Darwin's legacy in South African evolutionary biology

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In the two decades after publication of the *Origin of Species,* Charles Darwin facilitated the publication of numerous scientific papers by settler naturalists in South Africa. This helped to establish the strong tradition of natural history which has characterised evolutionary research in South African museums, herbaria and universities. Significant developments in the early 20th century included the hominid fossil discoveries of Raymond Dart, Robert Broom, and others, but there was otherwise very little South African involvement in the evolutionary synthesis of the 1930s and 1940s. Evolutionary biology developed into a distinct discipline in South Africa during the 1970s and 1980s when it was dominated by mammalian palaeontology and a vigorous debate around species concepts. In the post-apartheid era, the main focus of evolutionary biology has been the construction of phylogenies for African plants and animals using molecular data, and the use of these phylogenies to answer questions about taxonomic classification and trait evolution. South African biologists have also recently contributed important evidence for some of Darwin's ideas about plant–animal coevolution, sexual selection, and the role of natural selection in speciation. A bibliographic analysis shows that South African authors produce 2–3% of the world's publications in the field of evolutionary biology, which is much higher than the value of about 0.5% for publications in all sciences. With its extraordinary biodiversity and well-developed research infrastructure, South Africa is an ideal laboratory from which to advance evolutionary research.

Key words: bibliometrics, biodiversity hotspot, speciation, research trends, South Africa, species concepts

Introduction

The publication of Darwin's *Origin of Species* in 1859[1] marked one of the great revolutions in science. Darwin's central idea, that species diverged through natural selection and are thus related by a branching pattern of common descent, provided a new materialistic explanation for the diversity of the natural world.

How did evolutionary biology develop in South Africa over the subsequent 150 years, and what were the milestones along the way? What are its current strengths and roles in a modern democratic South Africa? To address these questions I review the South African literature on evolutionary biology, first as an historical narrative, and second with respect to noteworthy research themes. I also consider the extent to which sociological misinterpretation of Darwin's ideas had an influence on the development of racist ideology in South Africa. Finally, I present the results of a bibliographic analysis of publication trends in evolutionary biology for South Africa, relative to other countries which cover the range from developing to developed economies and low to high biodiversity.

The biological sciences, together with geological and medical sciences, have historically been relatively strong components of the research system in South Africa.[2,3] In the case of biological and geological sciences, the most likely explanation for this is that these benefit particularly from the rich natural resources of the region.[4] Evolutionary biology, in particular, has benefited from the extraordinary diversity of plant, mammal, bird and invertebrate species, as well as the key fossil hominid discoveries in the region.

One indication of the prominent position of evolutionary biology in South Africa is that seven of the ten most cited papers in the multidisciplinary *South African Journal of Science* are in this field.[5–11] Pockets of South African excellence can be identified in several subdisciplines of evolutionary biology, including hominid palaeontology, systematics, species concepts, speciation research, the study of adaptation, and coevolution. Before considering the specific contributions that have been made to these subdisciplines, I sketch the historical development of evolutionary biology in South Africa from the time of Darwin.

Darwin's correspondents in South Africa

Towards the end of its famous voyage (1831–1836), the *Beagle* docked in Cape Town from 31 May to 18 June 1836.[12,13] Darwin used this opportunity to meet local scientists, such as the astronomers John Herschel and Thomas Maclear, and to explore the adjacent coastal plain and mountains.[12] Seemingly unimpressed, and apparently oblivious to the great botanical richness of the region, he commented that there 'was very little of interest' to be seen on these excursions.[13] Darwin did not travel abroad after returning to England and, in later years, seldom even attended scientific meetings in London. He consequently relied heavily on written correspondence with fellow naturalists around the world in order to obtain scientific information. Settler naturalists in South Africa were inspired by Darwin's books and papers, and several corresponded regularly with him. Of interest here is that many publications by these settler naturalists in the *Journal of the Linnean Society* were personally facilitated by Darwin.

One of Darwin's most valued correspondents in South Africa was J.P. Mansell Weale, a naturalist who farmed in the eastern Cape region between 1860 and 1878. Weale shared Darwin's interest in the pollination mechanisms of orchids and other plants, and Darwin personally communicated several of Weale's papers for publication in the *Journal of the Linnean Society.* In 1871, Weale published a seminal paper on protective mimicry in the journal *Nature,* which was based on his field observations in South Africa.[14]

During the research leading up to the publication of *The Expression of the Emotions in Man and Animals* in 1871, Darwin distributed a questionnaire with a view to learning more about the cultural traditions of the 'native' inhabitants of the colonies. In particular, he was interested in testing his hypothesis that universality of expression of emotions reflects common descent. Darwin was interested in the expression of emotions in the Xhosa people of the eastern Cape, and enlisted the help of Weale to distribute copies of his questionnaire.[15] An interesting

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historical aside is that Darwin, who had expected his questionnaires to be completed by settlers, was somewhat taken aback to receive one with answers written in English by Christian Ngqika, a Xhosa constable working in the frontier town of Bedford.

Darwin also corresponded with Mary Elizabeth Barber, an amateur naturalist based in Grahamstown. Barber was the first woman to be admitted as a member of the South African Philosophical Society (later to become the Royal Society of South Africa) and was an accomplished painter and plant collector. Like Weale, Barber was interested in the pollination mechanisms of plants and published several papers on the topic with the assistance of Darwin.[16]

Barber readily incorporated Darwin's concept of natural selection into her own settler ideology of race. In several of her letters, she expressed views that made it clear that she considered the dominant position of Europeans in the colony to be a consequence of a natural biological hierarchy. In a thoughtful paper, Robert Shanafeldt[15] argues that Darwin should have foreseen the potential for his ideas to reinforce and justify the existing attitudes of the settlers. He describes Darwin's own views as 'tepid humanism', meaning that he neither condoned nor actively opposed these developments.

As amateur naturalists, Weale and Barber did not leave any institutional legacy of evolutionary biology in South Africa. By contrast, Roland Trimen, another of Darwin's correspondents, played an important role in the development of the South African Museum as its first director. Trimen was initially the private secretary to the then Colonial Secretary Sir Henry Barkly (1815–1898), who was also an amateur botanist and instrumental in encouraging the development of science at the Cape.[17] Darwin facilitated the publication of Trimen's first scientific paper, which was on the functional morphology of the orchid *Disa grandiflora* (now *Disa uniflora*),[18] but Trimen is best known for his work on the butterflies of South Africa, including a book he coauthored with James Henry Bowker (Mary Barber's brother).[19] Trimen, like Weale and Barber, was very interested in mimicry.[17] In a pioneering paper, Trimen, with help from Barber and Weale, identified various mimetic female forms of the butterfly *Papilio dardanus.*[20]

Natural history declined towards the end of the 19th century both in South Africa and abroad, although it was kept alive by systematists working in museums. Several universities were established in South Africa around the turn of the century,[21] but it would be some time before evolutionary research would be an integral part of their curricula.

The early 20th century

The most significant South African contribution to evolutionary biology, and arguably the most important contribution of the country to science generally, resulted from the discovery in 1924 of a well-preserved skull of a juvenile hominid in a limeworks quarry at Taung, near Kimberley. The significance of this specimen as a potential 'missing link' between apes and modern humans was recognised by Raymond Dart, the newly appointed head of the Department of Anatomy at the University of the Witwatersrand, who named the 'ape-man' *Australopithecus africanus.*[22] Dart inferred from the skull morphology that *A. africanus* was bipedal, and (with considerable verve given that he was just 32 and outside the scientific mainstream) wrote that the discovery could vindicate the 'Darwinian claim that Africa would prove to be the cradle of mankind'. This claim was met with considerable skepticism by the palaeontological community, first because Darwin's prediction about the emergence of man in Africa in his book, *The Descent of Man,* had been overlooked in favour of the idea that humans evolved in Asia, and second because it had been assumed that bipedalism evolved only after the evolution of a large cranium (which the Taung child did not possess). Robert Broom, a physician and palaeontologist, who had described many new fossil mammal-like reptiles in the early part of his career, became Dart's major ally in South Africa. Broom discovered several adult specimens of *A. africanus,* as well as a new robust hominid *Paranthropus robustus* from the Kromdraai diggings in the 1930s and 1940s.[23] These and other discoveries eventually vindicated the Darwin-Dart hypothesis about the African origin of humankind.

Recent historical research has uncovered a number of important links between biological science and the development of racist ideology in early 20th century South Africa.[24] Harold B. Fantham, the first Professor of Zoology at the University of the Witwatersrand from 1917–1932, was an outspoken proponent of eugenics and, in a series of articles published in this journal, argued for the need for the state to take measures to maintain 'race purity'.[24] Fantham also had an influence on the geneticist Gerrit Eloff, head of the Department of Genetics and Breeding Studies at the University of the Orange Free State and an admirer of the German Nazi movement, who developed pseudo-biological arguments for the adaptiveness of Afrikaners to Africa and thus the supposed imperative to maintain the purity of their gene pool.[24]

Jan Smuts, prime minister from 1919 to 1924 and again from 1939 to 1948, was an amateur botanist with a strong interest in evolutionary theory, biogeography, and human origins. While at Stellenbosch University, Smuts had studied taxonomy under Rudolf Marloth, the author of *Flora of South Africa,* whom he later accompanied on many plant-collecting expeditions. Smuts served as the president of the South African Association for the Advancement of Science (S2A3) in 1925, and even intervened personally to secure a position for Robert Broom at the Transvaal Museum. The two men had a close relationship and shared rather unorthodox teleological views on evolution. Saul Dubow has termed Smuts a 'scientific nationalist'.[21] However, Smuts' 'holism' is scarcely compatible with Darwin's theory that selection acts on individuals, although it does share with Social Darwinism the dangerous premise that biological laws should be the inspiration for human society.

Jeffrey Lever[25] has described Social Darwinism as an 'intellectual pathogen' that was imported from Europe and used to reinforce the pre-existing folk ideologies of racial superiority among white South Africans. However, with some notable exceptions,[21,24] there have been few studies of the actual extent of its influence on the development of policies of racial segregation. By and large, Christian Nationalists tended to justify racial segregation on the basis of a divine mandate, rather than the pseudoscience of Social Darwinism. Darwin's theory, its main buttress, was rejected on religious grounds by nationalists that took power in 1948, and it was not until after the first democratic elections in 1994 that evolution was even permitted to be taught again in schools.[25]

South African evolutionary biologists had very little to do with the evolutionary synthesis of the 1930s and 1940s, and the second half of the 20th century, until 1990, was characterised by the academic isolation of the apartheid era.

The late 20th century to the present day

The groundbreaking work by Dart and Broom helped to establish palaeontology as one of the strongest branches of science in South Africa during the second half of the 20th century, with a steady stream of new discoveries, and the development of top-class facilities, such as the Bernard Price Institute for palaeontological research at the University of the Witwatersrand. Leading palaeontologists of this period included Philip Tobias, Bob Brain and Elisabeth Vrba, while groundbreaking work on the genetics of modern humans was conducted by Trefor Jenkins and Himla Soodyall.

The University of the Witwatersrand (Wits) was indisputably the leading centre for evolutionary biology in South Africa during this period. The zoologist Hugh Paterson, who was based at Wits, developed the 'recognition' species concept in the 1970s, which strongly influenced a generation of South African biologists. Paterson's influence is especially evident in the book *Species and Speciation,* edited by Elisabeth Vrba.[26] This book contained contributions from a wide range of botanists, zoologists and palaeontologists who had participated in a symposium at the Transvaal Museum in 1982. The 1980s were also characterised by the emigration of many leading evolutionary biologists; this is evidenced in the change of addresses for fully one third of the authors in *Species and Speciation* between the time of the symposium and publication of the book in 1985. The published opening address by the then chairman of Anglo-American Michael O'Dowd was singled out in a review of the book by the leading American systematist Michael Donoghue for containing 'a form of biological determinism' that could be cited as justification for apartheid.[27] Although these charges were perhaps unfair since O'Dowd had actually emphasised the distinction between biological and social evolution, they nevertheless highlight the considerable political tensions of that decade.

The end of apartheid and the first democratic elections in 1994 brought an end to the formal and informal isolation of academia in South Africa. New collaborations with scientists in other countries were forged, and evolutionary biology was strengthened in many universities. This period of optimism also coincided with the new availability of the technique of automated DNA-sequencing that gave biologists a source of vast amounts of new molecular data with which to construct phylogenies for plant and animal groups. And in 1999, Sterkfontein and other fossil hominid sites received recognition as the UNESCO 'Cradle of Humankind' World Heritage Site.

In this penultimate part of the review I explore specific themes which have been a focus of research efforts by South African evolutionary biologists in both the past and the present centuries.

Species concepts and speciation

Darwin considered species as arbitrarily defined entities resulting from adaptive divergence.[1] He explained the discontinuities between species as the result of extinctions rather than breeding barriers.[28] His view that species did not differ in any profound sense from intraspecific levels of the taxonomic hierarchy was probably a deliberate attempt to counter the prevailing creationist notion that species have a special status in nature. This led to later claims that Darwin failed to solve the 'species problem' and that the title of his book *On the Origin of Species* was misleading.[29] However, Darwin's uniformitarian view of species has enjoyed considerable support, particularly from botanists,[30] and is being increasingly advocated by zoologists who find the idea consistent with both morphological and molecular evidence.[31]

In contrast to Darwin, Dobzhansky[32] and Mayr[33] considered species to have a distinct property: reproductive isolation from other species. There are now a plethora of different species concepts, but their biological species concept (BSC) is by far the most widely accepted, especially among zoologists.[29] The BSC was attacked by the South African biologist Hugh Paterson in a series of articles, many published in this journal, during the 1970s and 1980s.[6,34] In its place, Paterson proposed the 'recognition' concept of species which emphasised the reproductive cohesiveness of species arising from a 'specific mate recognition system' (SMRS). As a concept of species, it was rather similar to the 'cohesion' concept developed by Templeton,[35] and Carson's (1957) concept of the species as a 'field for gene recombination'.[36] The recognition concept had a major influence on the development of evolutionary thought in South African universities and museums.

Paterson was particularly opposed to the idea that reproductive systems evolve through a process of reinforcement (selection for traits that limit hybridisation in a secondary contact zone).[6,37] His dismissal of the latter possibility was based on the simple observations that most speciation is allopatric and that even if traits were selected through reinforcement in a secondary contact zone, such traits would not have fitness value outside the contact zone and therefore be unlikely to be fixed at the species level. However, Paterson has been justifiably criticised for over-emphasising the dependence of the BSC on reinforcement and then attacking this formulation of the BSC as a straw man.[38] While it is true that Dobzhansky, in particular, commonly invoked reinforcement to explain differences in reproductive characters,[32] Mayr tended to emphasise pleiotropy as the explanation for divergence in reproductive characters.[33]

Mayr's emphasis[33] on pleiotropy as the explanation for the building of reproductive isolating barriers in allopatry was plausible for some aspects, such as genetic incompatibility, but was an unsatisfactory explanation for divergence in the complex reproductive characters, e.g. genitalia, that are often used to diagnose species. By contrast, Paterson[6,39] emphasised the direct role of selection for traits that improve mating success as an explanation for divergence in reproductive systems. He, and others at the time, tended to emphasise the role of the physical environment in this process,[40] but sexual selection provides another, even more potent, force for allopatric divergence in reproductive systems. Mary West-Eberhard's classic review of the role of sexual selection in speciation[41] provided some of the missing pieces of the puzzle of why adaptive radiations so often involve reproductive traits, although she was seemingly unaware of Paterson's work at that stage. Her apparently independent conclusion that sexual selection could drive the divergence of systems of 'species recognition' in allopatric animal populations was uncannily close to Paterson's concept of speciation.

Paterson struggled to develop a useful definition of an SMRS in plants, and specifically excluded asexual organisms from his concept, and thus, like Mayr, did not succeed in developing a universal genetic species concept. With the hindsight of history, Paterson made a valuable contribution in emphasising the importance of allopatric divergence of reproductive systems under selection for increased mating success, and inspired South African biologists (and the few elsewhere who read his work) to think more deeply about the process of speciation. However, he did not provide a species definition that was much more useful than the BSC, and this may be because he accepted the prevailing dogma that species are special units of organisation in nature, as opposed to a convenient label for profoundly divergent forms, as advocated by Darwin and several contemporary evolutionary biologists.[30,31]

The extraordinary biodiversity of South Africa has been a major inspiration for evolutionary biologists. Why are there so many species, and why are there particular concentrations of species in some regions? Elisabeth Vrba[8] made an important early contribution by emphasising the role of natural selection in changing environments at a time when most models of speciation involved non-adaptive processes, such as drift. In recent years there has been a special focus on speciation of plant species in the Cape floristic region.[42,43] Dating using calibrated molecular clocks suggests that some groups have radiated very rapidly[44,45] while others have been present in this region for at least 30 million years.[43] Hypotheses for high rates of diversification have ranged from habitat heterogeneity combined with short-distance gene flow,[46] to the role of fire in enforcing isolation between populations,[47] to selection imposed by a geographical mosaic of pollinator availability.[30] All of these models have at least some empirical support[48–52] and current consensus favours a plurality of explanations, including the possibility of low extinction rates which allows species to accumulate in a particular region.[53,54]

Adaptation: from functional morphology to the comparative method

Studies of functional morphology were the main focus of evolutionary studies in the Darwin era. This was premised on the idea that if a trait could be shown to have a function it was likely to have evolved through natural selection. In the 1970s, Stephen Jay Gould, in collaboration with Richard Lewontin and the South African palaeontologist Elisabeth Vrba, published two important caveats to this approach, first pointing out that many traits are, in the historical sense, 'exaptations' whose current utility differs from their evolved function,[55] and that other traits are simply byproducts of the *Bauplan* (blueprint) of the organism, rather than direct products of selection.[56]

Evolutionary ecologists in South Africa have long sought to understand how the plants in the wide diversity of biomes in the region have adapted to their local physical environments.[48,52,57] Notable contributions include studies of the significance of resprouting,[58] resource allocation in grasses adapted to different soils,[52] and the adaptations of plants to fire.[57] Fire is a major shaper of ecosystems in South Africa and models show that in its absence large areas of the subcontinent would be covered in forest.[59]

One of Darwin's favourite research themes was the floral adaptations of plants to their pollinators.[60] South African biologists have provided some of the clearest examples of floral adaptation, including striking examples of Batesian floral mimicry (non-rewarding flowers that imitate the advertising signals of rewarding flowers).[61]

The first conceptualisation of coevolution was made in Darwin's book on orchid pollination[62] in which he speculated that the very long spurs of the Malagasy orchid *Angraecum sesquipedale* evolved under selection for efficient pollination by an as-yet-unknown giant hawkmoth with an exceedingly long proboscis which, in turn, evolved under selection to obtain the 'last drop' of nectar at the tip of the orchid's spur. This idea that reciprocal coadaptation could lead to exaggerated traits became known as 'Darwin's race' and some of the best available evidence for its occurrence in nature has come from biologists working in South Africa.[63–65] For example, in a mutualism between oil-producing flowers and oil-collecting bees in the Drakensberg mountains, there is striking population-level covariation between the flower depth in a guild of flowers and the length of the highly elongated front legs of one of the bee species (they use their front legs to scrape oil from the flowers).[63] Similarly, long-proboscid flies and their nectar host plants show geographically structured patterns of covariation that are consistent with coevolution.[64,65]

Because species tend to share trait values through common descent, any statistical analysis that assumes independence among species trait values may be invalid.[66] The phylogenetically informed 'comparative method' can overcome this problem when exploring the adaptive significance of traits.[67–69] In one study,[70] the comparative method was used to establish the significance for cross-pollination of the time taken for orchid pollinaria to reconfigure after withdrawal from flowers (an issue that particularly intrigued Darwin). In another,[68] it was used to identify large variations in patterns of metabolic rate in mammals, corresponding to the major zoogeographical zones of the world. These regional differences appear to reflect adaptation to climate, especially ambient temperatures and rainfall unpredictability,[69] and thus challenge the prevailing paradigm of a non-adaptive mechanistic determination of mammalian metabolism. Studies on insects also point to metabolic adaptation to climate.[71]

Darwin contributed many important secondary ideas to the science of evolutionary biology, including sexual selection and coevolution. Avian biologists have been at the forefront of sexual selection studies in South Africa. Some of the most notable contributions have included the demonstration that the multiple ornamentation of a red collar and long tail in male widow birds represent the result of selection through male–male competition and female choice, respectively, with a trade-off evident in investment in these two signal functions.[72,73] Avian biologists have also provided convincing evidence for egg mimicry by parasitic birds.[74] South African researchers Jenny Jarvis and Nigel Bennett have played a leading role in understanding the evolution of eusociality in mammals.[75,76]

Systematics

Systematics, the study of evolutionary relationships among organisms and their classification, is a scientific field which benefits directly from the rich biodiversity of South Africa. Systematics has always depended on collections and has thus been a key aspect of research in the major South African museums and herbaria from the time of their formation in the late 19th century.

Botanical systematics was a core function of the South African National Botanical Institute, which in 2004 became the South African National Biodiversity Institute with an expanded mandate to cover animal diversity. Other important developments were the formation of the Southern African Society for Systematic Biology in 1999 and the South African Biosystematics Initiative, a National Research Foundation (NRF)-managed funding initiative of the Department of Science and Technology (DST), which supports research in the general field of systematics. The past two decades have seen a considerable strengthening of phylogenetics, the specific component of systematics that deals with evolutionary relationships, and a weakening of capacity in traditional taxonomy, especially for species-rich groups like insects.

The phylogenetics of the Cape flora has received close scrutiny over the past two decades,[42,43] with notable contributions including a phylogeny based on exemplars of most of the genera in the flora,[77] evidence for rapid radiations in some groups,[44] and the use of dated phylogenies to answer questions about the age of the Cape and Namaqualand floras.[43,78] An important spin-off from these phylogenetic studies has been the gaining of deeper insights into biogeographic affinities of floras.[79,80]

South Africa does not have a unique zoogeographical region equivalent to the Cape flora, but has a notable diversity of mammals, birds and some insect groups. Phylogenetic studies of mammals have focused on the relationships within the Afrotheria, a largely African clade that includes elephants and aardvarks,[81] and the relationships of this group to the other placental

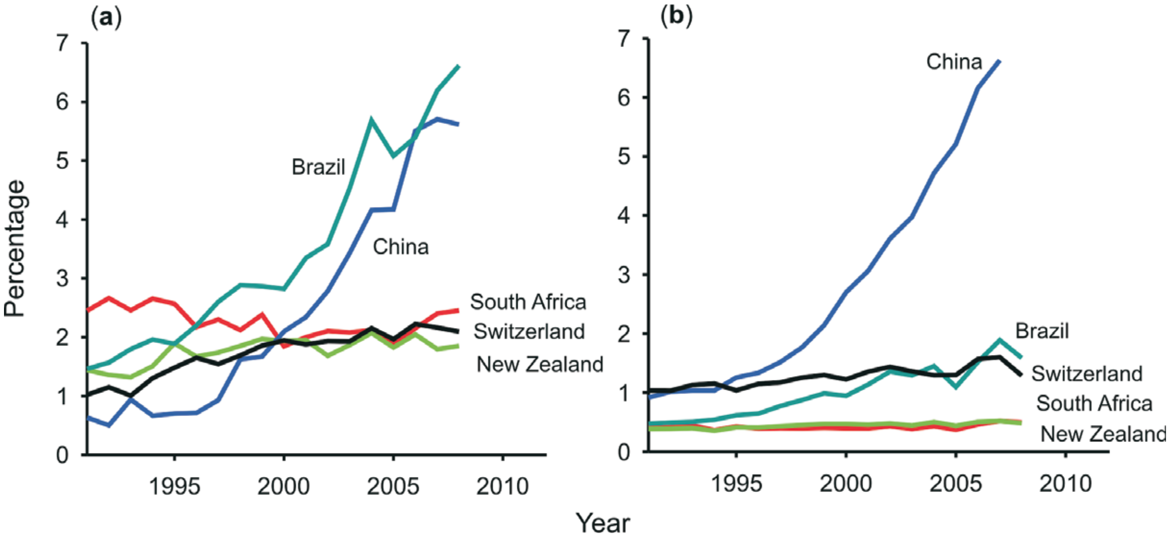

Fig. 1. The percentage of global publications in (**a**) evolutionary biology, and in (**b**) all sciences, contributed by authors based in South Africa, Brazil, China, Switzerland and New Zealand over the period 1990–2008.

mammals.[82] Studies of the population genetics and phylogeny of fishes have been valuable in understanding the evolution of river drainage systems in South Africa.[83]

Publication trends

To assess the position of evolutionary biology relative to other fields in South Africa and to determine how the global contribution of this field in South Africa compares with four other countries varying in development status and biodiversity, I conducted a bibliographic analysis using the Thomson Reuters ISI Web of Science®. Countries that were compared to South Africa were New Zealand, a southern hemisphere country whose total research output is almost identical to that of South Africa and which, like South Africa, has a natural advantage in evolutionary biology on account of its highly endemic fauna and flora and isolated biogeographical position; Brazil, a developing country with a megadiverse fauna and flora; China, which has one of the world's fastest growing economies and research environments; and Switzerland, a wealthy developed country with relatively low levels of biodiversity.

I first calculated the year-by-year (1990–2008) trends in the percentage of papers in the ISI Web of Science® database that are contributed by authors in the five countries. This was done to assess the performance of the overall science system in these countries. I then did a year-by-year (1990–2008) search for the keywords 'species', 'speciation', 'phylogeny' and 'adaptation' within six of the major biological knowledge fields (plant sciences, zoology, entomology, evolutionary biology, biology and ecology) in the Science Citation Index. This was done for the five countries, as well as the entire database, to assess the performance of the countries relative to global output in the field of evolutionary biology. This analysis cannot provide an absolute measure of outputs because of the limitations of the keywords, but can provide relative measures among countries and the entire database. The analysis proved robust to removal or addition of search terms. For example, the keyword 'species' was included on the grounds that taxonomy is part of evolutionary biology, but the trends obtained with and without this keyword were almost identical.

South Africa contributes about 2–3% of world output in the field of evolutionary biology, a value which has declined slightly over the past two decades (Fig. 1a). Very similar percentages and trends were obtained for New Zealand and Switzerland (Fig. 1a). In contrast, China and Brazil have shown a steep rise in their 'market share' of world publications of evolutionary biology papers, from positions similar or below those of South Africa, New Zealand and Switzerland in the early 1990s to contributions of about 6% and 7% of the world's output in 2008, respectively (Fig. 1a).

The contributions of South Africa, New Zealand and Brazil to evolutionary biology are all about four-fold greater than their proportional contributions to all world science publications (Fig. 1), suggesting that they have particular strengths in evolutionary biology and this is likely related to their natural advantages in terms of biodiversity. For China and Switzerland, on the other hand, the strength of evolutionary biology is roughly equivalent to that of the other sciences (Fig. 1).

These analyses are admittedly crude and do not take the citation impact of publications into account.[3] However, analysis of author affiliations of papers published in the leading journals in evolutionary biology over the past five years revealed a relatively healthy level of contributions from South Africa: *Biological Journal of the Linnean Society* (2.4%), *Evolution* (0.8%), *Journal of Evolutionary Biology* (1.1%), *Proceedings of the Royal Society (London): Biological Sciences* (2.1%), and *Molecular Phylogenetics and Evolution* (3.5%). This suggests that South African authors are making important conceptual advances in this field.

Conclusion

This review has identified evolutionary biology as a particularly strong field within the South African research system with a long tradition that can be traced back to Darwin. However the natural advantage that South Africa enjoys in this field has not yet been exploited to the full. Over time, it would be expected that countries with the richest biodiversity should make the most important contributions to evolutionary biology. Questions must be raised, therefore, about why other developing countries, such as Brazil, have managed to increase their share of world publications in this field over the past two decades, while South Africa has not (Fig. 1). One constraint on future growth is the legacy of years of willful neglect of evolutionary biology in the school curriculum,[25] combined with the persistence of poor schooling conditions for the majority of South Africans. These factors probably explain why ordinary citizens of South Africa fared the worst of those in any of the countries recently surveyed for understanding of Darwin's theory (British Council Press Release http://www.

britishcouncil.org/darwinnow-survey-global.pdf). Equipping citizens with the means to comprehend the enormous relevance of evolutionary biology is essential, not only for the basic sciences, but also for applied disciplines that are impacted by evolutionary processes, such as medicine,[84] invasion biology,[85] and conservation biology.[86]

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