Biological invasions and the conservation of biodiversity

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Summary
Consideration of definitions of 'biological invasion' and 'biodiversity' shows why invasions have recently generated great interest among conservationists. Many studies show that invasion numbers have increased drastically over the last five centuries, that this exponential increase is not levelling off, and that human activities are the only reason for the phenomenon. Many mechanisms are portrayed in an evolutionary framework and their consequences for biodiversity are described at three levels of life – gene, species and ecosystem. Examples from islands show that insular ecosystems are especially prone to damage from invasions; they also serve as 'laboratories' to elucidate the nature of invasion impacts. An important management approach – eradication – is discussed. Eradicating invaders not only aids understanding of their impacts on native species but also in understanding how ecosystems function. In fact, biological invasions can be seen as 'experiments', providing a rare opportunity to help answer certain fundamental scientific questions.

Keywords
Alien invasive species – Biodiversity – Biological conservation – Biological invasion – Eradication – Evolution – Invasive species – Islands – Science and society.

A biological invasion: an hypothesis that can be refuted

'Biological invasions' and 'the conservation of biodiversity': to suggest a relationship first requires a definition of each of these terms; in fact, to ask if they are scientific terms or vague concepts (74).

For a recent synthesis of the Holocene evolution of the vertebrate fauna of France (95), the definition of biological invasion provided by Williamson (131) – 'Biological invasion happens when an organism, any sort of organism, arrives somewhere beyond its previous range' – was rephrased as: 'Biological invasions happen when species achieve self-reproducing populations in ecosystems outside their natural distribution areas.' Though the spatial and temporal ranges of Williamson's definition remain, the

term is restricted to the taxonomic level of species, and the requirement is added that populations persist in natural environments, which excludes taxa represented only by captive individuals or in an enclosed space. A recent example illustrates this distinction. The sacred ibis (*Threskiornis aethopicus*) was introduced into France in zoological parks during the second half of the 20th Century. During the period in which it reproduced only in these parks, it was not viewed as having effected a biological invasion of France. It was considered an invader only when it reproduced outside the parks and the persistence of its new populations no longer depended on an influx of individuals from such parks (26, 95).

This is the definition adopted by the Delivering Alien Invasive Species Inventories for Europe programme (DAISIE), which aims to take a census of all animal and plant species that have invaded any region of Europe

during the last five centuries (www.europe-aliens.org/). According to this definition, to determine the native or introduced status of a species at a site requires critical analysis of information from palaeontologists, archaeozoologists, historians, biogeographers and ecologists. It is a matter of establishing an hypothesis from observations. However, the hypothesis can subsequently be refuted, which is the criterion for an enterprise to be truly scientific, according to Karl Popper (103).

Biodiversity: fuzzy concept or scientific reality ?

Thomas E. Lovejoy seems to have been the first person, in 1980, to use the term 'biological diversity', which was shortened to 'biodiversity' by Walter G. Rosen in 1985, during preparation for the National Forum on BioDiversity in Washington, DC, in 1986 (120). In 1988, the International Union for Conservation of Nature (IUCN), at its 17th general assembly, provided the following definition of biodiversity:

'Biological diversity, or biodiversity, is the variety and variability of all living organisms. This includes genetic variation within species and their populations, variation among species and their life forms, the diversity of complex associations of species and their interactions, and that of the ecological processes they influence or of which they are the actors [so-called "ecosystemic diversity"].'

Although Edward O. Wilson (132) used the term for the first time in a scientific publication while reporting on this assembly, he hinted at the difficulties of the concept in the definition he gave in 2000 (133): 'Biodiversity is the diversity of all forms of life. For a scientist, it is all the varieties of life studied at three levels: ecosystems, the species that make up ecosystems, and finally, the genes found in each species.'

The species level

The central object of activity by naturalists, the description of species, began to be intensively and rationally undertaken in the 18th Century by the explorer-naturalists. It is still pursued and routinely brings to light a great many new species, almost all of which remain unknown to the public at large. However, in the early 1980s, around the time of the emergence of the biodiversity concept, an important event shattered naturalists' perspectives. In 1982, in one fell swoop, Terry Erwin (45, 46) killed all the arthropods on a single tree in the Amazonian forest by fogging it with an insecticide: the number of insect species found on this one tree was the same order of magnitude as the number of all insect species known from all of North America! The estimate at that time of the total number of species on Earth, around 1.8 million, which had been established by extrapolating from the number of described species, suddenly exploded to numbers like 10, 50 and even 100 million species. Disagreements over these estimates reflected the inability to get adequate data (86, 87). As a result, the naturalist's dream – to describe exhaustively all species, record them and classify them – receded, and to fulfil it would require an entirely different approach from the one current in those days, of a few isolated naturalists undertaking relatively short expeditions, usually without much support. Moreover, it became abundantly clear that most species live in tropical and equatorial regions, the poorest areas economically and the ones with the most threatened environments. This fact, in turn, meant that, at precisely the moment when our perception of the extent of species-level biodiversity expanded radically, it became necessary to question just how strong our interest was in protecting it and by what means this might be accomplished.

The ecosystem level

The ecosystem level of biodiversity, recognised more recently than the species level, is the research object of many ecologists who seek to identify, understand and quantify the relationships that the living organisms of an ecosystem have with one another and with the physical components of the environment. Knowledge of these functional relationships is indispensable because, given the current state of understanding, simply having a list of the species contained in an ecosystem does not allow us to 'reconstruct' its structure. Both levels of description – species and ecosystem – are therefore needed, and, with respect to conservation, it is often easier to protect the ecosystem in which a threatened species is found than to focus simply on preserving the species itself. It was primarily research in conservation biology that led to this recognition (76).

The gene level

In the footsteps of Charles Darwin (37), population genetics teaches us that intraspecific variation is an important datum to quantify the 'health' of a species, because it is this variation that allows natural selection to operate. Substantial intraspecific genetic variation means that a species has a higher probability of evolving to deal successfully with environmental changes. In other words, evolution cannot occur without variation. Hubby and Lewontin (58) thus wrote in 1966:

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'A cornerstone of the theory of evolution by gradual change is that the rate of evolution is absolutely limited by the amount of genetic variation in the evolving population.… it is clear that genetic change caused by natural selection presupposes genetic differences already existing, on which natural selection can operate. In a sense, a description of the genetic variation in a population is the fundamental datum of evolutionary studies; and it is necessary to explain the origin and maintenance of this variation and to predict its evolutionary consequences.'

The environment into which a species is thrust is not only a physical environment but also a biological one, and all the variation residing in each and every one of these environmental compartments exerts a greater or lesser selective pressure on a species. By virtue of the reciprocal interactions among co-existing species, they co-evolve.

This is the mechanism by which the objects studied by geneticists, the genes, are tied to those studied by ecologists, the relations between species in an ecosystem. For a given species, this set of relationships constitutes the biotic part of the hyperspace that is its ecological niche, and the biotic functioning of an ecosystem is governed by the network of relationships that links the niches of all species in the ecosystem. Since every species interacts with others in the ecosystem, the arrival of a new species causes the redistribution of the resources at the base of the network, as the new species is forced to interact with the various biological and physical components of its new environment. This fact casts into doubt the validity of the concept of the 'empty niche'. Ultimately, every resource is always used, even if only by decomposers such as bacteria.

Two interacting species therefore exert selective pressure on each other. For example, co-evolution between a host species and its parasite leads to better adaptation of the host (for instance, by an immune response) that will be countered by a better adaptation of the parasite (for example, improved ability to inhibit the immune defences of the host). Despite the evolution of both partners, the degree of 'balance' in their relationship remains the same. This phenomenon has been called the 'Red Queen' (123), referring to the quandary of Lewis Carroll's famed character, Alice, in *Through the Looking-Glass*, who is suddenly forced to run with the Red Queen until she is exhausted and, on asking why, receives this response: 'Now, *here*, you see, it takes all the running *you* can do, to keep in the same place.' If 'the same place' corresponds to the situation of the species in the ecosystem, and 'the race' to the evolutionary process, the analogy is apt (27, 28, 29). But, in order for there to be a race, and for the species to persist as they are transformed by their evolution, there must be genetic variation. Knowledge and protection of this variation is therefore essential for the conservation of biodiversity.

Moreover, this variation has been used by humans since the Neolithic revolution, with the beginning of agriculture and the rearing of livestock. Agronomists today always look at wild stock for genes to improve the ability of cultivated varieties to resist pathogens or to thrive in particular cultivation conditions (e.g. 8, 12, 44), and genes can be transferred by genetic modification techniques between very distantly related species for purposes unrelated to agronomy, such as the synthesis of molecules for medical use or the extraction of metals from ore. Biodiversity has thus come to be seen as a giant reservoir of genes for agronomic (23), zoological, medical or industrial use.

Though the term 'biodiversity' remains the same, the underlying political rationale for its conservation has therefore become economic, and far removed from the reasons proposed by systematists, ecologists and geneticists. Among the objectives and results of the Rio Earth Summit of 1992 (122), it is the economic – and therefore political – motivation that has become the major one, surpassing scientific considerations.

Major difficulties for a scientist

Ecosystems, species, genes: different levels, but far from independent of one another. What can one say about a scientific object that we do not know how to quantify? To describe biodiversity in its totality implies simultaneously knowing ecosystems, species and genes, and the last two have themselves long posed grave problems of definition (72, 73). One might as well say biodiversity is an object of which at least some components are currently inaccessible. Is it, nevertheless, of real interest?

These gaps in general knowledge mean, as a corollary, that scientists are unable to respond to some questions that are essential for the preservation of biodiversity. Can we determine the minimum number of species that constitute a functioning ecosystem? Can we establish a threshold of genetic variation, below which a population is no longer viable? The answers are still uncertain and, though some cases have been well studied, it is difficult to generalise from them.

Moreover, to some extent, the task of the biologist entails different approaches and tools to deal with each of the three levels. Many biological sub-disciplines and specialties must be combined in research at the forefront of biodiversity science. To the fuzziness of the concept is thus added the multiplicity of approaches and techniques.

Although the three levels of biodiversity have been determined through biological knowledge, they have also been chosen to reach heralded goals; an effective conservation biology, on the one hand, and the

preservation of genetic resources, on the other. These goals, which are partly economic and political, have come to the fore in spite of the conceptual difficulties. Can these difficulties be surmounted?

In lieu of overcoming them, at least in the near future, a scientist who may be sought out and questioned on diverse facets of a field that can be called 'pre-scientific' finds him- or herself viewed as an expert, a situation for which academic science has not prepared them. Without going into detail, if someone soliciting advice considers a scientist an expert, the scientist can decline to be regarded in this way. If, however, the scientist accepts this designation, this means that they believe themselves qualified to give advice based on coherent, documented research. Moreover, they accept the possibility that subsequent evidence can contradict their advice. Whatever this advice, subsequent actions based on it are ordered by the decision-makers who sought out the expert. It is they, not the expert, who are held responsible, whether the results are seen as positive or negative. At least, this is the case as long as the expert, having given the advice, does not participate directly in the decision, no matter how heartfelt his or her convictions. Though the authors are not giving formal expert advice here, it is in this spirit that they will present a group of facts that appear to be important in understanding and managing biological invasions.

Biological invasion: a process that has gone on since the beginning of life, but that humans have recently accelerated to an unprecedented degree

Life did not have to wait for humans in order to move around, and the process of biological invasion, as it is defined above, occurred when life arose *circa* three billion years ago (16, 53). However, although Charles Darwin discussed invasions in his classic *Origin of Species* in 1859 (37), and the following century was witness to a dramatic increase in the rate of invasions, it was not until the 1958 publication of Charles Elton's book, *The ecology of invasions by animals and plants* (43), that widespread attention was drawn to this phenomenon.

In fact, although biological invasions began with the initial appearance of life, humans have played an undeniably major role in moving species around and have allowed

some species to cross barriers that were once totally impassable. Vertebrates are an instructive example. Although this is a taxon with rather few species, compared to insects, for instance, vertebrates have long been the object of special attention from several scientific disciplines, including archaeozoology, and the history of their settlement in France is well documented. One conclusion of a previously cited work (95) is that the rate of biological invasion into France was less than one invasion per century during the first eleven millennia of the Holocene (9200 BC to 1600 AD) but that it has risen to 136 invasions during the last 50 years. This remarkable acceleration was recently confirmed for all of Europe, and the exponential character of this growth shows no sign of flagging (51).

Moving beyond the vertebrates, the European DAISIE project reported its conclusions in January 2009. The most fundamental of these conclusions is that at least 11,000 plant and animal species have been introduced into Europe in the last five centuries (59). During the same period, at least 6,000 species were introduced to the continental United States (William Gregg Jr, personal communication). In the special case of one well-studied island, Morat *et al.* (89) determined in 1995 that New Caledonia has 3,322 indigenous plant species, of which 77% are endemic to the island (61, 62). In 2006, Meyer *et al.* (88), updating studies by MacKee (83) and Gargominy *et al.* (50), estimated that between 1,410 and 1,570 non-native plant species are naturalised on the island, according to the botanical definition of that term. One-third of the present plant inhabitants of New Caledonia are therefore introduced species, almost all of which arrived during the last two centuries.

The authors could cite many other examples, but what general conclusions can be drawn?

– These estimates are recent and rely on a body of research conducted during the last 20 years. A programme on invasions in the 1980s, undertaken by the Scientific Committee on Problems of the Environment of the International Council of Scientific Unions, unleashed a global concern with the phenomenon of invasions (117). The Convention of Biodiversity, opened for signature at the Rio Earth Summit in 1992, was marked by a strong statement on the need to combat biological invasion.

– All of these estimates show a large number of invasions.

– These invaders include many taxa of both plants and animals.

– The frequency of invasions has increased exponentially over the last 500 years, with no sign of slowing down.

– Human activity is the cause of nearly all recent invasions.

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Biological invasions: human actions have recently assumed a global dimension

Although human activity is the cause of nearly all recent invasions, it is striking that *Homo sapiens* never figures on the list of invasive species. Surely humans should have been included in the number of partly introduced species in the Holocene vertebrate fauna of France, in the work by Pascal *et al.* (95) on this subject, because humans colonised Corsica after the start of this period (125). During the last 15,000 years, an extremely short period on a geological time scale, humans have greatly increased their geographic range. They arrived in the Americas 14,000 years ago (52); 10,000 years ago they began to colonise the large Mediterranean islands (125); 5,000 years ago, humans from what is now Indonesia began their eastward migration, successively colonising all the Pacific archipelagoes, including Hawaii, Easter Island and New Zealand (84), and also moved westwards, arriving in Madagascar and the Comoro Islands (121). More recently, in the last five centuries, Europeans colonised, not always permanently, a large fraction of the sub-Antarctic islands (30).

Moreover, humans often deliberately introduced a number of species for their own use, especially after the advent of agriculture and livestock-rearing, but also, inadvertently, a number of hitchhikers, including commensal species. The commensal rodent species, all originally from Asia, are a good example. In chronological order of introduction, they are: the ship rat (*Rattus rattus*) and house mouse (*Mus musculus*), the Pacific rat (*R. exulans*) and, finally, the Norway rat (*R. norvegicus*). In less than three millennia, the Polynesians introduced the Pacific rat to all the archipelagoes they colonised, probably because this rodent was used for food, at least in the initial stages of colonisation (85). Atkinson's pioneering review (2), which merits an updating, shows that the ship rat and the Norway rat have been accidentally introduced to 82% of the world's archipelagoes over the last five centuries. Nor have continents escaped these invaders.

In what is now Israel, the house mouse established populations 12,000 years ago, as humans developed a sedentary lifestyle, based on cultivating and harvesting grain and constructing the first villages (7). The mouse reached Cyprus by 8000 BC (35) but did not colonise Western Europe until the Iron Age, *circa* 500 BC (34). The oldest accounts of the presence of the ship rat outside Asia come from Egypt and trace back to the middle of the second millennium BC (5). Later, at a relatively recent date, and apparently after the end of the Neolithic, this rat colonised the entire region surrounding the Mediterranean, as a human commensal. In fact, if remains from the Bronze Age found at Neuchâtel Lake (108) represent temporary incursions that probably died out, it was not until the end of the first millennium BC that stable ship rat populations arose in the western Mediterranean Basin. The arrival of this rat in Corsica has been dated exactly and found to be between the fourth and second centuries BC (126), at about the time it arrived in Pompeii. Beginning in the First Century AD, the ship rat appeared in non-Mediterranean Western Europe, where it remained restricted to urban ports, and it was not until the beginning of the Middle Ages that the frequency of its appearance increased in archaeological excavations, reaching 100% by the 14th Century (5, 6). As for the latecomer, the Norway rat, originally from northern China or Mongolia, it reached the West just before the 18th Century (24, 25). Naturalists of this period are sufficiently precise about the dates of its arrival in the great ports of northern Europe that one can reject the idea of a single decisive phase of invasion at this time (127). The Norway rat also has a similar history in parts of Africa. From approximately 1550 onwards, the ship rat and house mouse, and then the Norway rat, were introduced by European navigators to North and South America and Australia.

These few examples testify to the recent role of humans in invasions by countless species into terrestrial and freshwater habitats of islands and continents. But what about marine environments? Knowledge of the composition of marine communities and biogeography of marine species is much more limited than that of their terrestrial and freshwater counterparts. Though some specific cases are well documented, such as the introduction of the 'Portuguese oyster' (*Crassostrea angulata*) from Asia into Portugal between the 16th and 18th Centuries (15, 92), reviews of biological invasions of marine environments are rare. However, the chapter on this subject in the European DAISIE project records 737 marine introductions into European waters during the last five centuries, of which the oldest, that of the soft shell clam, *Mya arenaria*, may date back to the period 1245 to 1295, but cannot be confirmed until the 16th Century (49).

Once again, further examples can be cited, but what general conclusions can be drawn from those given here?

– In 15,000 years, humans have greatly expanded their biogeographic range.

– In their wake, they have deliberately or inadvertently introduced very many species.

– These 'hitchhikers' have established continuing populations in almost all ecosystems on Earth, whether continental or insular: terrestrial, aquatic or marine.

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Consequences of biological invasions for biodiversity

The stages of a biological invasion

To tally the consequences of biological invasions for biodiversity requires us to consider the general processes that occur during an invasion. Richardson *et al.* (105) and, more recently, Lockwood *et al.* (78) identify four main stages that every invasion must pass through, each entailing surmounting an obstacle. First, the species must somehow arrive alive at the new site; in this case, if the voyage is courtesy of humans, the swifter the voyage, the more likely the arrival is to be successful. The recent great increase in speed of both ships and aeroplanes therefore favours survival of potential invaders. The second stage consists of the new arrivals surviving. To do this, they must find whatever resources are necessary for their survival, particularly food and shelter. The third stage, which botanists call 'naturalisation', is reproducing and thus founding a continuing population that is restricted to anthropogenic habitats. Finally, the fourth stage is the invasion of new, more or less 'natural' habitats as the species spreads from the site of its introduction.

This division of the invasion process helps us to recognise several major difficulties in the overall perception of the scope of invasions and their consequences. In fact, the readily available information is almost all on successful invasions, with most failed invasions never being noticed (112). Among the many species that have recently arrived in new regions, some disappear without establishing populations and, among those that have established populations, some disappear before they become invasions. Given this fact, how can we determine the likelihood that an incipient introduction actually leads to an invasion? In addition, the time between the third stage (naturalisation) and the fourth stage (invasion) can be long; the consequences of an introduction may be seen only after a long time lag. Many important questions such as these cannot be fully answered yet. This is why the famous 'tens rule', proposed by Williamson (131), is the subject of lively controversy today. This rule, based on data from a group of attempted plant introductions in Great Britain, states that only around 10% of new arrivals establish populations and, of these, only about 10% become problematic (that is, invasive). However, for some taxa, the rule seems incorrect. For example, Jeschke (63) found much higher percentages of introduced birds and mammals establishing populations.

Biological invasions and species-level biodiversity

In a remarkable review of more than 30 years of archaeological research on Pacific islands, Steadman (119)

convincingly estimates that, in less than 5,000 years, humans, by colonising these islands and introducing pigs, dogs, Pacific rats and jungle fowl, caused the extinction of between 641 and 1,778 bird species. This number, compared to an estimate of *circa* 9,000 current species by De Juana (39), caused Steadman to call this the greatest vertebrate extinction caused by humans. Moreover, it has been determined that, since 1600, biological invasions have been responsible for 90% of the 30 documented reptile and amphibian extinctions (56), 93% of the 176 extinctions of bird species or subspecies (67), and 81% of the 65 mammal extinctions (21). Although the vertebrate extinctions are particularly well documented, which has allowed this generalisation to be drawn, the phenomenon of invasion-induced extinction has also been demonstrated for other taxa, such as terrestrial gastropod molluscs, whose rich diversity of endemic species on Pacific islands has been drastically reduced since the arrival of the Polynesians.

Robert Barbault records an incident in which, while he was walking with the parasitologist Claude Combes, they spotted a pigeon. Combes said to him, 'For you, it's a pigeon; for me it's a community of parasites!' (10). This observation emphasises the fact that all animals and plants harbour a collection of parasites, bacteria and viruses, so that, when a species is introduced, this group of fellow-travellers is carried along. In the past, when transport was slow, individuals infected by pathogens had little chance of arriving safe and sound, unless they were resistant, which probably explains the spectacular epidemics of plague, *Yersinia pestis*, in the Middle Ages in Europe, following the arrival of the ship rat, its reservoir, and the rodent flea, its vector (4).

The increased speed of modern transport greatly increased the probability of infected individuals arriving, even if they were doomed ultimately to sicken. This helps to explain the fact that 37% and 27%, respectively, of emergent diseases afflicting wild animals are either confirmed to have resulted or are highly suspected of resulting from introduced pathogens (41). Even beyond the role of 'carrier', a species new to an ecosystem can also collect pathogens from that ecosystem (e.g. 101) and, by becoming a new reservoir, can enhance the pathogen populations and their dispersal, which has consequences for the local species (28, 29). Finally, the co-evolution of new host-pathogen pairs is accompanied by an evolution of pathogenicity for various susceptible native species (64).

The role of biological invasions in many recent extinctions is no longer in doubt. But should we be speaking of 'the sixth extinction', as in the title of the book by Richard Leakey and Roger Lewin (75), which refers to the five mass extinctions brought to light by palaeontologists (38)? To call the current spasm 'the sixth extinction' is valid only if it is comparable in scope and nature to those described by

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the palaeontologists. However, the palaeontologists, unable to detail extinctions and new appearances at the species level for technical reasons, have quantified them at the family level. Now, how many families have disappeared in the last 15,000 years? The answer to this question shows that the current loss of biodiversity, though catastrophic, does not yet merit being called the sixth extinction. We should be heartened by this fact but must bear in mind that the tallies recorded by the IUCN are worrisome and the Red List of Threatened Species (60) suggests that extinction rates are poised to accelerate. For, in addition to extinctions that have already occurred, the IUCN profiles those likely to happen soon. It is instructive, in this regard, to add to the previous discussion of birds of Polynesian archipelagoes that, among the 28 native terrestrial bird species still present in French Polynesia, seven are listed as 'vulnerable', seven as 'endangered' (that is, in danger of rapid extinction), and five as 'critically endangered' (the most dire category). This means that 68% of this 'relictual' avifauna is now threatened with extinction (54). Finally, though it is true that each of the five palaeontological mass extinctions was succeeded, on a geological time scale, by a proliferation of new life forms, would these extinctions really therefore be called 'beneficial'? With such high stakes, is humanity ready to accept a bet that, over a very long time, a spurt of newly evolved species will follow current and future extinctions?

Managing biological invasions: the island case

It is on islands, which have relatively simple ecosystems, that the consequences of biological invasions are most obvious.

True 'oceanic' islands are those that have never been in contact with a continent. Biogeographers and ecologists often include in this category islands that have, in fact, touched continents in the past, but only in the very distant geological past, such as New Caledonia, Corsica and Sardinia. This extremely long or total isolation has resulted in the fact that insular plant and animal communities are 'depauperate' (low in species number) in relation to nearby continental regions of comparable size. Some entire groups of species with particular ecological roles are absent, a phenomenon called 'disharmony' (20). Insular food webs are therefore simplified. Finally, islands have a great many endemic species (91, 130). These have long evolved without undergoing the pressures of natural selection that continental species face, so they have lost or never evolved morphological, behavioural and chemical defences that could, for instance, protect them against introduced carnivorous or herbivorous mammals (3, 13, 17, 70). This is why the great majority of bird extinctions discussed above occurred on islands (11, 14, 32). Of extinctions of island bird species since 1600, 55% were caused by biological invasions (124).

Introductions of species have thus, so far, had a much more important impact on island biodiversity than on the biodiversity of continents. Over the last 50 years, many aggressive management operations targeting introduced species have taken place on islands; specifically, to lessen the risk of seeing still more endemic species become extinct. This is especially the case for the most drastic of such operations, eradication. Two other reasons, one technical and the other having to do with scientific research, have also led to most eradication campaigns being conducted on islands. The limited area of most islands means that it is easier to eliminate all individuals of a species from an island than from a continent, and the isolation of islands means the risk of reinvasion following a successful eradication campaign is also less. Moreover, an eradication constitutes an experiment at the ecosystem scale that is hardly feasible on continents. In addition, post-eradication monitoring allows identification and quantification of the impact of the eradicated species on native species and the functioning of the ecosystem, which, characterised by a simplified food web, is easier to understand on islands than on continents. It is also worth noting that, although island ecosystems are quickly affected by aggressive introduced species, one might expect their recovery to be equally rapid once an invader is removed. Finally, islands are often parts of archipelagoes, and this situation, offering the possibility of treating different islands differently so as to have controls and replication, lends itself to experimentation (22, 31, 93).

This is why at least 48 islands have been rid of their feral house cat populations; the largest is sub-Antarctic Marion Island, South Africa (290 km²) (90). Goats have been eradicated from 120 islands, of which the largest is Flinders Island, Australia (1,329 km²) (19). Among 344 attempts to eradicate island rat populations, 318 have succeeded: the Norway rat has been eliminated from 104 islands, the ship rat from 159, and the Pacific rat from 55; the largest of these are, respectively: Campbell Island, New Zealand (113 km²), L'Hermite, Chile (10 km²) and Hauturu or Little Barrier Island, New Zealand (31 km²) (57).

Literature on the consequences of eradications is voluminous, and the authors will give only a few examples from a recent review (80). In 1958, K.E. Stager (118) eradicated the pig population from Clipperton Atoll, which lies 1,000 km off the Pacific coast of Mexico. The populations of masked boobies (*Sula dactylatra*) and brown boobies (*S. leucogaster*) on this island, which were estimated at fewer than 150 individuals and 500 individuals, respectively, at the time of eradication, grew by 2003 to 112,000 and 25,000, respectively, allowing this small atoll to harbour the largest colony of masked boobies in the world and the second largest colony of brown boobies (102). In the five years following the

eradication of the Norway rat from Trielen Island in the Molène Archipelago (Brittany), the number of nesting pairs of the rock pipit (*Anthus petrosus*), the winter wren (*Troglodytes troglodytes*) and the dunnock (*Prunella modularis*) increased by factors of six, three and two, respectively, while those of 13 other terrestrial bird species remained remarkably stable (66). After the eradication of ship rats from the island of Lavezzu and its surrounding islets (Corsica), the nesting success rate of Cory's shearwater (*Calonectris diomedea*) jumped from 47% to 87% (97). A similar result was obtained for Audubon's shearwater (*Puffinus lherminieri*) in the nature reserve of the Islets of Sainte-Anne in Martinique after elimination of the same rodent (94). The complete destruction of hawksbill turtle (*Eretmochelys imbricata*) nests on the island of Fajou (Guadeloupe) ceased the year after the eradication of the small Indian mongoose (*Herpestes auropunctatus*) (81). These various experiments allowed a much better estimate of the scope of the impact of introduced species on native species, even when the existence of the impact had been suspected.

Eradication can also reveal an unsuspected level of interaction between an introduced species and native ones. This is what happened after the eradications of island populations of Norway rats in Brittany, where the abundance index of the lesser white-toothed shrew (*Crocidura suaveolens*) increased several ten-fold on Bono Island (Sept-Îles Archipelago) and Trielen Island (Molène Archipelago), as did that of the greater white-toothed shrew (*C. russula*) on Tomé Island, near the Sept-Îles Archipelago (98). Moreover, a trapping grid operated identically for nine consecutive years on a neighbouring island that had never had Norway rats (Béniguet, Molène Archipelago) showed that the abundance index of the lesser white-toothed shrew varied by no more than four-fold during that period, which included the eradications (96).

These examples show that:

– it is feasible to eradicate island populations of introduced species

– the maximum size of islands where successful eradications have occurred is constantly increasing

– the results can sometimes exceed expectations.

Managers have noticed these successes and an increased interest in eradication is the result. However, each campaign must be well planned, and it is important not to underestimate the preparation needed to overcome the inevitable difficulties. In fact, not only must the logistic, technical, human and financial resources be amassed but sometimes sociological impediments must be surmounted, and enough research must be conducted to show that the eradication will not be followed by an even worse

ecological problem. This can happen if the targeted species plays an essential role in the ecosystem that had previously been filled by a native species that is now extinct, or if the targeted invader is controlling some other invader that could have an even more drastic impact. Some failures along these lines are outlined by Loope *et al.* (79). To understand the risk, one must have detailed inventories of the native and introduced species on an island and a good sense of their roles in ecosystem function. Finally, the reasons for the eradication must be clear and plans must be in place to monitor the results of the eradication, to derive the full benefit of the experiment (31).

Island ecosystems are widely seen as precarious because they are in a sort of 'fragile' equilibrium, with their species having been subjected to much less rigorous selective pressures (82, 111, 114). Nevertheless, it is really more accurate to speak of 'instability' than 'fragility', and the difference between an island and a nearby continent has more to do with a difference in the dynamics of instability than with island communities being inherently unstable and continental ones stable. Because continental populations are large in size, they have great inertia and their evolution is slow. For islands, it is exactly the opposite, which explains the high rate of endemism among island species but also a high rate of extinction and, in parallel, a high rate of speciation, although it is difficult to amass evidence on the latter.

Biological invasions and the preservation of biodiversity

Political and economic goals have presided over the emergence of the concept of biodiversity, and the constraining scientific framework, with its focus on genes, species and ecosystems, tempts us to move beyond a purely scientific perspective. Two complementary viewpoints contribute to this temptation. One is that of philosopher and historian of ancient history, Pierre Hadot, who, in 2004 (55), published a work on the concept of the 'unveiling of nature', while the other was espoused by Heinrich Rickert (1863-1936), a logician and neo-Kantian epistemologist of the transition between the 19th and 20th Centuries (106, 107).

Hadot structured his work in two parts, each associated with an attitude that governs a method of studying nature. They are summed up in the conclusion of his book:

'Throughout my narrative, I have been able to observe two fundamental attitudes about nature's secrets: the voluntary and the contemplative. I have located the first under the patronage of Prometheus, who, in consecrating himself to the service of man, uncovered by ruse or by violence the

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divine secrets… Magic, mechanics, and technology are found in this tradition, and moreover, they have as a goal, each in its own manner, to defend the vital interests of man… As for the other attitude, I have located it under the patronage of Orpheus. In this case, nature wants to be hidden, because the discovery of her secrets is dangerous for man. By intervening technologically in natural processes, man risks disturbing them and, worse yet, unleashing unforeseeable consequences. From this perspective, it is the philosophical or aesthetic approach, that is, rational discourse or art – two undertakings that are ends in themselves and that assume a disinterested attitude – that will be the best way of understanding nature. Alongside scientific truth, it is therefore necessary to admit an aesthetic truth that constitutes a valid knowledge of nature.'

Is it possible that the combination of these two attitudes that seem *a priori* strongly opposed (although there can be an Orphic attitude in basic research, in economics and in politics) can yield a solution to the intrinsic difficulty in the definition of biodiversity, which does not belong solely to scientists? The Promethean attitude corresponds to:

– the study of ecosystem function

– analysis of species-level biodiversity

– protection of genetic resources

– the economic aspects of biodiversity.

The Orphic attitude refers to protection of key, highly visible species, landscapes and sacred places, but also to the biodiversity of cities and agro-ecosystems. To reconcile and pursue the two approaches, the aesthetic and the scientific, would produce the greatest and most effective constituency for preserving biodiversity.

Rickert, opposed to the long-standing classification of sciences said to be 'natural sciences' (physics, chemistry, biology) and those said to be 'social sciences' (psychology, history, etc.), distinguishes between fields that search for general laws and those that focus on particular cases and singularities:

'In order to obtain two concepts that are purely logical, and thus purely formal… I [Rickert] have myself sought to formulate the logical, fundamental problem posed by a classification of sciences according to two methods: reality becomes nature when we envision it as if it is universal, and it becomes history when we conceive of it in terms of particularities and the individual; and I want, therefore, to oppose the generalising approach of the natural sciences to the individualising approaches of history.'

This is the basis on which Rickert proposes a classification into sciences of nature and sciences of culture, while

recognising that certain endeavours partake of both approaches.

These two viewpoints, one emphasising the 'biological' facet, the other the epistemological aspect, show the confusion engendered by a concept that is too broad in scope, such as that of biodiversity.

Biodiversity and its preservation: science of nature or science of culture? To paraphrase Rickert is to say that biodiversity and its preservation are part of the sciences of nature when conceived under the aspect of the universal, and of history, the science of culture, when envisioned under the aspect of the particular, the individual. For example, when politicians and managers ask scientists the two fundamental questions relevant to invasion biology: what traits of a species are likely to make it invasive and damaging? and what characteristics of an ecosystem are likely to make it susceptible to damage from invasions? they are asking for general laws allowing an unambiguous response. When the same people ask what measures should be put in place to save the Tuamotu kingfisher (*Todiramphus gambieri*) on the Niau Atoll in the Tuamotu Archipelago, an endemic species reduced to *circa* 60 individuals and subject to predation by feral cats and two rat species, they are interested in the details of that particular species. To respond to this question requires integrating not only ecological knowledge but also the history of the arrival of mammalian predators on this island.

To address this history is to bring to the fore the big forgotten underlying basis for biodiversity, the theory of evolution, which teaches us that every species, every gene, every ecosystem is the result of a history, a history that explains its singularity. This fact brings to light the difficulty of speaking about biodiversity: what can we say in general if it is not drawn from the elements of ecology, population genetics or the structure of the genome? And is it not rather the singularities, the idiosyncrasies, that are so fascinating about biodiversity? The singularities that make sense only in the light of evolution, to paraphrase Theodosius Dobzhansky (42).

Biological invasions – a conceptual refocus?

Biological invasions constitute experiments, even if the experimenters or their descendants have often forgotten to leave behind the essential elements of the experimental protocol (93, 99). To think of invasions in terms of experiments that ought to be interpreted in the light of biological evolution is the object of an article by Sax *et al.* (109). Sax and colleagues identify a series of questions

that invasion biologists may be able to answer in ways that interest politicians and managers.

Are ecosystems saturated with species?

One interpretation of the equilibrium number of species in MacArthur and Wilson's theory of island colonisation (82) rests on the hypothesis that ecosystems become saturated with species. The only cases in which saturation has been clearly demonstrated are those of areas less than one square metre, which calls into question the ability to generalise from such observations (9, 129). Moreover, many data on the evolution of insular faunas and floras – as, for example, the recent evolution of the composition of the New Caledonian flora mentioned above – also cause us to question this hypothesis.

Competition rarely causes global extinctions in the short term

This fact is well demonstrated for plant species as well as for marine invertebrates, and is doubtless explained by the length of time involved. Global extinction of a widespread species caused by an introduced competitor probably takes hundreds if not thousands of years. However, competition may cause extirpations of local populations much more frequently than species extinctions. By contrast, many quite rapid extinctions of endemic species are well documented as having been driven by the introduction of a predator or pathogen, especially onto islands. It is important to bear in mind that all these forces, including competition, are always ongoing and important in the natural selection that drives evolution.

Communities often arise by ecological 'fitting together'

Recent studies seem to show that assemblages of species with greatly differing evolutionary histories may come together by a kind of ecological sorting, due to both biotic and abiotic variables, so that they *fit* together and, despite their heterogeneous pasts, the ecological community functions. This observation suggests that introduced species can sometimes find their places in native communities without causing catastrophes. Island ecosystems are often composed of species that have not had a long co-evolutionary past together, as has been demonstrated, for example, by Schoener *et al.* (110). However, any community 'functions', even a community in a devastated ecosystem; nutrients cycle and energy flows. There has been no systematic effort to determine if such rapidly assembled communities differ in characteristic ways from long-standing, presumably co-evolved, ones (115).

Adaptive genetic change can occur rapidly

Although genetic changes can be produced in a few years or even less in the laboratory, or in response to strong anthropogenic pressures, such as the evolution of resistance to pesticides and antibiotics, it has been shown that equally rapid changes can arise in nature in response to selection pressures exerted on newly introduced species or on native species confronted with newly introduced species. Studying such cases may aid managers of threatened populations to maintain genetic diversity.

Severe bottlenecks need not prevent rapid adaptation

A 'bottleneck' occurs when population size is drastically reduced. One event that produces bottlenecks is when a small number of individuals found a newly introduced population. In theory, the founders will have a small subset of the genes in the original population, while subsequent genetic drift will cause other genes to be lost, at least while the population remains small. This reduction in genetic diversity, in turn, should reduce the ability of the introduced population to evolve adaptively in response to new environmental pressures. Although such bottlenecks have been demonstrated for some introduced species (e.g. 1), there are also cases in which a population initiated by a small number of founders has not undergone a bottleneck (e.g. 65) or at least not a severe one. Such populations are believed to have escaped the consequences of a bottleneck by a rapid increase in population size, preventing genetic drift from operating. Moreover, some introduced populations are supplemented by new additions, bringing additional genetic variation, and if the new additions come from different regions, the introduced population may even have more genetic variation than any native ones (e.g. 69). In such cases, the introduced population should have an increased capacity to respond evolutionarily if the environment changes.

The 'climatic envelope' of a species need not predict the range of introduced populations

The native geographic distribution of a species depends on the combined physical and biotic selective pressures and the dispersal abilities of the species. Since it is often very difficult to estimate the magnitude of the biotic pressures, researchers have frequently used the 'climatic envelope' approach, based solely on the values of the physical environmental variables, to predict the ultimate range of a species when it is introduced to a new region (e.g. 100), or to predict the evolution of this distribution area under the pressure of climate change (36). However, observations of the spread of several introduced species show that such predictions can be very erroneous (e.g. 48). 'Ecological

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niche models' based on climatic envelopes do not take account of interactions of a species with other species in its native or introduced range, nor do they account for the possibility of evolution, so they may be inaccurate in predicting the success or failure of an introduced species, or how ranges will be affected by climate change.

Many introduced species undergo a substantial time lag before becoming invasive; often the reasons are mysterious

Sax *et al.* (109) did not mention the time lags – sometimes persisting for decades – that often typify invasions, as noted above. Although these have long been remarked upon (33), no general explanation has proven satisfactory. Research has shown some previously mysterious lags to be due to subtle environmental changes, a slow build-up of propagule pressure, the arrival of propagules bearing new genes, or the arrival of a previously absent mutualist (116). However, many lags remain puzzling, and the frequent existence of such time lags complicates management, because it implies that an introduced species that initially seems innocuous, not meriting management, cannot simply be ignored.

A new hypothesis: the pattern of specialisation within a community influences its degree of resistance to invasions

Sax *et al.* (109) emphasise a recent hypothesis by Callaway *et al.* (18): that biological invasions will be favoured if native predators and parasites tend to be specialised and, therefore, would be unlikely to attack a newcomer, and if native mutualist species are generalised, which means they would benefit new arrivals. Callaway and his co-workers provide supporting evidence for aspects of this hypothesis from several invasions of grasslands by particular species. However, it would be difficult to gather quantitative data for many systems to allow this hypothesis to be rigorously tested – the hallmark of an important scientific hypothesis – and applying this hypothesis to policies on introduced species and their management seems remote.

What can be concluded about biodiversity from the various facets of this conceptual refocus? Since ecosystems are unsaturated, they can receive new species and thereby increase in terms of species-level biodiversity. In some instances, the newcomers will be integrated into the ecosystem without major disturbances (including species extinctions), and this is especially possible if they are not predators or pathogens (or vectors of pathogens) of dominant or keystone species (see also 113). Unfortunately, many invaders worldwide have been precisely such predators, pathogens or reservoirs and, even worse, many of these have been generalists. Moreover, the most species-rich ecosystems have a high proportion of specialist species, which, according to the hypothesis, tends to favour the survival and high impact of invaders. As these high-impact invaders tend to be generalists, the proportion of generalist species in ecosystems tends to grow as that of specialists decreases, and this trend is accentuated by introduced predators and pathogens. In the end, ecosystems become enriched in generalists and impoverished in specialists. Quammen (104) envisions a world dominated everywhere by the same global 'weeds', both plants and animals.

Conclusion

There is no doubt that the number of biological invasions has increased greatly over the last ten millennia, and especially over the last 50 years; no doubt that the frequency of invasions is not slowing down; no doubt that they occur in every type of ecosystem – terrestrial, freshwater, marine, continental, insular; no doubt that many invasions have had enormous consequences to the functioning of invaded ecosystems, with impacts on plant and animal species going all the way to local extirpation or global extinction; no doubt that invasions induce genetic changes in both invaders and natives; no doubt, finally, that humans have recently been the agent of all introductions, with rare exceptions.

It is now more than 50 years (see also 43) since scientists have had some insight into these facts, but only 25 years since invasions have become a major research focus (117). Thus, invasion biology is a very young science and intensive management of invasions is largely a very recent phenomenon. Even today the effort is incommensurate with the global importance of biological invasions. Research teams are usually small and often poorly supported by their supervisors. Nevertheless, the extent of the impacts of biological invasions is now widely known internationally; the details of many invasions are well understood, and management approaches and likelihoods of success are better appreciated.

There is also no doubt that humans have benefited greatly from some invasions, especially through the deliberate introduction of animal and plant species from the dawn of agriculture and livestock-rearing, leading to the year-round availability of food. This innovation, in turn, has led to the great growth of the human population and massive increase in its geographic range.

Why, then, this change in perception, from the 19th Century enthusiasm for botanical gardens and acclimatisation societies (77) to the current distaste and fear, which can go so far as to lead governments to attempt to forbid the introduction of any species, deliberate or

accidental? Doubtless it was because of the realisation by a growing proportion of the population of the enormous recent increase in the scope of invasions and some of their impacts. Doubtless also because this recent perception is associated with the recognition of how greatly and quickly many familiar and even emblematic environments have changed, reflecting a disturbing instability, especially troubling because it is perceived within the lifetimes of individuals.

However, instability is a characteristic of life, of genes, of individuals from birth to death, of populations, of ecosystems, in short, of biodiversity. Is it possible to define an optimal instability? Does this question make sense, at least for evolutionists? The answer is not yet clear, and although palaeontology teaches us that massive changes in biodiversity occur at the scale of geological time, science cannot yet answer this question.

If the difference between an island and a neighbouring continent derives from a difference in the dynamic of instability, does the heavy footprint of human impact on islands provide a foretaste of what will happen on continents? Will the proliferation of introductions, one of the major causes of loss of species globally (40, 128), reach a level on continents that will cause the hecatomb of extinction observed on islands? This notion is purely speculative, but the parallel between islands and continents can be taken further by examining another major cause of biodiversity loss noted by Diamond (40) and Vitousek *et al.* (128): habitat fragmentation. Fragmentation confers some island-like features on continental areas. By isolating populations, habitat fragmentation reduces local population sizes and increases their instability. Whether this increase will lead to increased extinction and, if so, under what circumstances, is far from clear (47, 70). Beyond the effects specific to each of these causes of biodiversity loss – invasions and fragmentation – their synergy may cause the continental impact of invasions to approach that on islands. This line of reasoning suggests that use of the island model is an appropriate way to consider the mechanisms by which biological invasions affect the three levels of biodiversity.

Moreover, although the human species has greatly reduced its own risk of imminent extinction by massively increasing its geographic range and population size, how should we consider the nature and importance of the pressures exerted on humans by the components of the urban ecosystem that now houses most of us? In fact, this type of ecosystem has some characteristics in common with islands – low species diversity and disharmony, for example. Within urban ecosystems, the interactions between humans and other species are greatly reduced; what will be the consequences of this reduction?

Aside from their environmental consequences, biological invasions can have economic, public health and veterinary impacts. Surely, therefore, we should reduce as much as possible accidental introductions associated with our activities, and we should not seek to introduce new species deliberately unless they have been subjected to rigorous scientific scrutiny and past experiences have been taken into account (as there are no general rules to guide us). This same sort of scientific foundation will be needed to establish strategies of ecological restoration, as introduced species will have to be removed or managed for restoration to succeed. In fact, the accrual of scientific information on an ever-increasing number of 'experiments' (that is, invasions) will inform resource management and restoration; this information is all the more important because it is ethically impossible, given our current state of knowledge, to undertake deliberately many of the experiments on environmental management that would be meaningful.

Coda

When Rudyard Kipling, 1907 Nobel laureate of literature, had 'The Cat that Walked by Himself' in *Just So Stories* (68) say, 'I am the Cat who walks by himself, and all places are alike to me,' was he not intuiting the formidable adaptability of the cat, which has followed humans to inhabit very many islands? Moreover, in the context of the story, Kipling made no secret of the fact that, from its point of view, the cat has 'domesticated' humans and not the reverse. Poetic licence or fertile paradox that our dominant anthropocentrism causes us unconsciously to consider absurd and so prevents us from considering seriously?

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