Introduction

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In the early 1930s, Julian Huxley, the prominent English evolutionary biologist, embarked on a visit across many British science laboratories to understand in which way the scientific knowledge they were producing was socially relevant. His account of this journey, published in 1934 (Huxley, 1934), is a compendium of applied scientific research in engineering, medicine, agriculture and so forth. In the final chapter of the book, a conversation with Hyman Levy (a physicist and mathematician, also a person concerned about the use of science for the good of all, not just a few), Huxley remarks that back then – as is also true now – the advancement of scientific knowledge was limited by funding, including funding for applied research. In a remarkably candid admission, he wrote that one of the reasons private firms kept their research budget secret was because sometimes 'they do not want their shareholders to know – the shareholders, you see, might think research a silly luxury, and become a nuisance at the annual meeting' (pp. 254–5). Later in the conversation, Huxley showed some support for the then very active field of eugenics, to which Levy disagreed, as do the vast majority of evolutionary biologists today. Levy subsequently pinned down some of the core issues of applied science:

> … but one of the first questions we have to ask as soon as we have accumulated adequate scientific knowledge … is, What objective have we? Can scientific men lay down an objective? We are to use science and scientific methods, but for what? What kind of society do we want? What kinds of society are possible at all? (p. 276)

Although he also added that 'That is too important a question to leave to scientists', the statement strikes at the core of the many issues of applied evolutionary thinking addressed in this book. We hope to prove that such evolutionary knowledge is useful and necessary to solve problems and

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establish objectives in our everyday life, but pointing to its immediate practical utility will not be sufficient to produce a better understanding of *evolutionary science* in society, and what role it can play for the improvement of our lot. The point that Levy was making is that specialists need to carry the rest of society with them, by listening and learning to communicate, so that the great decisions, especially when they are taken within a democratic system, are also based on solid knowledge of the relevant science. His final remark is especially poignant, as it reminds us that it is our responsibility not to be alienated from the mainstream thoughts and needs of society.

Fifteen years later, another evolutionary biologist, John Burdon Sanderson Haldane, also addressed the need for ethical applications of scientific knowledge, to dispel the fear and apprehension expressed by society at large with regard to science (Haldane, 1949). Complementing both Huxley's and Levy's views, he also mentioned that divorcing science from its applications may risk making science 'intellectually barren'; he did not mean it literally, but it remains an interesting statement coming from one of the great contributors to the development of modern theoretical evolutionary genetics.

Ultimately, however, Huxley, Levy and Haldane understood perfectly well the importance of 'pure' or 'basic' or 'background' science (that is, theoretically driven science), and the last thing they had in mind when they were thinking about 'applied science' was to use this to quash the imagination and intellectual courage often expressed in theoretical works. After all, scientific progress (including *applied* scientific progress) ultimately relies on our ability to think outside the box, beyond the current paradigms. However, the message that today's evolutionary scientists can draw from these first-half of the twentieth century thoughts about science and its applications is that scientific progress, and with it improved human (and environmental) welfare, depend on both basic *and* applied science; and the mutual synergy of both, appropriately conveyed to the broader community through education and also through the visible and palpable results of it, will go a long way towards counteracting the ideologically driven misinformation that is currently homing in on evolutionary science.

A more specific point about applied evolutionary science was made more explicitly in the mid 1990s by Doug Futuyma in an article published in the journal *Science* (Futuyma, 1995). Futuyma reported on the outcomes of a meeting, carried out the year before in New Jersey (USA), between evolutionary and other scientists and representatives of industry, conservation organisations and various funding agencies. The objective was 'to identify applications of and opportunities for evolutionary science and to recommend mechanisms for future interchange and technology transfer'. To the cynic, this may seem just like a last-ditch attempt from the part of a few desperate and underfunded evolutionary scientists to try to stay afloat by clinging on to the purse of industry. Such a superficial reading of what applied evolutionary

science is about would not only completely miss the point, but, far more importantly, would preclude us from reaping the maximum societal benefits from a solid and ever-growing field of scientific research.

Six years later, in 2001, James Bull and Holly Wichman published an article in *Annual Reviews of Ecology and Systematics* entitled 'Applied evolution', where they provided evidence to argue the case for the social relevance of evolutionary biology. I could not agree more with their statement that 'The time has arrived for wide public understanding of the importance and relevance of evolutionary biology in everyday lives' (Bull and Wichman, 2001, p. 212).

By the early 2000s, the time was finally ripe for this issue to start taking centre stage. The better understanding of applied evolutionary science received a big boost in 2006 with the publication by David Mindell of his book *The Evolving World: Evolution in Everyday Life* (2006). Mindell provides a simple yet thorough introduction to various areas of application of evolutionary science. In fact, his chapter on *Domestication: Evolution in Human Hands* is such that I decided to leave the issue of domestication largely out of this book and refer the reader to Mindell's work. Here I would just like to make the following comments on evolution and domestication. Although it was domestication that, at least in part, inspired Darwin in the development of his theory of evolution by natural selection, we seem to have a certain tendency to regard domestication as 'unnatural', a process driven by the human mind and craft that somehow 'escapes' the natural laws governing adaptive change in biological systems in the wild. It is probably time to return domestication to its proper place within the biological processes of evolution. Domestication is not just a metaphor that inspired Darwin; it is instead an actual process of evolutionary change driven by the interaction between two species: humans and the species being domesticated. That this process includes a purposeful objective that depends on the properties of our mind (e.g. selection for breeds that produce more milk, or higher grain yield per hectare, or extravagant feather patterns) is just an effect of the specific biological characteristics of one of the two interacting species, humans in this case. That is, Darwin's inspiration notwithstanding, domestication is not just a metaphor for evolution, but a specific case of evolutionary process that happens to produce outcomes that we humans find useful. Through domestication we use (consciously or unconsciously) evolutionary mechanisms to achieve an ultimate goal of increasing our own fitness or, more proximately, economic wealth and also emotional satisfaction, as in the case of pet animals and ornamental plants. In the words of Elliott Sober (quoted by Hart, 1999, p. 144):

> Artificial selection is not selection that takes place *outside* nature, but selection that occurs within a particular niche found *in* nature . . .

For a recent review of evolutionary aspects of domestication see Driscoll *et al.* (2009), and for a truly remarkable case study, see the domestication of the

silver fox, a long-term experiment started in the former USSR by Dmitry Belyaev in 1959 and that is continuing in today's Russia under the leadership of Lyudmila Trut (Trut, 1999).

Another area of application of evolutionary science is that of phylogenetics, widely used in medicine and epidemiology. Being a professional phylogeneticist himself, Mindell's treatment of this topic is both detailed and comprehensive, so much so that again I refer the interested reader to his book.

Indeed, the production of this edited book was organised in such a way that the two books could be considered complementary. This also means that many of the themes that are developed here are missing in Mindell's volume. In addition, I have also benefited from reading the reviews of his work. For instance, running through those somewhat critical reviews, there is a *leit motiv* that reflects a concern that what evolutionary science is presenting as applications are just methodologies and techniques developed independently from evolutionary theory, but that could be interpreted, *a posteriori*, in an evolutionary manner. That is, some critics stress that evolutionary thinking is not pulling the cart of technological progress; instead, it is just sitting on it and enjoying the free ride (see, for instance, the reviews by Jerry Coyne, 2006, and Ben Oldroyd, 2008). I agree that they have a point. The criticisms were somewhat addressed by Mindell (2009) in a later article, but I took special care during the editing of this book to make sure that all chapters clearly stress the novel and specific applications that directly derive from evolutionary considerations in the various fields. Admittedly, the chapters are not homogeneous in this regard, partly because some fields are better 'preadapted' for the production of practical evolutionary applications (see agroecology and medicine) than others (see palaeontology), but they all make clear and valuable contributions.

In 2008, two years after the publication of Mindell's book, Louis Bernatchez and Michelle Tang launched the new journal *Evolutionary Applications*. In their message to the readers, the editors stress the motivation for the production of this new journal in this manner:

> Evolution now permeates all aspects of biology and evolutionary tools and approaches are increasingly being applied to problems of considerable socio-economical importance. For instance, evolutionary theory guides research aimed toward reducing drug resistance of pathogens and parasites, ensuring the long term genetic health of endangered species and crops, improving the understanding of the ultimate causes of medical diseases, and predicting the genetic response of populations to climate change and exploitation.

Such a new forum for the introduction, analysis and critique of evolutionary applications across many fields is not only welcome, but I hope that it will grow in importance and influence. Some universities around the world are already opening centres and new courses for the study of evolutionary applications (e.g. in Finland, Denmark, New Zealand, USA), but the number and

scope of such courses and research centres will hopefully increase in the future. Evolutionary think-tanks are also appearing, such as the *Evolution Institute* (http://evolution-institute.org) with the mission of using 'evolutionary science to solve real-world problems'.

Practical applications of evolutionary theory may hopefully also help defuse some of the nastiness in the current religion–evolution debate, perhaps by injecting a bit of pragmatism into the sometimes ideological tone of the debate. In a recent study of the degree of public acceptance of the theory of evolution across 34, mainly European, countries, but also with the inclusion of Japan and the USA for comparison, Jon Miller, Eugenie Scott and Shinji Okamoto (2006) showed that the USA had the second lowest percentage of respondents believing that the theory of evolution was true (40%); the lowest percentage was reported from Turkey (less than 30%) (see Figure 15.1 in Futuyma's chapter). In the past 20 years, the percentage of adults who reject evolution has declined from 48% to 39% in the USA, but only because the percentage of people who are unsure about evolution has increased. In the rest of Europe and in Japan, acceptance of evolution was much higher, reaching a peak of around 80% in Iceland and Denmark and a low of over 40% in Cyprus. Miller *et al.* suggest that the literal belief of the account of the creation of humans and the rest of life as it appears in the biblical book of Genesis explains the pattern (note that most countries surveyed have mainly biblical religions: the only country with mainly non-biblical religions, Japan, shows an acceptance rate of evolution of around 70%). However, acceptance of evolution increases – in countries where biblical religions are prevalent – whenever such religions are more favourable to a metaphorical reading of Genesis. Interestingly, such flexibility in religious matters allows believers to retain those aspects of their faith that help them operate in life, whilst at the same time providing them with the opportunity to incorporate potentially useful knowledge produced by scientific evolutionary research. That is, by being flexible and pragmatic they enjoy the best of 'both worlds'!

Right at the outset I should clarify that the use in this book of the expression 'evolutionary theory' is meant to point to the fact that our understanding of evolutionary processes is achieved through the scientific method. The scientific method is based on the proposal of hypotheses that are tested empirically and rejected or retained on the basis of the results of such empirical evidence. Current acceptance of a well-supported theory is a pragmatic step, limited by the requirement to keep our eyes open for the eventuality of future potential falsifications. Therefore 'evolutionary theory' is simply shorthand for 'the scientific theory of evolution'. At this point in time, the scientific theory of evolution has been shown to be far superior to any other alternative to explain the diversity of life and its variable expressions over time. In fact, strictly speaking, the many applications of evolutionary theory that will be mentioned in this book are indeed further tests of the

theory. A theory that is false cannot produce consistently successful applications, let alone consistently successful applications in a myriad of different specialised areas. As we apply a theory for various purposes, sooner than later the truth will surface and any sham will be unmasked for what it is. In addition, commercially successful applications of the theory demonstrate not only that the theory is empirically supported but that, after all, evolution 'does … cash out' (Coyne, 2006).

Needless to say, the list of topics that are covered by the various chapters in this book is but a tiny fraction of the topics that could have been included. Many readers will undoubtedly come up with additional interesting examples that are within their field of expertise. On the other hand, I would not be surprised if the title of some of the chapters may puzzle a few readers (this has already happened during the process of production). I did my best to expand the topics covered in this book into some areas that although they have attracted a degree of controversy in the past, are both important and currently the subject of very sophisticated scientific research (e.g. music therapy, evolutionary basis of homosexuality). Finally, readers will notice that the word Darwinism is sometimes used in this book. By Darwinism, we simply mean the scientific theory of evolution that specifically stresses the central role of natural selection as the mechanism explaining adaptation (not all evolution is adaptive, but adaptive evolution critically proceeds through the mechanism of natural selection, whether via its more *gradualistic* – favoured by Darwin – or more *punctuated* modality – favoured by Eldredge and Gould). Darwinism could also be understood in the sense of 'using Darwin's ideas for ideological reasons, that is as a kind of secular religion – this would cover Social Darwinism but also the New Atheists' use of Darwin to promote the cause of anti-religion' (I thank Michael Ruse for this definition). I do not personally regard this book as a flag-bearer for ideological Darwinism. The purpose of this book is simply to illustrate how practical applications can be derived from evolutionary theory across many fields. It is such successful applications, and other empirical evidence, that establish a link between theory and reality.

I conclude this introductory chapter with a brief explanation of the organisation of the book, followed by summaries of all chapters that are supplemented with some personal comments and ideas. The book is organised into six parts addressing broad areas of evolutionary applications: *Evolution, Ecology and Conservation*; *Evolution and Food Production*; *Evolution and Medicine*; *Evolution and Psychology*; *Evolution and Computing*; and *Evolution and Society*. Some of the major issues in each of those broad areas are critically discussed in a variable number of chapters, from two to four. In order to facilitate the comparison across chapters, they are all structured following a common format that includes a brief introduction, followed by a 'The Main Issues' section, where a review of the relevant aspects of the field is provided. A 'Looking Forward' section comes next, where the specific evolutionary

applications in the field are discussed. Finally, a 'Conclusions' section drives home the main message of the chapter.

We start with the section *Evolution, Ecology and Conservation*, with John Long contributing the first chapter: *Evolution, missing links and climate change: recent advances in understanding transformational macroevolution*. Long introduces what may be regarded as one of the most important of evolutionary sciences: palaeontology. Fossils not only provide the most tangible evidence for evolution (macroevolution in particular), but they are also a window to the past of our planet and the effects that environmental changes had – and may again have in the future – on life. Long invites us to see the major transitions in the evolution of life as specific solutions to novel challenges: living on land that requires specific modes of locomotion such as the use of limbs; lifting one's body through the air that requires a light skeleton along with powerful muscles and wings; producing offspring that become independent soon after birth requiring mechanisms to nourish those offspring during the initial stages of development. When new environments are colonised, evolution seems to proceed through a burst of biological diversity that could be interpreted metaphorically as many 'proposed solutions' to living in such an environment; with time, only some of those solutions are retained. Such a pattern of high initial biological diversity followed by a decrease could be explained, for instance, by the association of environmentally induced stress with increased rate of mutations, and subsequent loss – through natural selection and genetic drift – of some of the variants. We can also learn from this process in our own search for practical solutions to the problems we face: a burst of creative ideas first, followed by pruning out those that do not quite work. If this sounds familiar, this is in a nutshell the description of the scientific method. As noted by the philosopher Karl Popper, science is, at its core, an evolutionary process. Life, however, is a bit less efficient than that, as it lacks the benefit of foresight. Thus, the solutions that are retained during evolution are not always optimal. In his chapter, Long points to various major applications of palaeontological knowledge to addressing current problems, such as what to expect in terms of biodiversity variation in the face of global climate change. Past records of climate change and mass extinctions suggest that the impact of climate on biodiversity will be variable and dependent on both current adaptations of the various taxa and the ability to experience accelerated evolution.

Biodiversity changes can occur not only in long-term geological time, but also in more short-term ecological time. Such short-term changes in biodiversity can be detected both through surveys of population sizes ('body counts'), and also through study of genetic diversity ('allele counts'). Kamal Ibrahim and Roberta Torunsky tackle genetic mechanisms as they are applied to biological conservation in their chapter *Evolutionary perspectives in conservation genetics*. Evolutionary changes rely on genetic diversity. Hence, the

conservation effort to retain such diversity directly impinges on the ability of taxa to undertake evolutionary change into the future, including adaptive evolution. In the shorter term, the loss of genetic diversity may increase the probability of extinction, especially in a changing environment; a pressing issue these days if we consider human impact on wild populations of animals and plants, compounded by broader-scale climate changes. For those species that can survive short-term environmental impacts, their longer-term viability may still be compromised by genetic effects, such as inbreeding depression.

The second part of the book deals with *Evolution and Food Production*. Agriculture may be regarded as a long coevolutionary process whereby humans nurture, breed and select (consciously or unconsciously) plants and animals as sources of food, fibres, and so on, whereas those plants and animals in turn exert a selective pressure on humans with regard to digestibility, defence against toxic compounds, defence against infectious diseases (e.g. zoonoses) and so forth. Steve Wratten, Mark Gillespie and Aldo Poiani open the series of chapters on evolution and food production with a chapter on *Evolution in agriculture* where they provide an overview of evolutionary applications to sustainable agriculture: the emerging field of *evolutionary agroecology*. Evolutionary applications to sustainable agriculture include use of pesticides at low doses to prevent adaptation from the part of pests against the chemicals used and, more importantly, to prevent side-effects of the pesticide on predators of those pests. Such a strategy favours biological control of pests. That is, interventions in agriculture should consider the ecosystemic nature of a cultivated field. One of the conundrums of evolutionary agroecology, as stated by Wratten *et al.*, is that sustainable agriculture relies on the 'collective performance of plant communities and ecosystems . . . i.e., we should improve the levels of organisation at which natural selection does not operate'. This will be achieved when studies of evolutionary dynamics of species relevant to agriculture are undertaken not in isolation, but in the context of concomitant evolutionary changes of other relevant components of the agroecosystem.

An example of such ecosystemic and evolutionary approach is provided by Martin Burd, Angelica Martínez Bauer and Mani Shrestha in their chapter, *The evolutionary ecology of pollination and the functional biology of agricultural plants*. Pollinators are central to the productivity of many crop plants, but the pollination process contains intrinsic stochastic features that constrain the evolution of maximum seed yield. Plants have evolved strategies to hedge their bets under such unpredictable circumstances, whereby each flower may produce many seeds if it happens to be pollinated. Moreover, pollination is a process that is affected by the structure of local communities and the interactions occurring among the different species. A rather neat example of the multispecies approach to pollination, involving the interaction between a flowering plant and two bird species, is described by Burd *et al.* in which

the evolution of greater attractiveness of flowers to a sunbird pollinator may induce territoriality in such species, thus producing the exclusion of a second pollinator bird species, a chat. Such exclusion may finally result in lower levels of pollination. This suggests that in agroecosystems, the achievement of maximum yield by means of managing pollination efficiency should at the very least consider interspecific interactions that occur at the guild level, the members of the community of pollinators for instance. However, one can very easily see how interventions that consider other trophic levels as well (e.g. predators) may also be helpful. In this context, evolution could be experimentally simulated by artificially altering some traits of specific components of the agroecosystem to determine the long-term effect on plant yield. If such an effect is considered useful in agricultural terms, then selection (or more direct forms of genetic manipulation) programmes may be implemented to produce components of the agroecosystem that have the required phenotypes. The only problem with this approach is that there is no guarantee that such designed system will be stable over time, or indeed that stability is necessarily a good feature. Environmental conditions are likely to change, thus establishing new limitations to the kind of communities of crop plants, pollinators, predators and so forth that will be associated with greater yield. Some organisms have evolved a degree of phenotypic plasticity that allows them to respond functionally to alterations of the environment; communities also respond to environmental changes. Whether it is possible to select for phenotypically plastic components of an agroecosystem that can respond functionally to altered environmental conditions in a manner that keeps crop production elevated and commercially viable, is something that seems prima facie far-fetched, but it certainly looks like an exciting challenge.

Commercial fisheries are another very important aspect of food production. Evolutionary issues relevant to fisheries are addressed by Mikko Heino, Adriaan Rijnsdorp and Ulf Dieckmann in their chapter *The dawn of Darwinian fishery management*. Commercial fisheries of wild stock tend to exert a selective pressure on fish populations that result in 'slower growth, earlier maturation, and higher reproductive investment'. That is, the long-term effect of commercial fisheries is to produce the conditions, via evolutionary processes, to potentially make themselves less commercially viable; certainly a rather undesirable outcome! Such evolutionary effects can be studied with the aim of reaction norms – that is, specific responses of various phenotypes (and genotypes) to environmental gradients – and also through laboratory experiments and modelling. One interesting evolutionary outcome of the effects of fisheries is that phenotypes that are more resilient to fishing should be selected. Hence, the objective of a more desirable evolutionary fishery programme would be that of producing viable and resilient populations of fish that also possess commercially useful characteristics, both in terms of individual fish size and population size. However, Heino *et al.* warn us that such an

outcome may be difficult to achieve given the usually negative effect that fish exploitation has on stocks and fish body size. On the other hand, this also suggests that fish populations that have adapted to fishing could be exploited commercially as food after they have been subject to a degree of processing (canned fish and so forth), whenever they lose their commercial appeal in terms of individual size, provided that population sizes remain sustainable. Alternatively, Heino *et al.* suggest the exploitation of fish populations at lowered intensities, or to selectively fish individuals of such a size that fishery-induced evolution is minimised.

In the third section of the book, the focus shifts to *Evolution and Medicine*, with four chapters exploring various evolutionary applications to the improvement of human health. The section starts with an introductory chapter by Randolph Nesse, *Evolution: a basic science for medicine*. Evolutionary aspects of disease that may suggest better prevention and/or treatment strategies are slowly being considered by the medical profession. Nesse rightly points out that there is still an apparent reluctance to use the word 'evolution' in the medical profession, even when clearly evolutionary processes are being considered. However, he also reminds us that a more explicit evolutionary approach to medicine may provide relatively easy solutions to some major public health problems – such as containing the spread of contagious diseases – that can save many lives, especially in economically developing countries or in less-privileged areas of economically more-developed countries where resources are at a premium. On the other hand, a better understanding of the physiological and adaptive role that some metabolic products have may help redress our views that some such products are just waste or potential causes or evidence of disease. Once an adaptive function of a metabolic product has been recognised, then currently acceptable threshold values for such a product in the body may be increased, thus helping the patient and also saving resources in the process. The same principle can be applied to mental health, where some behaviours, such as anxiety or psychological distress, may be adaptive responses to emergency situations that could be controlled relatively easily by means of some changes in lifestyle, rather than by undergoing radical and expensive medical interventions. Solid, scientific knowledge of evolutionary medicine will empower not only the physician, but also the patient.

Some of the issues addressed by Nesse are further developed by Paul Ewald and Holly Swain Ewald in their chapter *Evolutionary insights for immunological interventions*. Ewald and Swain Ewald point to a very important feature of the physiology of organisms: the interconnectedness of mechanisms and functions. Researchers have been focusing on such interconnectedness for some time now, so much so that new disciplines such as Neuroimmunoendocrinology have emerged in recent years to address the study of interconnected systems. The hope is that from such knowledge a more