repeatable among-individual differences in behaviour. This reflects a major current interest in animal personality research. However, we also acknowledge that metabolism is labile, which is one of the reasons why we highlight the need to consider covariation between energy metabolism and behaviour at different hierarchical levels (see also [8]). Careau and Garland additionally suggest that an important question is what explains among-individual covariance in these complex phenotypes, and whether they are part of coadaptations to environmental conditions. Again, this touches on outstanding questions from our Opinion, in which we point out the need for studies that explicitly consider feedbacks between energy metabolism and behaviour, and for studies exploring the development of correlations between energy metabolism and behaviour over ecological and evolutionary time scales.

Concluding remarks

Many of the points raised by Careau and Garland developed topics we highlighted in the Opinion as future perspectives. We take this as a promising sign, suggesting that despite terminological disagreements, we share common views on some of the key challenges in this field. Their response to our Opinion [1] and their earlier papers (e.g., [9]) point out the need for a better understanding of the mechanistic basis for individual differences in metabolism. We do not dispute this view, but we argue that an adaptive framework also has much to offer, particularly in terms of predicting the types of covariance structures that will be favoured by natural selection.

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Evolving away from the linear model of research: a response to Courchamp *et al.*

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The end of the linear model of ecological research

We agree with Courchamp *et al.* [1] that research in fundamental ecology must be promoted. However, they create an artificial dichotomy between 'applied' and 'fundamental' ecology, and suggest that applied ecology could jeopardize fundamental ecology (Figure 1, scenario 1). We disagree and see ecology as a young science whose future rests on better integration of all aspects identified by Courchamp *et al.* [1] as fundamental and applied. All domains of ecological sciences must be developed, and are intellectually rich, demanding inquisitiveness and curiosity.

The traditional model for science (known as the linear model [2]) considers a continuum where knowledge flows directionally from fundamental research to applied research and to decision-making. Basic research, as described by Courchamp *et al.* [1], is generated free of constraints towards real-world problem-solving, which is addressed later by applied research. Pielke [2] proposed the 'stakeholder model' as an alternative, where knowledge generation results from complex interactions and dynamic feedback between researchers and users of science. This new paradigm is

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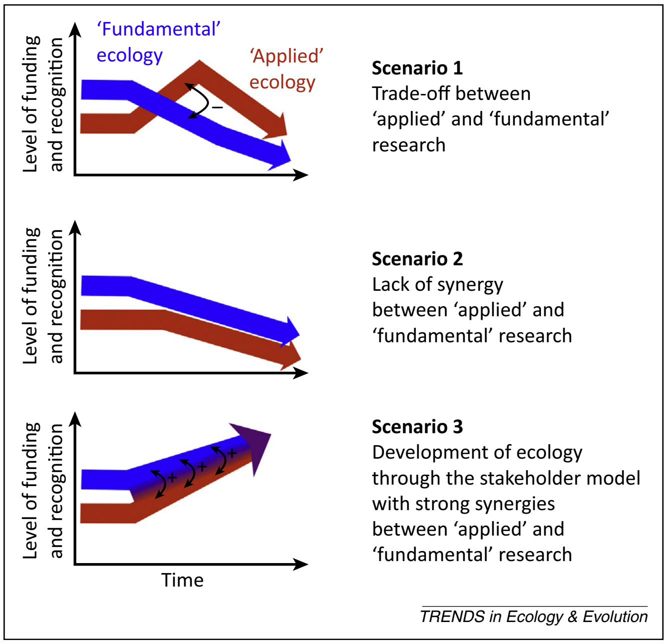

Figure 1. Three possible scenarios for the development of ecological sciences. Courchamp *et al.* [1] fear that competition between resources allocated to 'fundamental' and 'applied' ecology could strongly weaken fundamental research, and this in turn could lead to a collapse of ecological sciences (scenario 1). We in fact see the major weakness of ecology to be its poor capacity to build synergies between 'fundamental' and 'applied' ecology and users of science (scenario 2). A shift towards another model of research allowing reinforced links between ecology and society is needed. This would improve the ability of ecology to understand the biosphere and to inform the design of more sustainable interactions between the biosphere and human societies. Ecology would then be considered as more central to human society, particularly by policy makers, leading to greater support (scenario 3). We contend that applying ecology to solve societal issues through mobilization of solid knowledge generated by all forces of the community is the acid test of ecology (to paraphrase Mitsch and Jørgensen on ecological engineering [11]). If ecological sciences pass this test, the material resources for both fundamental and applied ecological research will increase [12]. Switching from the linear model of research to the 'stakeholder model' is central to this scenario.

increasingly being adopted in many sciences, with tight and efficient connections between the different types of research. This is the case for fundamental biology and for the development of medical applications. For example, it would be difficult to decide whether Pasteur conducted applied or fundamental research.

Towards synergies between 'applied' and 'fundamental' ecology

In the case of ecology, the distinction between fundamental and applied ecology is extremely fuzzy because of the key role humans play in the biosphere. Human have a tremendous impact on the entire functioning of the biosphere [3]. The study of this impact includes fundamental ecological and evolutionary mechanisms [4]. Ecological research increasingly recognizes the complexity of human–nature interactions because these involve many feedback mechanisms. This recognition underpins the notion of the socio-ecological system [5], and has led to the design and development of new, broad research fields studying complex feedback between humans and the biosphere. In addition, human-altered ecosystems and global changes provide long-term and large-scale 'experiments' that can be used to unravel basic ecological and evolutionary processes [6].

Courchamp *et al.* [1] neglect the potential synergies between 'applied' and 'fundamental' research. Research aimed at problem-solving feeds back to fundamental ecology and can be developed conjointly with fundamental ecology in the same research projects. Tackling broad environmental issues, such as mitigating and adapting to climate change, preserving and managing biodiversity and ecosystem services, or understanding the causes of the pollinator decline, requires the integration of knowledge from all ecological domains, which triggers the development of original fundamental research of the highest scientific impact. Courchamp *et al.* [1] suggest that research projects in applied ecology are essentially short-term and short-sighted projects. While some funding agencies strongly push towards projects that are intended to lead quickly to turnkey solutions, this is not always the case. By contrast, we suggest that ecologists need to contribute sound arguments to support the long-term research programs on which societally relevant solutions depend, and they should have a key role in the design of these programs. For example, developing sustainable agriculture, forestry, and fisheries is a long-term task. It requires many disciplines and approaches, including 'fundamental' research, on various subjects and their integration within a common framework [7].

Academic ecology has often been somewhat polarized towards fundamental ecology, and Courchamp *et al.* [1] complain that funding agencies are now polarized towards applied sciences. We suggest that polarization is unhelpful. It leads to many current problems separating science from solutions. Most importantly, owing to the rapid increase in global human population during the 20th century, as well as to the way we use ecosystems and natural resources, the biosphere faces many threats, which in turn threaten human societies [8]. This highlights a global failure of the development of ecological sciences. As ecologists, by largely focusing on the linear research model we have not effectively conveyed some major take-home messages to society as a whole (e.g., biological resources and material cycles are limiting at all scales of the biosphere, and human societies depend on biodiversity and the functioning of the biosphere) [9]. Continuing to adhere to the linear model will likely decrease resources allocated to 'fundamental' and 'applied' ecological research (Figure 1, scenarios 1 and 2). We should thus shift from the linear model of research to a transdisciplinary model where science is co-designed with stakeholders at multiple levels (scenario 3). This could for example help to shift towards science-based environmental policies [10].

Next steps forwards

Each individual scientist can position him/herself anywhere on the gradient between 'fundamental' and 'applied' ecology depending on skills, inclination, and career stage [2]. Scientists engaged solely in 'fundamental' or 'applied' research are needed equally as much as we need individuals ready to be mobile across postures. It is crucial to allow scientific curiosity to express itself as freely as possible in all types of ecological sciences. We also need a research system that collectively abandons the linear model of research. All aspects of academic life can promote a dynamic interface between basic understanding and solving societally relevant problems. Research institutions, laboratories, evaluation of scientists and research, congresses, scientific societies, journals, and educational programs can help to intermingle applied and fundamental aspects of ecological sciences as well as scientists and users of science.

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Back to the fundamentals: a reply to Barot *et al.*

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We appreciate that Barot and coworkers [1] recognize that our proposed model [2] advocates the end of the linear model of research. We indeed highlighted the importance of feedback mechanisms and multi-level integration in this model to illustrate the interdependency of the different types of research. However, Barot and colleagues appear to go a step further and essentially argue that the distinction between fundamental and applied ecology has little justification. They propose that ecological sciences should become an unpolarized discipline that uses fundamental knowledge of ecology and social sciences to tackle environmental issues. They further argue that future ecological research should contain some applied component to be accepted in current political and societal contexts. Whereas we accept and argued in our article that applied ecology should have a firm foundation in basic ecology, their argument contradicts our view that ecologists should strive to keep fundamental ecology distinct, and prevent it from becoming gradually assimilated with applied ecology.

Barot and colleagues make several unfounded claims of how we downplayed the importance of applied ecology, but instead of addressing these one by one we wish to focus on what we believe is the central misconception in their commentary: whereas fundamental and applied research can be integrated towards particular societal objectives or goals, an orthogonal pursuit is to understand nature without regard to if or how it affects humanity or human concerns. Our study describes the primacy of this endeavor, how and why it should be promoted, and the danger of it being reduced to a component of applied research. We stress, therefore, that there is a highly productive and meritorious continuum and interaction between the fundamental and the applied. However, there is also an ecological research domain of 'fundamental for fundamental's sake' that should be unfettered by the needs of humanity, and should instead satisfy the needs of human curiosity.

Our mutual disagreement is exemplified in their claim that: 'We should thus shift. to a transdisciplinary model where science is co-designed with stakeholders at multiple levels'. Recently, transdisciplinarity, as well as interdisciplinarity, have sometimes been advocated as a panacea for research, while in fact there are many examples in ecology where purely disciplinary research has resulted in outstanding findings [1]. Although such approaches may be useful in domains such as conservation sciences, agroecology, or epidemiology, these are primarily fields of applied research, and the same does not necessarily hold

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