Opinion

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Fundamental ecology is fundamental

Franck Courchamp[1,2], Jennifer A. Dunne[3], Yvon Le Maho[4], Robert M. May[5], Christophe Thébaud[6], and Michael E. Hochberg[3,7,8,9]

[1] Laboratoire d'Ecologie,Systématique, et Evolution, UMR CNRS 8079, Université Paris-Sud, Orsay, France
[2] Department of Ecology and Evolutionary Biology and Center for Tropical Research, and the Institute of the Environment and Sustainability, University of California Los Angeles, Los Angeles, CA 90095, USA
[3] Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA
[4] Institut Pluridisciplinaire Hubert Curien, UMR CNRS 7178, Université de Strasbourg, Strasbourg, France
[5] Department of Zoology, University of Oxford, Oxford OX1 3PS, UK
[6] Laboratoire Ecologie et Diversité Biologique, UMR CNRS 5174, Université Paul Sabatier, Toulouse, France
[7] Institut des Sciences de l'Evolution, UMR 5554, Université Montpellier II, Montpellier, France
[8] Kavli Institute for Theoretical Physics, University of California, Santa Barbara, CA 93106-4030, USA
[9] Wissenschaftskolleg zu Berlin, 14193 Berlin, Germany

The primary reasons for conducting fundamental research are satisfying curiosity, acquiring knowledge, and achieving understanding. Here we develop why we believe it is essential to promote basic ecological research, despite increased impetus for ecologists to conduct and present their research in the light of potential applications. This includes the understanding of our environment, for intellectual, economical, social, and political reasons, and as a major source of innovation. We contend that we should focus less on short-term, objective-driven research and more on creativity and exploratory analyses, quantitatively estimate the benefits of fundamental research for society, and better explain the nature and importance of fundamental ecology to students, politicians, decision makers, and the general public. Our perspective and underlying arguments should also apply to evolutionary biology and to many of the other biological and physical sciences.

What is fundamental ecology?

Fundamental ecology, or basic ecology, is the study of organismal diversity and of the interactions between organisms and their abiotic and biotic environments [1]. Its main goal is to advance knowledge and understanding, and its results, even if sometimes predictable, are not known with certainty in advance. By contrast, applied ecology is usually motivated by particular, well-defined objectives, typically to solve environmental problems, including the management of natural resources such as land, energy, food, or biodiversity [2]. Because applied ecology often involves the development of interventions to alter events (e.g., exotic species invasions, endemic species decline), this research is essentially an attempt to achieve a defined objective. Box 1 summarises the different types of research and Figure 1 presents a conceptual model of their relationships.

One of the central objectives and achievements of fundamental ecology is to develop and test general theory in ecology [3]. At the broadest level, a general theory is an entire domain of science and a set of interwoven fundamental principles, like the theory of evolution by natural selection [4].

Fundamental research is sometimes called pure science or 'blue-skies' research. The term blue-skies research has its roots in the idea of curiosity- and inquiry-driven studies (Box 1). It is said that under Eisenhower's presidency a prominent politician unsympathetic to basic research claimed 'I don't care what makes the grass green!', which was later rephrased as 'what makes the sky blue' [5]. Interestingly, 50 years earlier, using vapours and light beams in glass tubes, Tyndall [6] explained the basis of the sky's colour and his work led to better and more effective processes and products unforeseen at the time of his discovery. These included a test for optically pure air, support for the nonexistence of spontaneous generation, particle filtering of lung airways, mould destruction by *Penicillium* bacteria, and even the precursors of the flexible gastroscope and bronchoscope [6].

Financial support for fundamental research in ecology, like in many other disciplines, is highly competitive. Many perceive stasis or a continuous decline in support, but accurate numbers are difficult to obtain to substantiate general trends, since funding categorization can be open to alternative interpretations and data can be difficult to obtain. This perception that support, be it financial or moral, is not improving is worrisome for ecologists, for their science, and ultimately for society. Here we show how the predominant support for objective-driven, applied science is relatively recent and why, in conjunction with this, fundamental research has seen limited investment in both relative and absolute terms. We then advocate increased and less constraining support for basic ecology, by presenting the principal drivers of fundamental research and some of its main benefits, including the satisfaction of human curiosity, the quest to explain our world, the creation of scientific knowledge, and the often unintentional,

Corresponding authors: Courchamp, F. (franck.courchamp@u-psud.fr); Hochberg, M.E. (mhochber@univ-montp2.fr).
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Box 1. Different types of research

We define fundamental research as theoretical or experimental work undertaken primarily to acquire new knowledge of the underlying foundations of phenomena and observable facts without any particular application in view [14]. Fundamental ecology is therefore often exploratory and curiosity driven. By contrast, applied research focuses on finding solutions and improving them and is thus goal driven. The distinction in objectives is important. Conducting research with a specific goal in mind makes achieving it more likely but also reduces the chances of obtaining unexpected results, a major source of scientific discovery. Curiosity-driven research often challenges accepted thinking and may generate new fields of investigation. Applied research feeds to some extent on the outcomes of fundamental research (see Figure 1 in main text). However, basic and applied research are not entirely discrete alternatives but rather can be viewed as a continuum [14]. This is especially pertinent to ecological research, where fields such as conservation biology, fisheries science, or global-change biology often integrate both fundamental and applied perspectives.

There are other, less discussed but nevertheless important research approaches. Development research aims to make products from newly discovered technologies. Strategic research is primarily directed towards understanding the fundamental basis of an applied, ultimate goal [Dos Remedios, C. (2000) The value of fundamental research. *International Union for Pure and Applied Biophysics* (http://iupab.org/publications/value-of-fundamental-research/)]. Finally, translational research seeks to rapidly transfer findings from fundamental research into practical applications of direct relevance to human needs. In contrast to applied research, which usually represents incremental improvements to current understanding, translational research strives to deliver breakthroughs, notably through the creative and multidisciplinary exploration of results from fundamental research. Most translational research is aimed at innovative, basic biological science to improve medicine, bypassing the typically long times separating basic research and concrete clinical application [39]. Ecology provides fertile grounds for translational research; for example, in conservation science. Unfortunately, translational research often competes for funding and attention with both fundamental and applied research, although its success obviously relies to a great extent on progress in the latter [48]. In principle, the boundaries between all of these different types of research should be more porous, since they have the potential to interact and instruct in achieving their respective aims.

more tangible, economic, social, and political outcomes, as well as many innovations. Finally, we present concrete propositions to promote further support for fundamental research in ecology.

Major trends in research funding

Basic versus applied research through history

Historically, fundamental approaches have played a dominant role in scientific research, with discoveries of all kinds and importance being the trademark of fundamental scientific research, from Antiquity to the Age of Enlightenment. The recent surge in the growth of institutionalised applied research stems, in part, from political perspectives of the role of scientific research in society [7]. This has created a new market-oriented and objective-driven approach to science to respond to economic and societal expectations [6].

Before the industrial revolution, funding sources were very different from what they are today, coming from personal funds (scientists were often aristocrats, with education, money, and time), sponsorship from the less-educated nobility without the time or interest to do research themselves, or funding sought by the scientists from the public through experimental demonstrations or natural history displays – the famed 'cabinets of curiosities'. After the Industrial Revolution, the costs of scientific research changed scale and funding became more organised, often through universities. Over time, university funding has become more tied to governmental and private funding. Now, universities and research institutions often seek sources through tuition fees, patent licensing, endowments, private sponsorship, or alumni contributions [8]. As a result, and not unexpectedly, the emphasis of research is increasingly being based on the expectations of these funders and is thus more often expressed in terms of direct and immediate benefits to society. Some funding calls prioritise projects in which scientists associate with industry and most universities now adopt business models [6] and develop entrepreneurial centres to encourage related technology transfer [9].

Current sources of funding

The private sector typically seeks short-term (i.e., 1–4 years), low-risk returns on investment, which is incompatible with the unpredictability and long-term (typically decadal) nature of returns on basic research [Dos Remedios, C. (2000) The value of fundamental research. *International Union for Pure and Applied Biophysics* (http://iupab.org/publications/value-of-fundamental-research/)] [6]. Because private investors usually dislike uncertainty, fundamental research is still mostly supported by governmental institutions. Basic research is also increasingly funded by philanthropic foundations and wealthy personalities [8,10]. The approach of benefactors has changed from supporting small research projects to large-scale programmes and earmarked research networks such as, in our field, deep-ocean exploration in the search of giant squid or paleontological expeditions to find remains of *Tyrannosaurus rex* [10]. In parallel, there is a recent trend towards smaller project budgets being sought directly from the public, through crowdfunding [11]. In both cases, there is thus an understandable concern that funded programmes can become idiosyncratic, at the expense of the coverage of a wider, less biased range of basic research topics. For example, of the US$19 billion of private funding for all research fields in 2006, nearly a quarter was spent on health-related topics, compared with less than 3% on basic biology, a considerable decrease compared with just a few years previously [12].

Shift of governmental support from basic to applied

Governments are the primary instrument for balancing the collective benefits of a research strategy and of personal interests and funding across disciplines so that research embraces the full spectrum of topics [13]. However, with governmental funding showing lower trends over the past several years in many Organisation for Economic Cooperation and Development (OECD) countries [14,15], there has been a shift in strategy towards more emphasis on the short-term goals of applied research, the creation of economic value even becoming a legal requirement of public research institutions in some countries. Thus, many institutions dedicated to basic research are expanding their associations

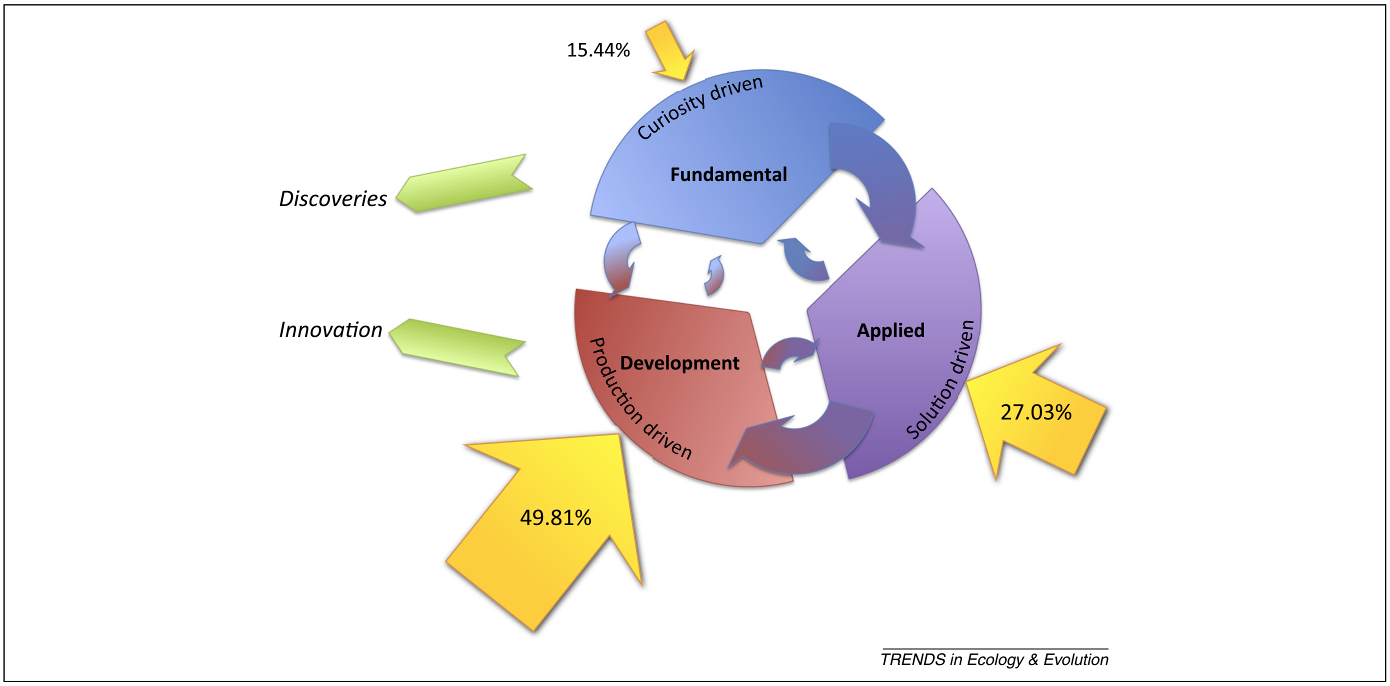

Figure 1. A conceptual model showing the links between different types of scientific research (Box 1). The width of the curved arrows is an indication of the importance of the transfers between research types. For example, fundamental research is the main basis of applied research, but outcomes of applied research may fuel, in turn, new studies in fundamental research. Similarly, transfers from fundamental research to development research are often called 'translational research'; the reverse results in innovative scientific equipment and technologies that can, in turn, open new lines of fundamental research. The green arrows indicate gains for society; yellow arrows represent relative funding [OECD (2012) Research and development statistics: R&D expenditure by sector of performance and type of R&D. *OECD Science, Technology and R&D Statistics* (http://www.oecd.org/statistics/)] based on average funding for the past 10 years in Organisation for Economic Cooperation and Development (OECD) countries.

with industry and are becoming increasingly concerned with government-encouraged transfer to application [8]. In OECD countries, funding for basic research over the past few decades has been at lower levels than for other major research categories [14] [OECD (2012) Research and development statistics: R&D expenditure by sector of performance and type of R&D. *OECD Science, Technology and R&D Statistics* (http://www.oecd.org/statistics/)]. For example, in 2011 funding for basic research was at 14% (US$85 billion), whereas applied research was at 24% (US$151 billion) and development at 62% (US$394 billion).

Sources of decisional shifts: politicians and the public

The increasing influence of politicians in research decision making [16] has lead to shorter funding timescales corresponding to political mandates and priority given to questions of direct relevance to the general public [Dos Remedios, C. (2000) The value of fundamental research. *International Union for Pure and Applied Biophysics* (http://iupab.org/publications/value-of-fundamental-research/)]. There is a growing political will to ensure that taxpayer-funded research is seen to benefit the public [17]. Governments face numerous competing demands for public funding, including some of more immediate and obvious benefits to society such as controlling emerging diseases or increasing agricultural yields. Limited and sometimes erroneous information obtained through education and the media combine to explain why some taxpayers are opposed to research that has no immediately obvious benefits for society. Stimulating themes in fundamental ecology such as understanding biological diversity – even with the applied aim of species conservation – can easily be made to sound frivolous and counterproductive in the context of economic growth and societal challenges [18].

Some scientists have echoed this trend by calling for 'more projects focusing on applied challenges, arguing that public funding should focus on public problems rather than fundamental curiosities' [19], while some have claimed that 'blue sky research should be brought back to Earth' [20]. With current environmental challenges, ecologists, especially younger scientists, are increasingly drawn towards applied ecology. In parallel, the current obsession in academia for quantity [21] reduces creativity, reflection, and risk taking and therefore, arguably, opportunities for fundamental discoveries.

What drives fundamental research?

Breakthroughs in research often result from a combination of curiosity, creativity, intelligence, passion, perseverance, and even chance [22], with curiosity being arguably the main driver of fundamental science. Exploring the wonders of life and the nature of things for the sake of knowledge alone is possibly one of the most ancient and noble of human aspirations.

Another driver of fundamental research is the innate desire to understand inherently complex systems. Most if not all ecologists marvel at understanding the intricate beauty of systems involving many interacting components, be they molecules, individuals, or populations. That many ecologists are now trained in the more quantitative sciences, such as physics, computer science and mathematics, is indicative of the general affinity across disciplines for understanding complex concepts and systems. Promoting the importance of fundamental ecology today seems a key component in continuing to attract skilled, creative, and curious students to ecology who can help to build and test a coherent body of fundamental ecological knowledge.

Why fundamental ecology is important

Understanding

Ecology is still a young discipline and we are only starting to reach an understanding of how species function and interact and of the processes underlying patterns in biodiversity. Nevertheless, there are numerous examples of progress in understanding basic ecology and in the fundamental ecological frameworks influencing applications. For instance, theory has contributed immensely to identifying relationships involving different temporal, spatial, and biological scales [3]. Using systems as diverse as hare–lynx interactions (e.g., [23,24]), host–parasite relationships (e.g., [25,26]), and insect pest outbreaks (e.g., [27]) ecologists have shown that mechanistic models can outperform many data-fitting statistical models in understanding how these complex systems function and in predicting future trends. Fundamental studies of trophic networks have shed light on the role of trophic cascades in ecosystem functioning and ecosystem services, in both oceanic [28,29] and terrestrial communities [30]. Fundamental studies on population dynamic modelling have highlighted the need to understand the interaction of demographic and genetic factors in extinction [31,32], which led to the International Union for the Conservation of Nature (IUCN) Red List of threatened species [33]. These are only a few among many examples demonstrating methodological or applied advances that arose from fundamental, entirely curiosity-driven work in population ecology. A general illustration comes from the recent compilation by the British Ecological Society of '100 influential papers' from the past 100 years [34], most of which involve fundamental ecology.

We cannot anticipate all the biological and environmental challenges that humanity will face in the future. A fundamental understanding of the problems underlying the current environmental and biodiversity crises is the most reasonable path to solving them. It is also probably a safer, less expensive, and ultimately time-saving option. This is yet another reason to foster the acquisition of knowledge with as few preconceived routes as possible.

Economic, social, and political perspectives

Economic theory has demonstrated the importance of fundamental research. Since the output of basic research is inherently intangible, unpredictable, and difficult for researchers to appropriate, it provides some of the largest spill-over benefits to society [35–38]. Although there are strong conceptual and methodological difficulties in assessing the many economic benefits of publicly funded basic research, several studies have demonstrated its importance, arguing for high levels of continuous investment, particularly by governments (reviewed in [13]). There are numerous ways through which benefits from research flow into the economy and society, including: (i) increase in the stock of useful knowledge; (ii) supply of skilled graduates and researchers; (iii) creation of new scientific instrumentation and methodologies; (iv) development of networks and stimulation of social interactions; (v) enhancement of problem-solving capacities; (vi) creation of new firms; and (vii) provision of social knowledge [13]. Because most attempts to assess the socioeconomic benefits of basic research focus on one or only a few of these (usually the first), the total benefits are often underestimated [13].

The current trend for seeking an applied component to ecological research, independent of the potential economic benefits of its fundamental components, may also reflect how society and, ultimately, policy makers often view ecology. This is exacerbated by the common confusion between ecology and environmentalism and suggests that the perception of ecology should be corrected through education to explain what exactly is the science of ecology and why it is important to understand its underlying processes [4]. In this regard, an emphasis is needed on various outreach activities, including formal programs early in education, and more systematic popularisation of fundamental ecology, for example through scientifically sound nature documentaries.

Fundamental ecology is also important for political credibility. With the unprecedented biodiversity and environmental crises, ecologists have a responsibility to provide insights into the functioning of highly complex systems. Politicians and decision makers need global predictions of ecosystem and biodiversity trajectories and ways of assessing the quality and uncertainty associated with these predictions, but they also require an accurate understanding of the underlying processes governing patterns and predictions.

Finally, fundamental research in ecology – and in other fields – is crucial for the development of societies. It is a great accomplishment of humanity that some individuals are encouraged to advance and spread knowledge and understanding for the potential benefit of all. Worldwide, societies have long been providing resources for research regardless of practical, short-term returns [22]. Indeed, it has been argued that fundamental research is not a luxury, but rather a cultural achievement and even the foundation of many types of benefit for the entire society [22].

A source of innovation

Probably the most common argument defending basic research is that it potentially leads to new discoveries. Novel applications without prior development are notoriously uncommon, ostensibly because major discoveries seldom emerge from strategically planned research. Innovations, when they do arise, often stem from surprising translations or recombinations of existing knowledge [19,39]. There are countless examples of unexpected applications from basic research (see Boxes 2 and 3 for examples in ecology). A typical illustration is the increased focus on organismal and system oddities with hopes of direct applications to industry. For example, The Biomimicry Institute (http://biomimicry.net/about/biomimicry38/institute/) compiled over 2000 examples of technologies inspired by basic research in the fields of ecology and evolution. Applications can also extend to fields remote from basic ecology. For example, models of prey–predator dynamics developed last century are now being used in both industrial economics [40] and political economics [41], insights from research

Box 2. Examples of basic research in ecology leading to environmental applications

In many areas of applied ecology, the urgency of problems such as habitat destruction or species extinction often calls for a rapid response. Conservation science is unique in being both a field of research and a field of action, but environmental challenges have naturally shifted emphasis towards action, sometimes at the expense of building a strong fundamental framework. For example, a few decades ago biological invaders on islands were typically ignored until their impact became a decisive factor for intervention, which was pursued without either pre-control survey or post-control monitoring [49]. Consequently, hysteresis and multiple stable states (including extinction) were generally overlooked, resulting in a number of 'surprise effects', typically the failure of eradication, or the unexpected outbreak of other, hitherto neglected invasive species [50]. Subsequently, incorporation of trophic-web theory allowed assessments of mesopredator releases [51], hyperpredation processes [52], competitor releases [53], and other ecological processes related to interspecific interactions and likely to interfere with or facilitate eradication [54,55]. Similar observations apply to the management of fisheries, with long-lasting stock collapses [29,56], algal blooms [57], eutrophication in freshwater and coastal marine [58,59], or regime shifts in terrestrial ecosystems [60].

Another illustration comes from a fundamental programme aimed at better understanding the mechanisms underlying the Allee effect (a positive relationship between the number of individuals in a population and their fitness [61,62]). Fundamental research has led to the questioning of the basic assumption that Allee effects are an intrinsic characteristic of populations and therefore cannot be created by human activities. Thus, the standard paradigm was that humans could only drive populations down to sizes where a pre-existing, unexpressed Allee effect would be activated. Questioning this premise led to the discovery of possible anthropogenic Allee effects, through which human activities can exert inverse density-dependent exploitation. According to this concept, the arbitrary value people attribute to rarity would confer an economic value on rare species that would maintain the incentive to exploit them, even at very high levels of rarity [63]. Rare species, being more valuable, would be more exploited, thereby becoming even rarer, precipitating a vortex of extinction. This process threatens, through many different wildlife-based markets, countless species of plants and animals.

A final poignant illustration of the importance of basic science is the increasing need to promote ecosystem services, where possible [64,65]. Only with an adequate understanding of the patterns and underlying mechanisms of ecosystem functioning can one justifiably and reliably protect, restore, and value the services provided by that ecosystem. Unfortunately, the current environmental crisis often elicits rapid responses with little fundamental basis, in which avoidable (and now irrecoverable) mistakes would have been averted. Recent estimates of the global value of pollination for agriculture – US$153 billion annually – provides a good illustration of the importance of better understanding the functioning and outputs of ecosystems [66].

on the stability and complexity of ecosystems shows future promise in the regulation of banks [42], while fundamental studies in the behavioural ecology of social insects are being used in robotics [43].

Nevertheless, that fundamental research often fuels applications should not be the main argument for why we need basic research. Unexpected applications of fundamental discoveries are only providential byproducts of other objectives. We believe it is important that fundamental ecology is a major source of application, but the primary justifications for conducting fundamental research should remain firmly grounded in satisfying curiosity, acquiring knowledge, and achieving understanding.

Promoting fundamental research

Ecologists can promote basic science in several important ways.

First, we need to regularly assess the state of and progress made in fundamental ecology through the publication of perspective, forum, review, and synthesis articles. In our view, one of the most influential ways to make both headway in specific areas and overall progress in the field is through discussing and recasting the most important questions in fundamental ecology [44].

Second, we must develop and draw on new approaches to communicate results to politicians and granting agencies and to reassure them that giving liberty to scientists is

Box 3. Examples of basic research in ecology leading to applications in health sciences

Since each species potentially has unique biological properties, it is unsurprising that an estimated 60% of antitumour and antimicrobial drugs are of natural origin [67]. Basic research is at the origin, for example, of the discovery in the naked mole rat (*Heterocephalus glaber*) of anticancer mechanisms [68]. Taking full advantage of such a potential 'gold mine' would not have been possible without research on understanding the causes of mortality in this species through necroscopies. Another example is the incubating male king penguin (*Aptenodytes patagonicus*), which preserves fish in its stomach for up to 3 weeks to feed to its young at hatching, should the mother be absent when the juvenile begs for food [69]. Searching for the mechanism permitting fish conservation at 37°C led to the discovery of spheniscin, a small antimicrobial and antifungal peptide. This molecule has since been shown to reduce the growth of the two main agents of hospital-acquired infections, the bacterium *Staphylococcus aureus* and the fungus *Aspergillus fumigatus* [70].

Basic research on plant–insect interactions has also led to important applications, such as alternative strategies for the protection of crops like maize and rice against herbivores. Plants possess many defence mechanisms based on secondary metabolites or defensive proteins whose toxic or deterring properties are harmful to herbivores. However, it was not known until recently that some plants release volatile signals that attract herbivore natural enemies, such as parasitic wasps above ground, and entomopathogenic nematodes below ground [71]. These defences are regulated by conserved signalling pathways [72]. In another striking example, fundamental studies of the microbial ecology of hot springs at Yellowstone National Park resulted in the discovery of hyperthermophiles, which incidentally led to the identification of the Taq polymerase, since then used in PCR [73]. This unexpected finding was key to innovations in agriculture and medicine and helped create the new field of biotechnology, which includes genomics, recombinant gene technologies, applied immunology, and the development of pharmaceutical therapies and diagnostic tests. These are just a few examples of how basic ecology can unexpectedly provide the molecular basis of important applications.

Environmental health is another field where basic ecological science has repeatedly proved to be of major importance. With the development of mathematical models of host–parasite relationships [74,75], ecological epidemiology has resulted in a better understanding of the spread of pathogens and parasites, paving the way for applications to manage the spread of infectious diseases. Examples include host–parasite modelling of epidemics such as measles, which subsequently informed control campaigns against the 2001 outbreak of foot and mouth disease in the UK [76–78]. Unfortunately, basic science was not sufficiently developed (or not identified as such) to realise its full potential in contributing to the control of the spread of avian (H5N1) and swine (H1N1) flu and the current Ebola epidemic.

not necessarily at the expense of accountability [6]. It is essential that funders realise that academic research programmes once thrived on intellectual freedom and that this is essential for discovery [16]. Defining clearly what ecology is and what ecologists are (i.e., not environmentalists) is key in this regard.

Third, we should consider creating programmes giving large and unconstrained blue-sky research grants to promising or experienced researchers. Such initiatives obviously should not be at the expense of other research programmes. Even a modest investment in supplementary, long-term grants, without externally imposed objectives, should contribute to considerable breakthroughs [16].

Fourth, we need to establish norms for funding fundamental research that will facilitate adherence by agencies and promote the long-term future of fundamental science. One possibility is to establish an international norm of a minimum level and/or percentage of research funding that participating agencies pledge to maintain for fundamental science. Participating national, international, and private funding bodies would then officially declare that they adhere to international norms. This highlights the necessity that politicians/decision makers, agencies, and scientists all be involved in institutional-, national-, and international-level discussion to establish such norms and to determine the extent of their application. We stress that promoting basic ecological research requires continued dialogue and need not result in reduced budgets for other research approaches (Box 1).

Fifth, we must find ways to quantitatively value fundamental findings. This would involve estimating the pay off and timescale of the returns of basic research, which, although known to be important [36,37], remain largely unquantified [16]. This could be one way of demonstrating unambiguously the importance of fundamental research in ecology.

Sixth, we need to reduce the pressure on ecologists to systematically provide short-term results to predefined questions. One approach would be to modify tenure rules to account for the importance of longer-term, less output-oriented research. Another possibility is longer grant periods, to promote the tackling of challenging and risky questions with possible unexpected outcomes. Despite risk being increasingly presented as a positive criterion, the current mindset on productivity discourages risky projects. Typically, reviewers are required explicitly to express their opinions on the expected impact of grant proposals, often in terms of output quality and certainty [45,46]. Precluding risk can constrain creativity and, therefore, discovery in the longer term [47].

Seventh, supervisors and mentors need to encourage their students to conduct side projects and pilot projects to foster the spark of curiosity and creativity. Supervisors and mentors should insist on the benefits of devoting time to thinking, to exploratory research, and to the importance of 'toying' with concepts and data (and thinking 'outside the box') rather than emphasising high scientific productivity or being drawn into applied research on the sole basis of better funding opportunities. They should also insist on the importance of asking difficult (but tractable) questions – that is, steeping out of one's comfort zone.

Finally, researchers themselves need to prioritise how to effectively defend basic research. Politicians have long recognised that research free of practical constraints is at the heart of technology and industry. For example, Vannevar Bush, scientific advisor to Franklin D. Roosevelt, stated in 1945 that scientific progress resulted 'from the free interplay of free intellectuals, working on subjects of their own choice, in the manner dictated by their curiosity for exploration of the unknown' [22]. Yet many politicians still view basic science as an unaffordable luxury, especially in times of financial stress [9]. Young and more senior ecologists must engage debate with policymakers to correct the common misconception that fundamental research is a luxury [Dos Remedios, C. (2000) The value of fundamental research. *International Union for Pure and Applied Biophysics* (http://iupab.org/publications/value-of-fundamental-research/)] [9].

Concluding remarks

We have developed several lines of reasoning supporting the promotion of fundamental research in ecology, although the same or similar arguments could apply to evolutionary biology [18] and to other sciences. We emphasise that we do not claim that applied research has less merit or intrinsic value than basic research or that promoting fundamental science should negatively impact budgets for applied research. We argue, however, that basic science is at the foundation of ecology and requires active support if it is to function at the highest level and continue to create intellectual capital in the future. This support encompasses project funding, but also endorsement by academics, governments, and society as a whole. Support includes fostering the building blocks of the ecological sciences such as taxonomy, as exemplified by the Global Taxonomy Initiative (http://www.cbd.int/gti/default.sht).

It is easy to depict a caricatured vision of the world a century from now, should fundamental ecology not gain greater support. Acquired knowledge and understanding would probably be put to good use, through high-level engineering, but this recycling of science would likely lead to fewer breakthroughs and fewer challenges to existing paradigms. Intellectual capital would be 'consumed' faster than it is replaced [16]. It might be a world where ecological tinkerers would, perhaps brilliantly, build on the current foundations of science, but those foundations would cease to be developed or would develop more slowly, with associated risks of failure to face future, novel challenges. To explain the living world around us, we need to meet the intellectual challenge of understanding life in complex, changing environments; to this end, fundamental ecology is our most fundamental instrument.

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Letter

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

Sébastien Barot[1], Luc Abbadie[2], Denis Couvet[3], Richard J. Hobbs[4], Sandra Lavorel[5], Georgina Mary Mace[6], and Xavier Le Roux[7]

[1] Institut de Recherche pour le Développement (IRD), Institut d'Ecologie et des Sciences de l'Environnement de Paris (IEES-P), UMR 7618, 46 Rue d'Ulm, 75230 Paris CEDEX 05, France
[2] Université Pierre et Marie Curie (UPMC), Institut d'Ecologie et des Sciences de l'Environnement de Paris (IEES-P), UMR 7618, 46 Rue d'Ulm, 75230 Paris CEDEX 05, France
[3] Centre National de la Recherche Scientifique (CNRS), Centre d'Ecologie et des Sciences de la Conservation (CESCO), UMR 7204, Muséum National d'Histoire Naturelle (MNHN), 55 Rue Buffon, 75005 Paris, France
[4] School of Plant Biology, University of Western Australia, Crawley, WA 6009, Australia
[5] CNRS, Laboratoire d'Écologie Alpine (LECA), UMR 5553, CNRS – Université Grenoble Alpes, BP 53, 38041, Grenoble CEDEX 9, France
[6] Department of Genetics, Evolution and Environment, University College London, Gower Street, London WC1E 6BT, UK
[7] Institut National de la Recherche Agronomique (INRA), Laboratoire d'Ecologie Microbienne (LEM), CNRS, UMR 5557, Unité Sous Contrat (USC) 1364, Université Lyon 1, 43 Boulevard du 11 Novembre 1918, Villeurbanne, France

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 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

Corresponding author: Barot, S. (sebastien.barot@ird.fr).

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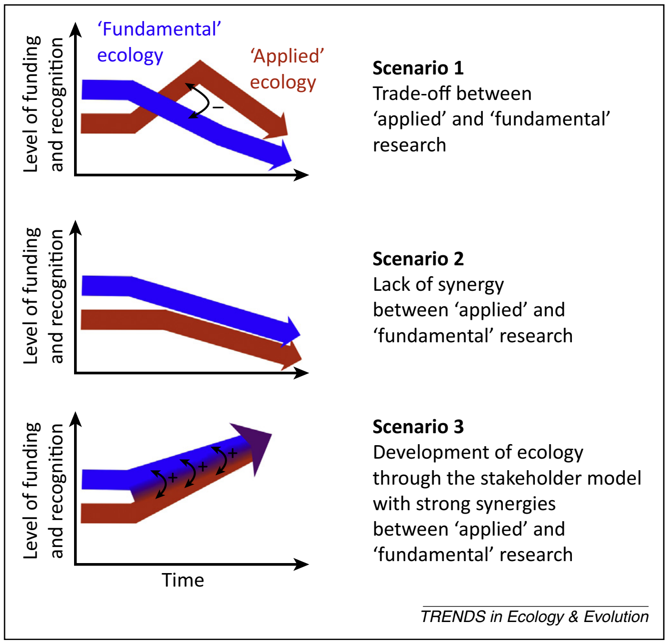

Figure 1. Three possible scenarios for the development of ecological sciences. Courchamp *et al.* [1] fear that competition between resources allocated to 'fundamental' and 'applied' ecology could strongly weaken fundamental research, and this in turn could lead to a collapse of ecological sciences (scenario 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.

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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Letter

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

Franck Courchamp[1,2], Jennifer A. Dunne[3], Yvon Le Maho[4], Robert M. May[5], Christophe Thébaud[6], and Michael E. Hochberg[3,7]

[1] Laboratoire d'Ecologie, Systématique, et Evolution, Unité Mixte de Recherche (UMR) 8079, Université Paris Sud, Orsay, France
[2] Department of Ecology and Evolutionary Biology and Center for Tropical Research, and the Institute of the Environment and Sustainability, University of California Los Angeles, Los Angeles, CA 90095, USA
[3] Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, USA
[4] Institut Pluridisciplinaire Hubert Curien, CNRS UMR 7178, Université de Strasbourg, France
[5] Department of Zoology, University of Oxford, Oxford OX1 3PS, UK
[6] Laboratoire Evolution et Diversité Biologique, CNRS UMR 5174, Université Paul Sabatier, Toulouse, France
[7] Institut des Sciences de l'Evolution, CNRS UMR 5554, Université Montpellier II, Montpellier, France

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 for fundamental ecology wherein most efforts remain centered on discovering patterns and understanding processes in ecology and evolution. Efforts to shoehorn fundamental ecology into an applied interdisciplinary framework are neither necessary or nor always useful. Failing to consider fundamental ecology as both an interactant with applied ecology (our view and the view of Barot *et al.*) and also an independent entity (our view) will cause a shift that results in ecology being subsumed into policy-based environmental sciences.

To conclude, we agree that researchers can easily reconcile a search for basic understanding with a quest to solve societally relevant problems. However, we do not see why all ecologists should do so, nor why any given ecologist cannot conduct research projects that are basic science, others with additional applied objectives, and yet other projects which are purely applied. Systematically intermingling applied and fundamental ecology may be tempting but, we argue, will result in the gradual demise of fundamental ecology, and will negatively impact on ecology as a science. While not foregoing support for applied ecology, we think that a plea for renewed support for fundamental ecology is incompatible with their merger. The basis of fundamental ecology is understanding. It must remain, be protected, and be promoted as an end unto itself.

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Corresponding author: Hochberg, M.E. (mhochber@univ-montp2.fr).

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