity of the dilution effect by connecting a reduction in diluter species with the increase in disease risk. The dilution effect probably explains links between host communities and transmission. In their model of virus infection of plankton based on life-history traits, Beckett and Weitz (2018) found that lysis rates were driven by the strains with the fastest replication and not those with the greatest abundance.

Compared to models with better resolved species-specific representations of physiological processes, improved representation of biodiversity was suggested in a biodiversity-based marine ecosystem model (Bruggeman and Kooijman, 2007). The model was based on a system of infinite diversity in which species were defined by continuous trait values for light-harvesting investment and nutrient-harvesting investment. The traits chosen affected all parts of the metabolism forming a trade-off between harvesting and net growth. Based on this model and a model by Bruggeman (2009), a trait-based model was developed to include mixotrophy, succession and evolution of unicellular planktonic organisms and to predict optimum trophic strategies of species under changing environmental conditions (Berge et al., 2017). This model contained three key resource-harvesting traits: photosynthesis, phagotrophy and inorganic nutrient uptake. To distinguish two different mixotrophic strategies, Chakraborty et al. (2017) extended the model by Berge et al. (2017) by explicitly incorporating cell size and introducing a pure heterotrophic strategy.

Different aspects of plankton ecosystems were recently scrutinized at greater detail, including trait-based ecosystem function predictions for a global lake data set (Zwart et al., 2015), biological interactions, species extinctions, nutrient uptake kinetics, and some theoretical properties as well as more applied implications of plankton models. Interactions were investigated in the form of temperature dependence of competition of phytoplankton species (Bestion et al., 2018) and of host-pathogen interactions between zooplankton and a fungal pathogen, which seem to be mediated by host foraging under climate warming (Shocket et al., 2018). Species extinctions strengthen the relationship between biodiversity and resource use efficiency (Smeti et al., 2018) based on a model studying phytoplankton succession (Roelke and Spatharis, 2015a) and assemblage characteristics (Roelke and Spatharis, 2015b). Based on insights from a size-based model on nutrient uptake kinetics of phytoplankton, Smith et al. (2014) emphasized that plankton ecology benefits from mechanistic trait-based models that account for physiological trade-offs. In a theoretical exercise, Gaedke and Klauschies (2017) showed that the knowledge of the shape of observed trait distributions is beneficial for the elegant analysis of aggregate plankton models, because it allows for data-based moment closure. With a new scale-invariant size-spectrum plankton model, Cuesta et al. (2018) explored the constancy of the relationship between biomass density and logarithmic body mass across scales. Finally, there were examples of trait-based plankton models that explicitly addressed applied questions such as the management of harmful algal blooms (Glibert, 2016; Follett et al., 2018).

The vibrant field of trait-based plankton models is a good example of how trait-based approaches can inspire ecosystem modelling. The relatively homogeneous conditions in aquatic environments lead to the dominance of one trait – size – over any other trait or any taxonomic category in explanations of community and ecosystem processes and patterns. Thus, trait-based approaches are more suitable than species-based approaches to model aquatic communities and ecosystems.

4. Trait-based models on microorganisms and soil decomposers

Microorganisms and soil decomposers are relatively new subjects of trait-based modelling and are still often represented as functional groups or functional types rather than traits. Therefore, the following seven examples also included classifications into functional groups. As in models of aquatic ecosystems, the models of microorganisms and soil decomposers were built around the key trait body size and were predominantly equation-based (Supplementary Material. Tab. 1) with the exception of one statistical model (Van Bellen et al., 2017). In terms of scale, all but one model in this section operated at the community level. This one exception targeted continental to global scales (Wieder et al., 2015). Such scales are surprisingly large for a model including microbial processes.

Nitrification by ammonia-oxidizing bacteria, ammonia-oxidizing archaea and nitrite-oxidizing bacteria was considered in a mechanistic trait-based model (Bouskill et al., 2012). It was based on traits connected to the enzyme kinetics of nitrite. Another version of this model simulated the influence of global change on ecological niches of soil nitrite-oxidizing bacteria types (Le Roux et al., 2016). This trait-based model grouped nitrite-oxidizing bacteria into a few functional groups. The authors demonstrate that this approach was successful because three main bacteria functional types expressed contrasting responses to environmental changes.

Using functional types can be inferior to using functional traits. This was demonstrated by another microbial model that addressed time lags in the enzymatic response of denitrifying microorganisms to changes in substrate concentration, including the interactive dynamics between enzymes and nutrients (Song et al., 2017). This model linked community traits with functional enzymes, not species or functional guilds as in previous studies (Taffs et al., 2009; Bouskill et al., 2012). With organisms whose multiple functions overlapped with one another, the guild-based (functional type) approach failed to properly represent these organisms. Enzyme- and thus trait-based implementations therefore provide tools for scaling up biogeochemical functions to the community level without involving the dynamics of individual species or their guilds.

A physiological trade-off between the traits of drought tolerance and carbon use efficiency was at the core of two modelling studies on soil decomposition(Allison, 2012; Allison and Goulden, 2017). In these models, the decomposition submodel of enzymatic traits was derived from the phytoplankton model by Follows et al. (2007) to predict litter decomposition rates in soil. The sensitivity of microbial traits, community dynamics, and litter decomposition to variation in drought tolerance costs was quantified in an updated model (Allison and Goulden, 2017). The model implied that, for the Mediterranean climate system, seasonal drought was a more important environmental filter than reduced precipitation during the wet season. These models were examples of successful exchange between disciplines.

There were few general trait-based models that are applicable to terrestrial and marine ecosystems alike. One of the rare cases, Harfoot et al. (2014), was a general ecosystem model based on eight traits thought to be the most important for determining rates of ecological processes. These traits were realm, nutrition source, mobility, leaf strategy, feeding mode, reproductive strategy, thermoregulation mode, and body mass. This model benefited from a coupled individual- and equation-based approach. The equation-based approach was applied to autotrophs and the individual-based one to all other organisms. In this way, ecosystem structure and function emerged from interactions at the individual level. However, the individuals in this model were in fact groups or cohorts of organisms (the super-individual approach, Scheffer et al., 1995). This model showed that highly complex models require the combination of different modelling approaches including simplification tools such as the super-individual approach.

All in all, the variety of models in all sections demonstrates that trait-based modelling approaches are useful tools that are able to facilitate modelling and improve the predictive power of model outcomes across taxa and disciplines. In this variety of models, we nevertheless see a number of trends. One of these is a shift from functional types to functional traits. There is also a search for generalizations across organisms with similar functions and a few examples that scale-up processes from the local to the global level. Techniques that appear to be useful, especially in individual-based models, are the super-individual approach and the incorporation of intraspecific trait-variability. Nevertheless, it seems clear from both empirical and modelling studies that the development of trait-based models did not produce a universal set of traits. Therefore, researchers should instead select traits according to the research question and strategies of the organisms under investigation.

Discussion and Conclusions

Based on our systematic review, it is clear that trait-based approaches are as valuable in modelling studies as they were earlier in empirical studies. They facilitate parameterization and scaling-up of models as well as the generalization of their results. Despite some inconsistencies in the terminology of trait-based studies, trait-based models have been implemented widely for different groups of organisms and ecosystems, in different model types, and for achieving a broad range of aims (See Supplement Material. Table 1). We observed productive exchange of trait-based modelling concepts and techniques, especially between vegetation ecology and other disciplines, and argue that this should be intensified and extended to more disciplines in the future.

Inconsistencies in terminology within trait-based approaches mainly originate from the unclear differentiation between functional types and functional traits as categories for grouping organisms. For example, Jeltsch et al. (2008) suggested three strategies for applying plant functional type approaches in modelling, where the “functional trait” strategy was one of them - together with “functional group” and “functional species” strategies. Jeltsch et al. (2008) also pointed to the fact that it was not possible to easily separate these strategies from each other. In any case, none of the modelling papers explicitly use the classification by Jeltsch et al. (2008). If researchers did so, it would certainly clarify terminology.

In our review, we distinguish between models applying functional types and functional traits, following the shift in the theoretical literature from describing vegetation types to describing vegetation function (Moore and Noble, 1990; Webb et al., 2010) reflected in the development of DGVMs (Van Bodegom et al., 2012). The inconsistent use of terminology biases systematic reviews that use key words in search engines. For example, some papers state that they implement a novel trait-based modelling approach although in practice they use functional types. Other papers clearly consider well-developed trait-based models but are not found using that key word (e.g. Seifan et al., 2012). Some studies develop crucial theoretical frameworks or methods that are probably useful for future model development and validation but do not themselves use any model. They advocate, for example, incorporating arbuscular mycorrhizal fungi in trait-based models (Treseder, 2016), including community trait distributions to overcome the challenge of estimating single traits (Edwards, 2016), considering intraspecific variability (Burton et al., 2017), or using remotely sensed data to parameterize trait-based models (McDowell and Xu, 2017). Nevertheless, not all facets of trait-based modelling seem to be sufficiently well known in all fields of ecology to warrant correct attribution of a study to this method. Thus, unambiguous terminology requires more attention in the future. Adhering to a consistent terminology will also simplify the exchange of trait-based concepts between different disciplines.

Exchange of ideas on implementing trait-based models occurred between the fields of vegetation ecology, marine ecology, limnology, animal ecology and microbial ecology. This exchange already started with the first trait-based approaches from plant functional ecology (Lavorel & Garnier, 2002; Wright et al., 2004) being adopted by animal studies of bats (Lentini et al., 2015) and birds (Scherer et al., 2016). In ecological modelling, ideas were transferred from phytoplankton research (Follows et al., 2007) to a litter decomposition model (Allison, 2012). We encourage the expansion of such exchange of trait-based modelling approaches between disciplines. These exchanges are likely to be most promising for cases where different organisms have similar functions in their communities.

Trait-based models have been implemented for answering a number of ecological research questions from basic and applied ecology. Basic ecological questions that were addressed with trait-based models included goals such as identifying which mechanisms drive plant growth, how populations develop over time and space, how communities assemble and biodiversity can be explained, as well as which factors influence community dynamics. Applied trait-based modelling studies investigated biological invasion conditions and consequences, responses of ecosystems to climate and land-use change, conservation and management planning, as well as the evaluation of ecosystem services. We see potential for the reinforcement of trait-based modelling approaches in areas such as the assessment of ecosystem services, invasion prediction and prevention, biodiversity studies, connection to demographic approaches (Salguero-Gómez, Violle, Gimenez, & Childs, 2018) and, especially, the prediction of community and ecosystem responses under climate and land-use changes.

Many model types were employed to implement trait-based approaches. The greatest proportion was equation-based models. The next greatest proportion was that of statistical models that describe patterns and demonstrate correlations between, for example, functional traits and environmental filters. The combination of trait-based approaches with process-based modelling, as one subcategory of equation-based modelling, is particularly interesting because the detailed representation of physiological processes in process-based models may not at first be compatible with the aggregated approach of trait-based models. However, once united in a model, it is possibly just these different perspectives on a study system that, by complementing each other, will overcome the limitations from which the constituent approaches suffer when used in isolation (Scheiter and Higgins, 2009; Ali et al., 2015; Holzwarth et al., 2015). Combined process- and trait-based models are also able to capture a broader range of scales than each approach alone. Trait-based models are challenging to implement at extreme scales because the trait concept aggregates information too much for very fine-scale models and too little for very broad-scale models. However, traits are successfully integrated into process-based models that implement plant physiology at fine scales and into DGVMs and earth system models at global scales. Furthermore, we see a specific advantage to implementing trait-based approaches in individual-based models (May et al., 2009; Scheiter et al., 2013; Weiss et al., 2014; Pontarp and Wiens, 2017). It is possible to link traits directly to environment conditions and they are therefore considered to be an adequate tool for investigating community responses to environmental gradients (McGill et al., 2006; Webb et al., 2010). Combined with individual-based models (Grimm and Railsback, 2005; DeAngelis and Mooij, 2005), trait-based approaches have several advantages: They are able to offer sufficient flexibility to simplify the description of individuals, to capture plant-plant interactions at the individual level and thereby explain local community-level phenomena (Jeltsch et al., 2008), and to facilitate model parameterization based on trait data that are becoming increasingly available through databases (Weiss et al., 2014; Grimm and Berger, 2016). Trait databases will become an even richer source for trait-based modelling once they expand their current focus on plants to other organisms and start collecting and offering information on abiotic and biotic interactions as well as intraspecific trait variation (Funk et al., 2016).

We conclude that although trait-based modelling approaches have rapidly increased in ecology over the past twenty years, the potential advantages of the method have not yet been fully exploited. Key terms should be uniquely defined and the main concepts of the theoretical framework should be unambiguously clarified. We recommend developing and applying trait-based models to study community structure and dynamics and to attempt predicting the direction and intensity of community changes under global climate and land-use change. The complexity of such community-level studies is outweighed by the usually lower parameterization effort and more general model outcomes of trait-based modelling approaches. We recommend combining individual-based with trait-based approaches more frequently to benefit from the enhanced flexibility. Moreover, trait-based modelling enables the capturing of the feedback from communities to the environment, as long as the model includes the effects as well as the responses of ecosystems and traits. Trait-based modelling is therefore able to become an important contributor to a comprehensive understanding of community structure and dynamics under global change.

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