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PERSPECTIVES

How can we bring together empiricists and modellers in functional biodiversity research?

Florian Jeltsch[a,q,*], Niels Blaum[a], Ulrich Brose[b], Joseph D. Chipperfield[c], Yann Clough[d], Nina Farwig[e], Katja Geissler[a], Catherine H. Graham[f], Volker Grimm[g,a], Thomas Hickler[h], Andreas Huth[g], Felix May[a], Katrin M. Meyer[i], Jörn Pagel[a], Björn Reineking[j], Matthias C. Rillig[k,q], Katriona Shea[l], Frank M. Schurr[m], Boris Schröder[n], Katja Tielbörger[o], Lina Weiss[a], Kerstin Wiegand[i], Thorsten Wiegand[g], Christian Wirth[p], Damaris Zurell[a]

[a]*Department of Plant Ecology and Nature Conservation, University of Potsdam, Maulbeerallee 2, D-14469 Potsdam, Germany*
[b]*J.F. Blumenbach Institute of Zoology and Anthropology, University of Göttingen, Berliner Str. 28, D-37073 Göttingen, Germany*
[c]*Department of Biogeography, University of Trier, Universitätsring 15, D-54296 Trier, Germany*
[d]*Department of Crop Sciences, University of Göttingen, Grisebachstr. 6, D-37077 Göttingen, Germany*
[e]*Department of Ecology, Philipps-Universität Marburg, Karl-von-Frisch-Straße 8, D-35032 Marburg, Germany*
[f]*Department of Ecology and Evolution, Stony Brook University, NY 11789, USA*
[g]*Department of Ecological Modelling, Helmholtz Center for Environmental Research UFZ, Permoserstr. 15, D-04318 Leipzig, Germany*
[h]*LOEWE Biodiversity and Climate Research Centre (BiK-F) and Department of Physical Geography, Goethe-Universität Frankfurt, Senckenberganlage 25, D-60325 Frankfurt, Germany*
[i]*Department of Ecosystem Modelling, University of Göttingen, Büsgenweg 4, D-37077 Göttingen, Germany*
[j]*Biogeographical Modelling, BayCEER, University of Bayreuth, Universitätsstrasse 30, D-95447 Bayreuth, Germany*
[k]*Plant and Mycorrhizal Ecology Lab, Freie Universität Berlin, Altensteinstr. 6, D-14195 Berlin, Germany*
[l]*Department of Biology, Pennsylvania State University, University Park 16802, PA, USA*
[m]*Institut des Sciences de l'Evolution, UMR 5554, Université Montpellier 2, Montpellier Cedex 05, France*
[n]*Landscape Ecology, Technische Universität München, Emil-Ramann-Str 6, D-85354 Freising, Germany*
[o]*Department of Plant Ecology, University of Tübingen, Auf der Morgenstelle 3, D-72076 Tübingen, Germany*
[p]*Department for Special Botany and Functional Biodiversity, University of Leipzig, Johannisallee 21-23, D-04103 Leipzig, Germany*
[q]*Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), D-14195 Berlin, Germany*

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Abstract

Improving our understanding of biodiversity and ecosystem functioning and our capacity to inform ecosystem management requires an integrated framework for functional biodiversity research (FBR). However, adequate integration among empirical approaches (monitoring and experimental) and modelling has rarely been achieved in FBR. We offer an appraisal of the issues involved and chart a course towards enhanced integration. A major element of this path is the joint orientation towards the continuous refinement of a theoretical framework for FBR that links theory testing and generalization with applied research oriented towards the conservation of biodiversity and ecosystem functioning. We further emphasize existing decision-making frameworks as suitable instruments to practically merge these different aims of FBR and bring them into application. This integrated framework requires joint research planning, and should improve communication and stimulate collaboration between modellers and empiricists, thereby overcoming existing reservations and prejudices. The implementation of this integrative

*Corresponding author. Tel.: +49 331 977 1954; fax: +49 331 977 1930.
E-mail address: jeltsch@uni-potsdam.de (F. Jeltsch).

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research agenda for FBR requires an adaptation in most national and international funding schemes in order to accommodate such joint teams and their more complex structures and data needs.

Zusammenfassung

Ein verbessertes Verständnis von Biodiversität und ökosystemaren Funktionen als Basis für Ökosystemmanagement bedarf eines integrierten Rahmens für funktionelle Biodiversitätsforschung (FBR). Dabei gelingt es aber bislang nur selten, sowohl empirische Forschung (Monitoring und Experimente) als auch Modellierungsansätze erfolgreich zu integrieren. Wir beleuchten die Ursachen dieser Schwierigkeiten und zeigen Optionen für eine bessere Integration auf. Ein wesentliches Element ist dabei die gemeinsame Orientierung an einer fortlaufenden Überprüfung und Verbesserung eines theoretischen Rahmens der FBR. Diese gemeinsame Ausrichtung verknüpft das Testen von Theorien und konzeptionelle Verallgemeinerungen mit angewandten Fragestellungen, die sich am Schutz von Biodiversität und ökosystemaren Funktionen ausrichten. Hierbei können existierende Entscheidungs-Unterstützungs-Konzepte eine wichtige Rolle in der Verknüpfung und praktischen Umsetzung der verschiedenen Ziele der FBR spielen. Der vorgestellte integrierende Rahmen bedarf einer gemeinsamen Projektplanung und führt zu einer verbesserten Kommunikation und Zusammenarbeit zwischen Modellierern und Empirikern. Dabei werden bestehende Vorurteile und Berührungsängste überwunden. Die Umsetzung dieser integrierenden Forschungsagenda bedarf einer aktiven Veränderung nationaler und europäischer Förderpolitik mit dem Ziel gemeinsame Forscherteams mit komplexeren Strukturen und Datenerfassungsbedarfen zu ermöglichen.

Keywords: Biodiversity theory; Biodiversity experiments; Conservation management; Decision-making; Ecosystem functions and services; Forecasting; Functional traits; Global change; Monitoring programmes; Interdisciplinarity

Is there a problem?

Concern about the ongoing loss of biodiversity (e.g. Butchart et al. 2010; Perrings, Duraiappah, Larigauderie, & Mooney 2011) has underscored the need for a better mechanistic understanding of current patterns of biodiversity and ecosystem functioning, their sensitivity to global change, and the implications for management and conservationefforts (Dawson, Jackson, House, Prentice, & Mace 2011). As a result there is an increased focus on functional aspects of biodiversity research (e.g. Körner 2011; Perrings et al. 2011). Functional biodiversity research (FBR) is research aiming to identify *mechanisms* that (1) determine and drive *biodiversity dynamics*, and/or (2) determine the *effects of biodiversity changes* on ecosystem functions and services (for various functional approaches see Agrawal et al. 2007; Hillebrand & Matthiessen 2009; Jeltsch, Moloney, Schurr, Köchy, & Schwager 2008; McGill, Enquist, Weiher, & Westoby 2006; Schurr et al. 2012). Which aspect of 'biodiversity' is considered depends on the particular research question and may be expressed as species richness, species diversity or any measure of functional or genetic diversity (Devictor et al. 2010; Mason, Mouillot, Lee, & Wilson 2005; Schleuter, Daufresne, Massol, & Argillier 2010). If FBR is to be effective in advancing our understanding of the link between biodiversity and ecosystem function and our ability to forecast the impact of global change on biodiversity and functioning, three research approaches, monitoring, experiments and modelling, must be integrated.

Long-term biodiversity research and monitoring programmes provide a crucial data resource but have been recently criticized as being often ineffective because of poor planning and/or lack of focus (Lindenmayer & Likens 2010). This includes a lack of focus on the functional basis of biodiversity as well as quantifications of ecosystem functions (Agrawal et al. 2007; Jeltsch et al. 2008; Webb, Hoeting, Ames, Pyne, & Poff 2010). Forest inventories are a notable exception and have been employed successfully in functional biodiversity research to quantify both diversity and a set of specific functions (growth, mortality and recruitment, e.g. Vila et al. 2007).

More recently, biodiversity experiments have been designed to shed light on functional aspects of biodiversity (e.g. Reich et al. 2012). Such experiments create artificial diversity gradients by assembling new communities or by enriching or diminishing existing ones through addition or selective removal of taxa, respectively. However, given that biodiversity patterns are influenced by factors acting at multiple spatial and temporal scales resulting in a complex mix of causal relationships under natural conditions, experiments alone are often not sufficient to provide a comprehensive mechanistic insight into the drivers and consequences of biodiversity (Clark & Gelfand 2006). Also, experiments in simplified artificial systems are often difficult to relate to real-world ecosystems (Cadotte 2006; Clark & Gelfand 2006).

The third approach, modelling, is also an important tool because it permits the systematic exploration of the consequences of a large number of interacting factors. This allows development and testing of hypotheses on mechanisms, biodiversity patterns, and functional consequences (e.g. May, Grimm, & Jeltsch 2009; Meyer, Mooij, Vos, Hol, & van der Putten 2009; Miller, Roxburgh, & Shea 2011). Modelling plays a key role in extrapolating empirical findings in space and time and in providing quantitative projections of future trends under stable or changing environmental conditions (Jeltsch et al. 2008; Zurell, Jeltsch, Dormann, & Schröder 2009). It can be used to evaluate possible outcomes of management and conservation measures and can thus support decision-making (Dawson et al. 2011; Wintle et al. 2011). However, without an active exchange with empirical work to determine input parameters, quantify their uncertainty and validate model predictions, biodiversity modelling can be of limited utility for solving real-world problems (Keddy 2005).

In short, experimental manipulations are needed to sharpen our understanding of mechanisms, models are needed to compare the relative importance and interactions of these mechanisms under changing conditions, and monitoring is essential for testing the real-world relevance of the proposed mechanisms at large spatial and temporal scales.

The need for an integrative FBR approach which strives for mechanistic understanding and theory development and is oriented towards the conservation and management of biodiversity and ecosystem functions is widely acknowledged (Dawson et al. 2011; Ferrier 2011; Hillebrand & Matthiessen 2009; Lindenmayer & Likens 2010; Perrings et al. 2011) yet few successful examples exist (e.g. Driscoll & Lindenmayer 2012). Here we identify practical and conceptual obstacles to such integration, and propose a possible pathway to overcome them. We emphasize a synergistic orientation towards the continuous refinement of the prevailing theoretical framework for FBR as a critical strategy for the integration of the three classical research approaches, and suggest incentives and procedures, which can help in establishing an integrative framework for FBR.

Reasons for limited integration between monitoring, experiments and modelling

Current FBR is far from being integrated, mainly due to practical challenges and different scientific cultures of sub disciplines. Both underlying causes also lead to reservations between empiricists and modellers that hinder further integration and progress in functional biodiversity research (see Box 1).

Practical challenges. The inherent complexity of FBR requires a multitude of skills. Monitoring, experimental and modelling studies all tend to be challenging and time-consuming. Linking more than one approach is often more than a single scientist can handle and/or requires time frames greater than the 3–5 years that are typically provided by research grants. This calls for interdisciplinary research teams that require additional coordination and higher amounts of funding or more flexible project time frames. While such options already exist, e.g. in the European Union funding framework, they only cover a very small part of FBR research and are yet no role models of the right level of integration of monitoring, experiments and modelling. Moreover, researchers, i.e. typically doctoral students, have to identify and pursue distinguishable and publishable research topics. This often limits data 'production' to support the joint overarching research agenda. For example, data collections specifically needed for model parameterization (e.g. demographic data for specific species) are often not relevant or not interesting for the empirical part of the project. Also, there is typically a temporal gap between project start and data availability for modelling.

Different scientific cultures. Biodiversity research started as a rather loose combination of several disciplines (e.g. plant, animal or microbial ecology, evolutionary biology, taxonomy, microbiology). Each discipline has separate sub disciplines, traditions and research foci. Current teaching and research often remains within these separate disciplines without a clear orientation towards successful integration. For instance, there is little tradition of jointly teaching empirical and theoretical skills in biodiversity-related university courses. This limits communication between empirical and theoretical scientific groups and supports subjective reservations (see Box 1). Similarly, few universities currently offer specific courses in functional biodiversity modelling, and modellers often spend little or no time in the field learning about empirical approaches to biodiversity research. It is thus not surprising that on the one hand monitoring schemes and experiments are often designed without beneficial input from modellers and existing models and – on the other hand – that models in functional biodiversity research are often developed without consulting empiricists and without considering available data sets to ensure sufficient orientation towards real world data and validation (Keddy 2005). This is further complicated by the fact that much of the monitoring component of FBR is usually performed by non-academics (e.g., state or provincial land managers, non-profit organizations). In this regard, the divisions in schools of thought between academics and non-academics may be even more relevant than the rifts between the academic fields described above.

The role of theory for integrative FBR

We argue that a major obstacle to successful integration of empirical and modelling approaches in FBR frequently is the lack of a joint orientation of the disciplines towards an overarching theoretical framework. Theory has the potential to bridge disciplines, approaches, or systems as well as basic and applied functional biodiversity research. A clearer orientation towards a theoretical framework can thus facilitate generalization and broader applicability of research output. Thereby, a theoretical framework, here applied in the pluralistic sense of Pickett, Kolasa, and Jones (2007), is a system of conceptual constructs rather than one grand overarching theory. Thus, even though we keep referring to "theory" and "theory development" in the following, it should be noted that by this we not only refer to theories that make testable predictions but also powerful concepts which help addressing the key questions in FBR in a coherent

Box 1: Some unreflected reservations

An empiricist's reservations towards model(ler)s

- Simple, theoretical models lack realism.
- Complex models are almost as hard to understand as real systems.
- Data requirements:
- Models require too much and often unmeasureable data.
- Data needed to parameterize or validate models are often not interesting in themselves and do not contribute to empirical research.
- Models do not fulfil the expectations raised by modellers. It is debateable whether models can really be used to test hypotheses.
- Modellers use 'our' data and want to do the clever bit themselves.
- Modellers try to guide and dominate the empirical research.
- Additional modelling takes too much time.
- There are too many competing models for the same questions. A reduction and standardization is urgently needed.
- Model output:

(1) Output is often not sufficiently transparent. Complex equations or simulation routines and data manipulations lead to untestable results.
(2) Model experiments often do not have the same structure as real experiments.
(3) There is little we can learn from models that we cannot learn from observations and experiments in the real world.
(4) Presentation of model results is often technical and boring; empiricists are not directly addressed.

A modeller's reservations towards empirical research(ers)

- Some empiricists focus too much on immediate return on investment; there is an unwillingness to record data other than that which can be published immediately.
- Modelling output is not valued or not seen as a valuable outcome of research projects.
- There is a lack of interest/knowledge about the opportunities associated with mechanistic approaches, possibly due to a bias towards correlative statistical models.
- There is a lack of interest in integrating across taxa, systems or scales.
- Design of empirical work:
- Typically modellers are not involved in the monitoring or experimental setup. As a consequence:
  (1) Biodiversity monitoring schemes and experiments do not sufficiently allow for concurrent or subsequent mechanistic modelling.
  (2) Monitoring/experimental design does not allow for applied questions to be addressed because of disparities in spatio-temporal scales. For instance, empiricists may prefer to implement high-tech methods in a single or few locations rather than collecting low-tech data at larger scales.
  (3) There is a lack of standardization in the methodology.
- Data provision:
  (1) There often is an insufficient availability of and access to existing data.
  (2) Data resolution often is not adequate (summary statistics instead of raw data).
  (3) Often there is a lack of appropriate documentation of data and metadata.
  (4) There is no adequate knowledge about measurement errors to permit modelling of observational uncertainty.
- Many empiricists are not willing to sacrifice detail for generality.
- There is a lack of interest in general overarching theories that go beyond the specific study system.

and productive way (e.g. "resilience", "metapopulation", or "traits"). This system of conceptual constructs goes beyond methodological specifics and is an indispensable basis for any principal research aim (e.g. understanding, forecasting or management; Fig. 1). Clearly, it should be subject to continuous testing and refinement based on both empirical and modelling studies that are closely linked to observable phenomena.

There are several excellent examples of the decisive role of a joint theoretical framework in FBR. Some of these examples had the overarching goal of further development and maturation of ecological theory while other, more applied, examples

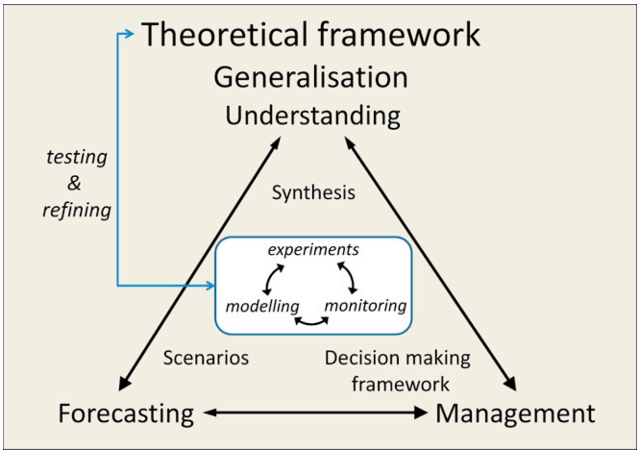

Fig. 1. Schematic description of how a joint orientation towards a theoretical framework in FBR can help to better integrate empirical and modelling research. Striving for generalization and theory refinement a joint theory orientation links both the primary research goals of understanding, forecasting, and conservation and the prevailing methods, i.e. experiments, monitoring, and modelling.

used an existing theoretical framework, e.g. to focus on conservation efforts. A prominent example is the development of metapopulation theory (Hanski & Gilpin 1997; Levins 1969) that, founded on field observations and a simple conceptual model (Levins 1969), stimulated decades of often integrative research including monitoring studies, experiments and conceptual as well as mechanistic models (Hanski & Gilpin 1997; Hanski & Ovaskainen 2000). This research built a solid theoretical basis for applied conservation efforts such as habitat networks and regional concepts of species conservation.

A more recent theoretical framework of specific relevance for FBR is the meta-ecosystem concept (Loreau 2010; Loreau, Mouquet, & Holt 2003), which explicitly couples spatially structured abiotic (e.g. nutrients or other resources) and community dynamics (Massol et al. 2011) on a landscape scale. Thus, it not only tackles mechanisms that generate or preserve biodiversity but also contributes to a better understanding of how biodiversity impacts ecosystem functioning. The latter aspect of FBR has recently gained more interest with a revival of trait-based ecology (Agrawal et al. 2007; Jeltsch et al. 2008; McGill et al. 2006; Webb et al. 2010). Trait-based approaches are not only used to better explain realized species' niches and predict future changes in biodiversity (e.g. Esther et al. 2010; Hillebrand & Matthiessen 2009; Jeltsch, Moloney, Schwager, Körner, & Blaum 2011; Jeltsch et al. 2008), but the focus on functional traits also provides a suitable basis to quantify biodiversity impacts on ecosystem functions and services (e.g. de Bello et al. 2010; Quétier, Lavorel, Thuiller, & Davies 2007). Though such trait-based approaches are assumed to open new avenues in linking models and empirical research, the integration of both approaches still lacks a more general theoretical framework (Webb et al. 2010). According to Körner (2011) the relative youth of functional plant ecology is the reason why applied questions in global change research tend to lack sound foundation in theory; applied questions came up before many of the more basic queries had been answered. We argue that a stronger orientation towards a joint theoretical framework regarding the functional consequences of biodiversity could also foster integration in the different aspects of FBR. It would have to be augmented by data collection and experiments on functional aspects (e.g. Hillebrand & Matthiessen 2009) linked with mechanistic modelling approaches (e.g. Grimm et al. 2005) and strategies that allow integration of processes and phenomena across scales (e.g. Körner 2011).

There is a growing emphasis on integrating correlative or even process-based models as an additional tool in otherwise empirical FBR in order to improve forecasts of specific species, communities or systems (e.g. Clark & Gelfand 2006; Ferrier 2011). Furthermore, it has been suggested that models should play a larger role in the design of empirical studies, e.g. by assessing alternative sampling schemes in simulation studies (Zurell et al. 2010) or by the direct evaluation of statistical models that identify data, which are most informative for prediction (Clark et al. 2011). However, without a clearer orientation towards an overarching theoretical framework that integrates basic and applied aspects we risk being stuck with a diverse bundle of research initiatives that only cover specific functional aspects of biodiversity research or specific systems, and lack comparability and generalization.

Clearly, integrative FBR also requires more specific improvements at the level of the joint research team, the individual participating researchers, and the funding organization (see Box 2 for a suggested checklist of key points to be fulfilled for a successful integrative project in FBR). However, we here specifically emphasize a joint effort for theory refinement as an integrating framework for FBR because it inherently involves a combination of methods (i.e., monitoring, experiments, modelling) and research goals (i.e., understanding, forecasting and management). It also requires conceptual clarity and statements of assumptions, a specified set of observable phenomena, and a variety of tools that allow for testing a broad range of hypotheses. All of this promotes and requires an active dialogue between empiricists and modellers.

Bridging the divide between FBR and management application

A theoretical basis in FBR does not only refer to development of ecological theory but should also be beneficial for informing conservation and management (Driscoll & Lindenmayer 2012). Realistically, FBR and subsequent recommendations for preservation of biodiversity, ecosystem functions and services need to be balanced against economic costs and interests. For this, we need an integrated analysis of the complex dynamics of ecological systems and effects of alternative management decisions or benefits of certain

Box 2: Elements of an ideal approach to an integrative FBR research project – a checklist

Research team

- Build a joint project team of FBR empiricists and modellers prior to project start.
- Identify research objectives based on thorough evaluation of existing theoretical framework in FBR.
- Identify most suitable system to study functional research objectives considering available data sets, models and constraints.
- Develop joint conceptual model oriented towards research objectives and questions to identify key knowledge gaps.
- Identify most suitable mix of approaches (monitoring, experiments, modelling) to fill these gaps.
- Identify data and information flow between different approaches and define procedures for possible modifications of research directions.
- Define iterative procedures to continuously refine joint conceptual model and relate research output to the theoretical framework.
- Identify which questions will be answered and which hypotheses will be tested by single or combined approaches (i.e. field measurements, experiments, modelling).
- Develop jointly monitoring and experimental designs that are informed by model predictions.
- Identify jointly the key processes, mechanisms and necessary output variables to be included in models.
- Identify needs and procedures for spatio-temporal extrapolations of empirical findings by modelling.
- Develop a strategy on how to integrate model and empirical findings for applied purposes (e.g. using decision-theory).
- Agree upon data sharing and publication policy.
- Jointly develop and manage the research project.

Modellers

- Identify type(s) of model(s) that is (are) most suited for research objectives.
- Carefully check applicability of existing models.
- Choose models that have parameters with high general data availability from public databases (thus saving the empirical counterparts time), that represent major axes of organismic variation, that retain the ‘trait meaning’ inside the model and that are sensitive towards the ecosystem functions under study.
- Fill (preliminary) data gaps with qualitative expert knowledge by interviewing empirical experts; conduct sensitivity analyses.
- Identify need for and approach to specific data gathering related to model parameterization and validation, e.g. functional trait measurements (McGill et al. 2006), demographic parameters (Jeltsch et al. 2008), pattern identification (Grimm et al. 2005).
- Provide model description that is understandable to non-modellers; communicate model assumptions, aims and outputs (Grimm et al. 2010).
- Refine model structure and parameterization with respect to first experimental and monitoring results.

Empiricists

- Aim for rapid data availability (including raw data), open data access to modellers and provide appropriate documentation of data and metadata.
- Determine appropriate sample size for rigorous testing of hypotheses and research questions
- Identify and quantify measurement errors.
- Identify what data are needed in models and evaluate if these can reasonably be collected within the framework of a research project
- Explain to modellers how data were collected and what they are intended to measure so that modellers can better integrate them into models.
- Adapt experimental and monitoring design with respect to first model results.

Funding organizations

- Provide specific calls for integrative FBR driven by theory testing and refinement.
- Provide funding opportunities for formation phase of integrative, interdisciplinary research teams.
- Build evaluation panels consisting of empiricists and modellers.
- Check if proposal is convincingly rooted in a theoretical framework for FBR.
- Check proposal for convincing procedures to test and refine theory in FBR (going beyond the testing of specific hypotheses).
- Provide funding for collecting, processing and storing of specific data and existing model code related to functional aspects.
- Provide stimuli for interdisciplinary training linking empirical and modelling disciplines.
- Provide easy tools/options to adjust research output as a consequence of modification of conceptual framework.

research and conservation efforts (Polasky, Carpenter, Folke, & Keeler 2011; Pressey, Cabeza, Watts, Cowling, & Wilson 2007; Schmolke, Thorbek, DeAngelis, & Grimm 2010).

Resilience concept. A promising candidate for an application-oriented theoretical framework in FBR is the resilience concept (Holling 1973). For example, this concept has been put forward by the Resilience Alliance (see www.resalliance.org, with linkages to decision makers and policy) to foster the understanding and adaptive management of socio-ecological systems. In this framework, *resilience* is the central concept defined as 'the amount of disturbance a system can absorb and still remain within the same state or domain of attraction' (Gunderson, Allen, & Holling 2009; Holling 1973). If changes exceed certain thresholds, the internal organization and structure collapses and the system changes to a different one, which usually has dramatic and irreversible effects on biodiversity and ecosystem function. For example, savannas can cope with a wide range of changes in rainfall patterns but if grass cover is reduced below a certain threshold (e.g. by overgrazing), the feedbacks between grass cover, fire, and tree establishment break down and the woody vegetation takes over (Jeltsch, Weber, & Grimm 2000). Clearly, the theoretical framework of resilience might mainly be interesting for a specific class of ecosystems which shows non-linear threshold dynamics. However, since degradation dynamics of most systems are unknown it is crucial to identify possible early warning signals before irreversible changes occur. The identification of such signals thus provides a key measure for sustainable management (e.g. Drake & Griffen 2010).

Decision theory. Another integrated framework is the decision-theoretic approach, that was, for example, put forward by the AEDA project (Applied Environmental Decision Analysis, www.aeda.edu.au). The decision-theoretic approach uses available empirical or expert information as well as mathematical models to make optimal decisions under clearly stated research or management objectives by balancing efforts and resources against overall benefit, and thus to maximize the chance of achieving the respective research and management objectives (e.g. Shea et al. 1998; Wintle et al. 2011). Such approaches of structured decision making are increasingly used for adaptive management and are, for example, strongly advocated by the US Department of Interior (Williams et al., 2009). Decision-oriented conceptual frameworks such as the resilience-based adaptive system management and the decision-theoretic framework, are excellent candidates for supporting integration within theoretical FBR frameworks. They allow researchers to ask targeted research questions that require a combined modelling and empirical approach to provide concrete conservation and management support.

Conclusion

Grounding functional biodiversity research (FBR) in a joint effort to test and refine the prevailing theoretical framework will significantly accelerate the urgently needed integration of monitoring (by academics and non-academics), experiments and models. With the help of existing decision-making frameworks, integrative FBR could combine the specific strengths of these approaches to enhance applicability of research results to specific conservation and management issues. However, such theory-driven integration is unlikely to occur by itself given existing divides between scientific disciplines and approaches, and incompatibility with short-term career goals and specific within-discipline achievements. It will need active steering and the provision of appropriate incentives by funding organizations, policy and higher education. A first step in this direction is a greater awareness and acknowledgement of the key role of theory development. This includes a systematic synthesis and evaluation of existing theories and approaches with regard to their potential to integrate FBR. Furthermore, incentives need to be put in place to encourage the adoption of such a framework in future FBR joint projects, including facilitating the research of individual workers and collaborative groups who make significant contributions to the entire framework.

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