Synthèses

Biological invasions, a question of nature and society

R. Barbault, M. Atramentowicz, coordinators

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Preface

Éric Vindimian

Our propensity for anthropomorphism conditions our imagination. We can thus all conjure up the image of our childhood teacher telling us of the great invasions: the Normans, those brave yet cruel seamen, the Huns with their unusual method of cooking meat, not forgetting the different groups of Goths, each as terrifying as the next. As soon as we mention biological invasions, that ancestral fear of the enemy ravaging everything in his path, under the horse's hooves where the grass no longer grows, invades our minds.

This fear is not completely removed from reality. Ecosystems are fragile. Communities are constructed over time and natural barriers condition their differential evolution. Thus, insular environments, more isolated by definition but also more unstable due to their size, are particularly vulnerable. This is all the more concerning as many endemic species restricted to isolated environments may disappear among competition for which they were unprepared.

However, the outlook is not all bleak in this complex world. The plague which ravaged human populations between the 12th and the 18th century partly owed its eradication to competition between the black rat *Rattus rattus* and the common rat *Rattus norvegicus* which arrived in Europe in the 18th century. The common rat, more resilient and prolific, almost completely exterminated the black rat, carrier of the infection. Within the Invabio programme itself, it has been shown that the invasion of Martinique by gastropods of the family Thiaridae has resulted in the eradication of schistosomiasis, a serious tropical disease, as the gasteropod *Biomphalaria glabrata* is no longer present to carry the terrible parasite *Schistosoma mansoni*.

The French ministry in charge of ecology was keen to find out more. As is its now well-established tradition, it called upon researchers to answer its questions. How can biological invasions be prevented? How can the risks they represent be assessed? What can be done to respond to current invasions? It was up to the ministry in charge of ecosystem management and protection to find answers to these questions.

As usual, as far as we are concerned, the approach was agnostic. The aim was not to establish new dogmas or to seek to restore nature to its untainted, wild form. Rather the research sought greater understanding of phenomena in progress and to put forward ideas for designing appropriate nature management tools.

Of course, and to no surprise of the ministry's research department, this all proved highly complex. The programme did not invent a universal formula against invasions. However it appears that we must act quickly, if we are to take action! Many non-native species become established without proliferating, some invasions spontaneously fail, others provide new services or even help to restore damaged ecosystem services.

The human dimension continues to have a strong presence in the management of biological invasions. An invasion is not necessarily perceived as such according to the people involved. For instance, some people see the *Prunus serotina*, which has invaded Compiègne Forest, as a magnificent tree producing edible fruit. Some do not see it at all! Many invasive species are also ornamental plants sought after for gardens. Human sciences help us to understand these factors, whose management strategies cannot be overlooked.

The Invabio programme gathered together a high quality, enthusiastic, interdisciplinary scientific community, harbouring the two-fold concern for scientific quality and support for public policies. Evaluation of the programme has shown that the national dimension is still lacking in terms of the distribution of results to managers. The gap between research which is conducted on a global scale and the different levels of management is a major factor in the future of programmes under the research department.

This programme would not have existed without its many supporters. We note the commitment of the Scientific Committee[1] and its President Robert Barbault, the valuable work of Éric Tabacchi and his team, the authors of the various reports and summaries in this book, the efficient coordination of Martine Atramentowicz within the research department and the enthusiasm of researchers and managers gathered together through this programme. I could not close this preface without sincerely thanking them, all the more as they gave me the opportunity to enjoy privileged times of dialogue and scientific reflection at the Moliets symposium (17-19 October 2006) during which the results were presented and discussed.

1. Members of the Scientific Committee: Robert Barbault (President of SC), Philippe Boët, Jean Boucher, Jean-Louis Chapuis, Jean Clobert, Sergio Dalla Bernardina, Alain Dutartre, Michel Echaubard, Pierre Joly, Jean-Noël Labat, Doyle McKey, Jacques Maillet, Yannis Michalakis, Serge Muller, Pierre Noël, Isabelle Olivieri, Michel Pascal, Bernard Picon, Jean-Sébastien Pierre, Jacques Roy, François Sarrazin.

Introduction

The ecology of invasions: old question, current news

Robert Barbault and Martine Atramentowicz

Since the pioneering work of Charles Elton, The Ecology of Invasions by Animals and Plants, published in 1958, the number of books produced on the problems caused by biological invasions and the questions they raise are countless. As for the phenomenon itself, it was not born yesterday, as it emerged upon the very appearance of living beings.

Indeed, it is rather misleading to confuse the propensity of all living beings to spread, which makes all species potential invaders, with what "defines" invasive species in the sense we understand them today. Here we will abide by the definition given by Williamson (1996) and adopted by Pascal, Lorvelec and Vigne (2006): "A **biological invasion** occurs when an organism, of any kind, reaches a site beyond its former area of distribution." What do we mean by "former distribution"? Let's not focus too much on that! Perversely, this would bring us back to the definition above, which we described as misleading. We simply note that from Williamson's definition there are two decisive points to be considered: the status of the species or exotic (not to be confused with foreign!) variety and the durable increase in the area of distribution of the taxon in question.

Should a third element, highlighted by various authors and advocated by the International Union for Conservation of Nature (IUCN) Invasive Species Specialist Group, also be included, whereby a true invasion only occurs when the introduced species is a damaging factor and is harmful to biological diversity? In this case, *Homo sapiens* are certainly the paradigm of invasive species! Should the "damage" parameter be included in the definition? Adopting a strictly scientific point of view, we will opt for the negative reply. And even if we were to approach the question from a manager's point of view, we have no reason to change our minds: it would not be wise for a manager of a protected area to wait until damages became apparent to raise the alarm.

Historical background

Much ground has been covered, it seems, since the appearance of Charles Elton's work. A short historical rundown will not do any harm (Davis, 2005). In 1964, the International Union of Biological Sciences (IUBS) held its first symposium in Asilomar (California). The aim? To bring together geneticists, ecologists, systematists and specialists in biological response to discuss "the kinds of evolutionary change which take place when organisms are introduced into new territories". The review was published the following year under the auspices of Baker and Stebbins (1965), with the title: The Evolution of Colonizing Species. Colonizing and not invasive species, you will notice. We had just emerged from the colonial period and the era of border control of foreigners was still far off – a research opportunity, in the passing, for colleagues in social sciences who focus on the phenomena of invasive species and those who are interested in them! Indeed, the terminology has changed, and Davis (2005) discusses this with great relevance. He notes that one must search carefully in Baker and Stebbins' work to find terms such as "**alien**", "exotic", "invader" and "invasion". Rather we find "colonizers", "founding populations", "introduced", "non-native", "new arrivals" and "migration". Elton's exuberant style, notes Davis, marked by the frequent use of analogy and metaphore, or even explicit military references, is almost absent from the vocabulary of the experts gathered in Asilomar – with the exception of Harper, close to Elton, although a botanist.

We must, however, note that Elton's work was particularly concerned with conservation (Davis et al., 2001), while in Asilomar discussions revolved around evolutionary processes. The fact remains that the movement launched by Elton gradually attracted more and more ecologists, as conservation concerns began to enjoy increasing importance. In 1980 – year of the release of Conservation Biology: An Evolutionary-Ecological Perspective by Soule and Wilcox, which marked the "seizure of power" by conservation biology – the third International Conference on Mediterranean-Type Ecosystems, held in Stellenbosch in South Africa, demonstrated great interest in biological invasions – a problem which particularly affected the Cape Province, home to rich endemic flora (Wicht, 1945; Taylor, 1969). This resulted in a proposal addressed to the Scientific Committee on Problems of the Environment (SCOPE) during its general assembly in Ottawa (1982) to set up a scientific committee dedicated to biological invasions and their impacts on ecosystems. This committee put forward three questions within the resulting SCOPE programme:
– what are the factors that determine whether a species will be an invader or not?
– what are the site properties that determine whether an ecosystem will be prone or resistant to invasion?
– how should management systems be developed using the knowledge gained from answering these two questions?

It was these three same questions that guided the Invabio programme. Thus, whether consciously or not, this programme followed in the continuation of the movement marked by conservation biology, in Elton's footsteps. Whether an upshot of the SCOPE programme or simply a consequence of the evolution of thinking (in the late 1980s the concept of biodiversity became established), research developed and publications dedicated to biological invasions multiplied, in particular in terms of

regional surveys. At the heart of the "battle", and this comes as no surprise, as their countries are among the most affected, we find researchers from the United States, New Zealand, Australia and South Africa. The SCOPE programme, launched in Stellenbosch, South Africa, produced its first report in 1984 on fynbos in South Africa (MacDonald and Jarman). Reviews on the subject for Australia (Groves and Burdon, 1986), South Africa (MacDonald and Jarman, 1984) and the United States (Mooney and Drake, 1986) then appeared at more or less the same time. Four years later, a review was released from the Mediterranean region (Di Castri et al., 1990). Not forgetting the state-of-knowledge review which concluded this succession of regional reports, Biological Invasions: a Global Perspective (Drake et al., 1989). SCOPE's action must be acknowledged. Thanks to Di Castri, France was not completely left out of this movement (Di Castri et al., 1990). This ripe harvest prepared the way for a new generation of works making the ecology of invasions a reality – or even a science in itself: a debatable point to which we shall return later. The international review Biological Invasions was launched in 1999.

Finally, the most recent publications following Williamson's widely quoted essay (1996) and Bright's "general public" work (1999), are highlighted (Box 1), including two French titles (Muller, 2004; Pascal et al., 2006).

Box 1 – Seven recent reviews.

Cadotte M.W., McMahon S.M., Fukami T., 2005. Conceptual Ecology & Invasions Biology. Reciprocal Approaches to Nature. Dordrecht, The Netherlands, Springer, 505 p.

Cox G.W., 2004. Alien Species and Evolution. The Evolutionary Ecology of Exotic Plants, Animals, Microbes and Interacting Native Species. Washington, Island Press, 378 p.

Lockwood J.L., Hoopes M.F., Marchetti M.P., 2006. *Invasion Ecology*. Chichester (UK), Blackwell Publishing, 312 p.

Mooney H.A., Mack R.N., McNelly J.A., Neville L.E., Schei P.J., Waage J.K., 2005. Invasive Alien Species. A New Synthesis. Washington, Island Press, 368 p.

Muller S. (coord.), 2004. Plantes invasives en France. Paris, MNHN, 168 p.

Pascal M., Lorvelec O., Vigne J.D., 2006. Invasions biologiques et extinctions. 11 000 ans d'histoire des vertébrés en France. Paris, Belin/Quae, 350 p.

Sax D.F., Stachowicz J.J., Gaines S.D., 2005. Species Invasions? Insights into Ecology, Evolution and Biogeography. Sunderland (MA), Sinauer Associates Inc., 496 p.

The Invabio programme

In response to concerns raised by the extremely rapid expansion of *Caulerpa* in the western Mediterranean basin, the French environment ministry implemented a specific action plan in 1997.

A research programme on *Caulerpa* seaweed invasions constituted one of the sections of this actions plan, alongside "observatory", "prevention" and "response means" sections. It aimed to initiate research on the impact of expansion on invaded ecosystems and on the related socio-economic activities.

Understanding the evolution of biodiversity in invaded areas, variations over time and space, determining the impact of expansion on populations and analysing social representations of this invasive seaweed among different groups concerned were some of the research questions for which management recommendations were expected (Box 2).

Very quickly, it proved necessary to extend the field of research to the different environments and invasive species which were creating problems in France. The questions raised by the expansion of *Caulerpa*, although they attracted considerable media attention, nevertheless remained limited to a few species and a defined ecosystem. The environments confronted with invasive, whether animal or plant, species are many and varied, demonstrating the vast diversity of questions related to their management. From 2000, the environment ministry thus launched a new programme focusing on research into the mechanisms underlying invasion phenomena, the socio-anthropological perception as well as control and management methods.

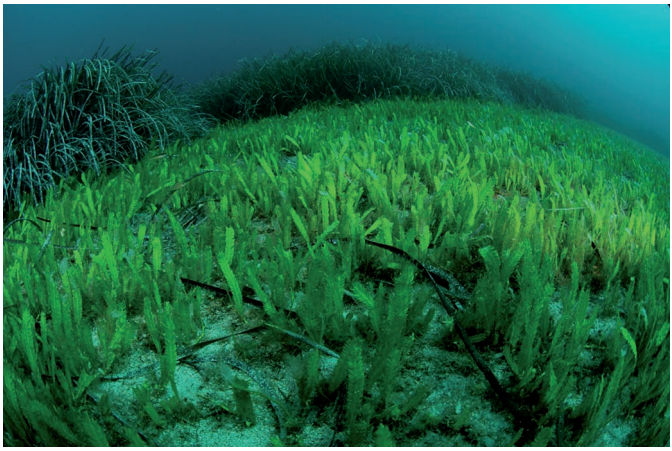
The main aim of this programme was both to improve conceptual and theoretical knowledge of biological invasions and to increase concrete knowledge of animal and plant invasions with which France is confronted, with a view to designing decision support tools for managers. This was the first national research programme specifically dedicated to invasions, working in close cooperation with environmental managers.

The vast diversity of the results from research projects funded through these programmes contributed to the analyses and recommendations presented in this book.

Box 2 – The projects funded through the research programme on the expansion of *Caulerpa taxifolia* seaweed in the Mediterranean (1998-2002).

The projects outlined below were selected and funded for their contribution to the understanding of the mechanisms associated with the spectacular proliferation of *Caulerpa taxifolia*:
– *Genetic status*: this seaweed was considered to be of Australian origin; the hypothesis of an introduction via the Suez Canal was refuted (Myriam Valero**,** CNRS).

…



The expansion of beds of the seaweed *Caulerpa taxifolia* on the Mediterranean seafloor, at Villefranche-sur-mer. This native species of Australia introduced in 1984 in Monaco has invaded the seafloor of six Mediterranean countries. These are areas of competition with the seagrass *Posidonia oceanica*, flowering plants of the Posidoniaceae family which constitute one of the major Mediterranean ecosystems (© CNRS Photothèque, R. Graille).

– ***Modelling the expansion of Caulerpa***: the modelling of the expansion of *Caulerpa* shows annual cycles, with a high growth rate in summer and a stagnation period in winter (Patrick Coquillard, Université d'Auvergne/Université de Nice-Sophia Antipolis).
– ***Impact on fish populations***: a high mortality in juveniles alters the recruitment of fish in *Caulerpa* beds, reducing the micro-habitats in which they protect themselves from predators (Patrice Francour, Université de Nice-Sophia Antipolis).
– ***Associated bacterial flora***: the specific composition of the bacterial flora associated with Mediterranean *Caulerpa* increases their resistance to low temperatures, boosting their proliferation properties (Yannick Le Parco, CNRS).
– ***Competition with Posidonia***: when in competition in the same biotope, *Posidonia* and *Caulerpa* adopt distinct strategies. *Posidonia* reduce their average leaf length and lifetime, a higher turnover of leaves increases the number of tannin cells. *Caulerpa* increase their leaf length and reduce their caulerpenyne content (Gérard Pergent, University of Corsica).
– ***The physico-chemical quality of water***: *Caulerpa* colonies develop indifferently in areas of little and of heavy pollution, presenting greater resistance to climatic variations in port areas with the highest metals concentrations (Pierre Rebouillon, Faculté de pharmacie de Marseille).
– ***The socio-anthropological perception of invasion***: symbolic treatment of *Caulerpa* invasion in the Mediterranean basin was understood in relation to symbolic treatment of other invasive phenomena associated with the Atlantic coastline (Sergio Dalla Bernardina, Université de Bretagne occidentale).
– ***The socio-economic impact of the invasion***: the commercial and non-commercial effects were studied and related to the difficulties of sea users (Stéphane Lucchini and Ghislain Géniaux, CNRS-EHESS-Université Aix-Marseille).

A few lessons

Generally speaking, a certain number of fundamental conclusions can be drawn from the rich literature accumulated.

The first concerns the impacts of biological invasions. From an ecological point of view, the majority of extinctions attributed to bioinvasion phenomena are located in isolated environments (Steadman, 1995). Things are far less clear-cut when it comes to continental flora and fauna, where many other factors appear to be more influential – the well-studied case of amphibians is one of the most illustrative examples (Stuart et al., 2004). From an economic point of view, the damage caused by invasive species is well documented and quite real (Pimentel, 2002). However, this is far from always the case. For instance, as concerns vertebrates in France, Pascal et al. (2006) note that "the ecological and socio-economic impact of 115 species of non-native populations, i.e. 75% of the total, is not documented. In terms of the ecological impact *sensu stricto*, it is only documented, mainly patchily, for the populations of 24 species, i.e. 16% of the 153 species currently represented in France by one or more non-native populations". These authors attribute this deficiency to academic science's disapproval of natural history work, as well as naturalists' lack of interest in non-native species.

The second, less regularly highlighted yet which appears to be of great importance, can be summed up by the titles of two articles which outline this point: "Are Invasive Species the Drivers or Passengers of Change in Degraded Ecosystems?" (Mac Dougall and Turkington, 2005; Didham et al., 2005). We are well aware that most ecosystems are subject to various sources of disturbance or even damage (Millennium Ecosystem Assessment, 2005) and it is therefore no easy task to decide between the hypothesis of "biological invasion as a driver of change" and the alternative, "the invasive species as a passenger of environmental change". By constantly repeating that invasive species are one of the main causes of the current erosion of biodiversity – which is true –, we end up forgetting that a large share of this observation is only based on simple correlations between the domination of an alien species and the decline of one or more **indigenous** species in damaged ecosystems. As highlighted by Didham et al. (2005), the direct causality hypothesis, although attractive, in this case, is not the only possible hypothesis. A plausible alternative hypothesis is that the success of the exotic species could be the indirect consequence of an alteration in the environment resulting in the decline of the indigenous species. MacDougall and Turkington (2005) provide direct evidence of this[1] (Box 3).

1. However there also exist other examples which show indirect impact, through the food chain of certain species, in particular predators, on the environment itself (Croll et al., 2005).

Box 3 – Invasive species, "drivers" or "passengers" of ecological change?

To answer this fundamental question, Didham et al. (2005) drew upon the experiment conducted by MacDougall and Turkington (2005) in the Quercus garryana oak meadows of south-western Canada and north-western USA to individually investigate the respective impacts of the disturbances endured by this ecosystem and the invasion by two exotic grasses, *Poa pratensis* and *Dactylis glomerata*, on the decline of native species.

MacDougall and Turkington applied the hypothesis that, if the interactive processes imposed by invasive species were indeed responsible for the decline of indigenous plants (which no longer represented more than 10 to 20% of the biomass), the removal of alien species should result in a direct increase in the richness and relative abundance of native species. If this was not the case, i.e. if anthropogenic disturbance was predominant, the eradication of these exotic species would have a minor impact.

After three years of exclusion of the two main exotic grasses, *Poa pratensis* and *Dactylis glomerata* (which represented 50 to 80% of total cover), a rapid, lasting decrease in total production was observed, as well as a gradual switch in dominance from perennial grasses to perennial forbs. The majority of compensation was made by the native forbs already established before experimental treatment. Little recruitment of either native or exotic perennial grasses was observed during the 3 year period. Dominance by native species under the "driver" model was not restored and the results suggest that the probable cause of alien species dominance in this ecosystem is likely to be found in the "passenger" model, i.e. through anthropogenic disturbance (fire suppression) imposed on the ecosystem.

According to MacDougall and Turkington (2005), the first model predicts that invaded communities are highly interactive, with indigenous species limited or excluded through competition with **dominant** exotic **species**. The second considers invaded communities are mainly structured by non-interactive factors (environmental changes, dispersal limitations), which are less restrictive for exotic species which will therefore prevail. Through an experimental approach developed on grassy swards of an oak savanna in British Columbia (Canada), these two authors showed that the relative abundance of indigenous and exotic species (two perennial grasses) was determined more by trade-offs related to environmental conditions (long-term fire suppression) than by traits connected to resource capture (which should most impact functionally similar species). This supports the exotic "passenger" model rather than the "cause" of change (Box 2). More generally, this shows that it is dangerous, in terms of biological invasions, to only consider the expanding exotic species and almost completely ignore the state and dynamics of the ecological system in which it is developing. This perverse effect of focusing on invasive species should not be underestimated (Teyssèdre and Barbault, 2009).

Having said this, a homogenisation of flora and fauna is emerging, as a consequence both of invasions by exotic species which become ubiquist, and of the decline or extinction of endemic species (McKinney and Lockwood, 1999).

The third, widely supported, lesson is the importance of biological invasions and their control in experimentally studying the dynamics of interactions between species (Cadotte et al., 2005; Sax et al., 2005). Thus, Courchamp and Caut (2005) wrote: "One of the difficulties of conservation biology is the general lack of experimental approaches". They add: "However there is an enormous set of ecological events that can be viewed as natural, large-scale experiments: biological invasions". However this knowledge is of little interest… for managers, except to develop their observations and actions through successful collaboration with researchers.

The fourth lesson (and this one is of great importance for managers, although they are already aware of it, and for good reason) is that in terms of exotic species eradication or control, the later we take appear in the phenomenon, the more difficult, or even impossible or dangerous, it is to take action. By dangerous, we mean ecologically (but that also means economically), as a, in this case exotic, species that is well established in a terrestrial or aquatic environment plays a role, or even ensures a balance, with which it may be risky to interfere. Sometimes it can be better to "naturalise" it than to attempt to send it back across the border! In point of fact, many species that have become familiar were once foreign. Here the question is raised of the frame of reference enabling us to determine the non-native or indigenous character of such and such a species, as is the question of human interference in the constitution of flora and fauna (Pascal et al., 2006). Muller (2004) reminds us that 9.4 % of French vascular flora (excluding overseas French territories!), representing 440 species, are naturalised non-native species (whereas for New Zealand this figure is 46.7 %).

These four general lessons that can be drawn from the scientific literature, and which may support managers' own appraisal when faced with a specific situation that requires quick answers without any possible recourse to research, give a rough outline of a few general conclusions confirmed by the results of the Invabio programme.

In conclusion

The first conclusion is that, in spite of considerable development of work dedicated to this field of ecology over the past twenty years, the outcomes remain fragile and are difficult to generalise. To the extent that distinguished ecologists speak about biological invasions as a *pseudoscience* (Slobodkin, 2001; Simberloff, 2004), while deploring the "bioxenophobic" overtones of certain mindsets. And our aptitude to predict the successful establishment and impacts of non-native species remains limited (d'Antonio et al., 2001; National Research Council, 2002).

The second conclusion is that biological invasion problems, whether we wish to understand them or control them, draw upon the general corpus of ecology, the whole of ecology – from ecophysiology to landscape ecology to population genetics (cf. Tabacchi et al. in this publication). Yet this ecology is marked by the way in which it treats or does not treat the vast field of relations between natural systems and social systems (Barbault, 2008; this introductive chapter).