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Biological invasions: Much progress plus several controversies

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Summary. Invasion biology has allowed to progress in our understanding of invasions and our ability to manage them. Recent research has largely focused on invasions that impact entire ecosystems. Molecular genetics has revealed the relative commonality of hybridizations between introduced and native species and between genetically different populations introduced into the same region. Controversies surrounding the findings of invasion biology and management include: i) The claim that most invasions are inconsequential, even if they have been scarcely studied. ii) The argument that invasions can increase local biodiversity, without recognizing that they decrease global biodiversity. iii) The statement that invasion biology is a form of xenophobia, downplaying evidence that fighting invasive species is motivated by their negative impacts. iv) The belief that there is little we can do to prevent or control invasions, ignoring successful eradication and management projects and promising novel approaches. iv) Animal rights objections to the management of invasive vertebrates, particularly mammals, which reflects different philosophical stances and will not be easily resolved.

Keywords: biological control · biological invasion · ecosystem impact · eradication · hybridization · lag time · maintenance management

Resum. La biologia de les invasions ha permès avançar en la comprensió de les invasions i de la capacitat per gestionar-les. La recerca recent s'ha centrat sobretot en les invasions que afecten ecosistemes sencers. La genètica molecular ha revelat la generalització relativa d'hibridacions entre espècies introduïdes i natives, i entre poblacions genèticament diferents introduïdes en una mateixa regió. Les controvèrsies sobre els resultats de la biologia de les invasions i de la seva gestió són: i) L'afirmació que la majoria d'invasions causen poc impacte, encara que hagin estat poc estudiades. ii) L'argument que les invasions poden augmentar la biodiversitat local, sense reconèixer que disminueixen la biodiversitat global. iii) L'afirmació que la biologia de les invasions és una forma de xenofòbia, restant importància al fet que la lluita contra les espècies invasores està motivada pels seus impactes negatius. iv) La creença que hi ha poc que puguem fer per prevenir o controlar les invasions, fent cas omís de l'èxit dels projectes d'eradicació i gestió i de nous enfocaments prometedors. iv) Les objeccions dels defensors dels drets dels animals a la gestió dels vertebrats, particularment mamífers, sent aquest un problema que no es resoldrà fàcilment.

Paraules clau: control biològic · invasió biològica · impacte a l'ecosistema · eradicació · hibridació · desfasament temporal · gestió del manteniment

THE RECOGNITION THAT BIOLOGICAL INVASIONS constitute a global change of the first order—along with changes in climate, nutrient cycles, and land use—came slowly. As early as the 18th century, the Swedish Finn Pehr Kalm noted fifteen European plant species and several European insects during his travels in North America [13]. Early phytogeographers, such as the Augustin Pyrame de Candolle, from Switzerland, greatly expanded the records of species believed to be introduced, deliberately or inadvertently, by humans to various locations around the world [13]. Victorian naturalist-explorers continued this tradition of documentation during the 19th century. Among them, Charles Darwin lamented the replacement of native plants by two invaders from the Old World into the Patagonian pampas [19], while Alfred Russel Wallace deplored the devastation wrought by some invasive species on various islands [107]. However, except for Darwin and Wallace, the focus of all these investigators was squarely on the geography of life—which species are where—and not on the impacts of non-native species.

In the early 20th century, George M. Thomson [94] wrote entirely about introduced plants and animals and their impacts in New Zealand, and James Ritchie [64] detailed the impacts of animal invaders in Scotland. Neither book led to new research efforts to study the effects of the entire gamut of biological invaders, although Thomson's work was rediscovered almost a century later and his data were used in analyses of bird introductions in New Zealand [23,24,99]. Through the mid-20th century, scientists would occasionally point to the impacts of particular species as meriting greater consideration [e.g., 52], but still no broad-based movement arose to study invasions. In 1958, Charles Elton published his famous monograph, *The ecology of invasion by animals and plants* [26], which is often cited as the founding document of modern invasion biology [62,63]. Although this book addressed the ecological impacts of invasive plants, animals, and microbes worldwide, it had little contemporary influence and did not inspire a wave of research on invasions [77]. Rather, modern invasion biology largely arose from a project of the Scientific Committee on Problems of the Environment (SCOPE) in the 1980s that engaged over 100 prominent ecologists and evolutionists in a series of workshops held in various countries and which resulted in several widely read books [77]. Thus, given the long history of the problem of invasive species, the modern field of invasion biology is remarkably young.

The first fifteen years

The SCOPE mandate was to determine: (i) Why are certain species particularly invasive once introduced, while others either disappear or remain restricted and innocuous? (ii) What makes certain habitats particularly prone to invasions

while others are relatively unscathed? (iii) How can the knowledge developed in response to these two questions be used to improve the management of invasive species? In fact, these questions (i) and (ii) dominated the SCOPE workshops and publications, whereas management was a lesser concern.

The SCOPE project as well as much of the research it inspired over the next decade greatly expanded our understanding of how particular invaders affect native species. The majority of cases could be placed in a few well-understood categories. The phenomenon receiving the most attention was predation by an introduced predator on native prey, with the most dramatic outcome being the complete loss of the native species. Striking examples include the extinction of more than 200 native cichlid fish species in Lake Victoria in response to predation by the introduced Nile perch, *Lates niloticus* [57], and the extinction of 15 species and subspecies of forest birds on Guam after the introduction of the brown tree snake *Bioga irregularis* [45]. Herbivory by invaders, both vertebrates and invertebrates, is also common. For instance, the South American nutria (*Myocastor coypus*), introduced into North America and Europe, has caused both the local extirpation of several aquatic plants and important crop losses [69]. In the 19th century, an insect from North America, the phylloxera *Daktulosphaira vitifoliae*, devastated European vineyards [56]. Invaders can carry diseases to which they are resistant such as the crayfish plague (*Aphanomyces astaci*) transmitted by North American to European crayfish [46]. Similarly, squirrel pox (*Parapox virus*), which arrived in Europe with the North American gray squirrel (*Sciurus carolinensis*), is currently devastating the native red squirrel (*S. vulgaris*) population in Great Britain and Italy [7,68]. Invaders can also compete with native species. In Spain, the African ice plant (*Carpobrotus* spp.) outcompetes native plants for light and water, while a North American turtle, the red-eared slider (*Trachemys scripta elegans*), excludes native turtle species from their optimal habitats [69].

During and in the wake of the SCOPE project it was determined that introduced species often hybridize with closely related native species [61]. Indeed, when native populations are small relative to the size of the invasive population, as was the case for the native white-head duck *Oxyura leucocephala* in Spain, which hybridized with the North American ruddy duck *O. jamaicensis* [51], this phenomenon can even lead to a sort of “genetic extinction,” as the original native genotypes become lost in a hybrid swarm. Moreover, hybridization can generate new species, as occurred in Great Britain when North American smooth cordgrass (*Spartina alterniflora*) hybridized with native small cordgrass *S. maritima* to produce the polyploid hybrid common cordgrass, *S. anglica* [93]. In this case, although the native parent *S. maritima* is never invasive [92], the new hybrid species is listed among a selection of 100 of the world's worst invaders [48].

Expanded and new research directions

The SCOPE contributions and the immediately ensuing research were largely focused on one-on-one ecological interactions—how does a single particular invader affect one native or a particular group of them? However, even in the initial SCOPE project, Peter Vitousek [104,105] called attention to the fact that certain invasive species can fundamentally alter an entire ecosystem, involving a large number of species that play various roles in the biotic community. In Vitousek's example, the particular invader was the Atlantic shrub *Morella faya* (or *Myrica faya*), introduced to the Hawaiian Islands. As a nitrogen-fixer in mid- and upper-elevation areas characterized by nutrient-poor volcanic soils—to which native plants were adapted—and in the absence of native nitrogen-fixers, *M. faya* effectively fertilized the soil, making it more hospitable to other non-native plants previously excluded by the low nitrogen levels. It also entrained a number of other changes in the ecosystem [4]. Further, this ecosystem change was exacerbated by “invasional meltdown” [87], in which the combined impact of two or more invaders is greater than their summed impact. The major seed-disperser of *M. faya* is the Japanese white-eye, *Zosterops japonicus* [111]; by clustering under *M. faya*, introduced earthworms increase the rate at which nitrogen is added to the soil [3].

Another ecosystem-wide impact of a single invader was described by Fukami et al. [31], who found that both the above-ground and below-ground communities differ profoundly on small New Zealand islands invaded by rats (either *Rattus rattus* or *R. norvegicus*) compared to rat-free islands. This type of research is distinct from many previous studies of the impact of introduced rats on islands [5,96]. Ecosystem-level research has now become a leading edge of invasion biology and it has shown that many ecosystem impacts are caused by changes in nutrient and fire regimes and in physical structure [25,78].

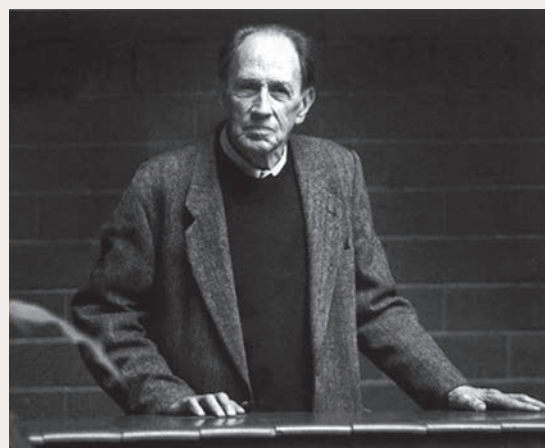
The other major new thrust of invasion biology research is the role of evolution in invasions. It is puzzling that, despite the participation of several prominent evolutionists in the SCOPE program and the obvious possible relevance of invasion events to evolutionary questions (e.g., the relative importance of founder effects and natural selection in small, newly established populations), evolutionary biologists did not join the rapidly growing biological invasions research program in great numbers for over a decade after SCOPE [77]. Spurred by the rapid increase in the development and availability of molecular genetic technologies, evolution has since become an integral part of the invasion biology research program. Yet, the first monograph on evolution and biological invasions was published only in 2004 [16].

Nowadays, molecular tools, particularly the study of microsatellite and mitochondrial DNA sequences, are used

Not in print

The achievements by great scientists can be usually found in the articles and books they have published throughout their careers. Many of their ideas and thoughts, however, are not always left in print, unless they write memoirs or books of essays.

Ramon Margalef used to say, in a tone half-humorous and half-sarcastic, that he felt suspicious—and had had good reasons for it—of the traditional systems of education, especially *higher* (i.e., university) education. On one occasion, when we were discussing an emergent and significant issue in the young science of microbial ecology, he told me: “This is so important, Ricard, that in twenty years it will already be included in textbooks”. *R. Guerrero*.



Professor Ramon Margalef. (Images courtesy of Gallery of Catalan Scientists, Institute for Catalan Studies).

to trace the origins of particular invasive species. An example is the demonstration that the Cuban anole (*Anolis sagrei*) in Florida must have undergone multiple introductions because many locations in Florida have a greater diversity of mtDNA haplotypes than does any one location in Cuba [38]. The same study was able to show that invasions by this lizard of Hawaii and Taiwan must have arrived from Florida rather than Cuba. This particular study did not demonstrate that the multiple origins had consequences for the invasion. However, for reed canary grass (*Phalaris arundinacea*) in North America [40] and the multicolored lady beetle (*Harmonia axyridis*) in North America and Europe [47], similar genetic analyses show that, as noted above, hybridization between individuals introduced separately from different regions can produce more invasive genotypes. Hybridization between a native and an introduced oomycete is responsible for alder blight (*Phytophthora alni*), a new pathogen that is killing alders (*Alnus* spp.) throughout Europe [113].

In general, the plethora of genetic studies on invaders has detected far more multiple introductions than had been suspected as well as frequent hybridizations between populations introduced from different regions. These studies also revealed that hybridizations between introduced and related native species occur more often than previously assumed based on simple morphological analyses. The frequency of multiple introductions at least partly resolves the “paradox of invasion genetics.” That is, it has long been noted that although very small populations are frequently presumed to be endangered by genetic deterioration, engendered by genetic drift and inbreeding-induced genetic depression [2,28], many strikingly successful invasions have originated from very small propagules, which greatly reduced genetic variation by virtue of the “bottleneck effect” [75]. However, we now know that some introduced populations, such as the Florida populations of the Cuban anole, have greater genetic variation than any one native population, thereby hindering the expected genetic deterioration [66].

Many introduced populations have evolved morphologically in their new homes. A remarkable example is the Old World fruit fly *Drosophila subobscura*, introduced into western North and South America. Old World populations have a pronounced latitudinal cline in wing length whereas in North American populations no wing length cline was detected ten years after introduction of the species; but after 20 years a cline had evolved that largely converged with the Old World cline [35]. However, different sections of the wing are responsible for the cline in North American vs. Old World populations. Thus, the evolution of geographic variation in wing length was predictable, but expression of the genes by which the cline was achieved depended on other factors. Introduced South American populations also rapidly

evolved a cline of increased wing length with increased latitude, but a different section of the wing is responsible for the cline in South American than in either North American or Old World fruit flies. Furthermore, many traits other than morphology have evolved in introduced populations, including changes in life history, physiology, and behavior [16]. Perhaps best known to the public are the many cases in which insects have evolved resistance to insecticides, either physiological changes to tolerate or detoxify the chemical or behavioral changes to avoid it [67,108]. Native species sometimes also evolve very quickly in response to invasions [91]. For instance, after introduction of the predatory green crab (*Carcinus maenas*) to the Atlantic coast of North America, the dog whelk (*Nucella lapillus*), a native prey species, evolved thicker shells [100].

The explosion of research publications on invasions has led to a proliferation of formal meta-analyses of that literature—as the method became known outside the field of medicine [11]—particularly regarding the first two questions of the SCOPE agenda: what determines the invasiveness of species and the invasibility of sites or habitats (e.g., [43,44,102]). However, it seems unlikely that such efforts will advance our understanding of invasions substantially for two reasons. First, particular invasions are highly idiosyncratic such that a fundamental requirement of meta-analysis is violated: the different studies can by no means truly be viewed as replicate tests of the same hypothesis. Second, this same idiosyncrasy implies that an effect size in an analysis in one case will have limited predictive value for an invasion by the same species or type of species in another. This is most clearly shown by the fact that a single species can be highly invasive at one site and either fail utterly or have minor impact at another [114]. What is needed most to advance our understanding of invasions is not the study of effect sizes but of actual effects, on the ground and in a multitude of cases [74]. Unfortunately, this sort of research is largely in the tradition of detailed natural history at the community level, which has fallen from academic favor precisely because community dynamics are too variable and idiosyncratic [41]. Yet, even though community studies are highly idiographic, they are precisely what is needed if we are to understand and successfully address many environmental and conservation issues, including invasions [73].

Controversies surrounding invasions and invasion biology

Aspects of invasion management and policy have been controversial since well before the advent of modern invasion biology [72], but for the most part criticism arose from the humanities and social sciences. More recently, these controversies have become more visible as the field of invasion

biology itself expands and matures. Matters came to a head with a Comment in *Nature* [20] signed by 19 ecologists and an immediate rebuttal [84] signed by 141 ecologists. Popular science writers, sensing a hot topic, have also entered the fray (e.g., [49,103]). In fact, there are several distinct criticisms, with different critics focusing on different ones [80,82]. These boil down to five main areas of contention.

(i) Which invasive species are harmful? It is widely acknowledged that a minority of biological invaders have harmful impacts, and critics of invasion biology (e.g., [20]) take that finding as evidence that the entire invasion problem is overblown. In fact, for three reasons the statistics on known invasion impacts should be interpreted with caution. First, the great majority of introduced populations have not been studied in any detail, so that their true impact is as yet unknown. For instance, of the over 10,000 non-native plants in Europe, the ecological effects have been studied in fewer than 11 % [101]. Second, in a number of instances invasions are substantial and even affect entire ecosystems, but their impacts are nonetheless subtle and not readily apparent. A good example is the fertilization of Hawaiian Islands by the nitrogen-fixing *M. faya* [104,105], discussed above. The gradual change was not obvious, but since the reporting of this phenomenon many similar examples have been uncovered [25]. Third, many introduced populations remain more or less restricted and innocuous for long periods, often several decades, before abruptly exploding across the landscape with broad-ranging consequences [17]. Thus, even if we were aware of the current effects of all introduced populations, their future impacts would be severely underestimated, even if no further invasions occurred. This phenomenon—that future impacts will arise because of populations already introduced—has been called the “invasion debt” [27].

The charge that most invasions are not known to be harmful is occasionally buttressed by either or both of two observations. First, some native species have ecologically or economically harmful impacts that are analogous to those caused by invasive non-natives. This is true, but the likelihood of such impacts is far less than for non-natives [53,86]. For instance, plant species introduced to the United States are 40× more likely than native plant species to generate harmful effects. In the relatively few instances in which this indeed occurs, it is almost always in the wake of an anthropogenic environmental modification, such as changed fire regime or overgrazing by livestock [86]. A second occasional observation is that sometimes non-native species actually aid conservation in some way (e.g., [71]). Of course, this is true; any time a species, including an introduced one, becomes common, some other species will use it as a resource. However, one must always consider the full panoply of impacts on the ecosystem and all of its spe-

cies; in this light, the instances in which non-native species confer conservation benefits are highly questionable [106].

(ii) Introduced species increase biodiversity. It has been frequently noted that introduced species increase local biodiversity in certain circumstances or even maintain local biodiversity in the face of extinctions (e.g., [70]). However, invasions cause a sharp decrease in global biodiversity. Consider the birds of the Hawaiian Islands [85]. Of 114 known bird species present at the time of human colonization of the archipelago, at least 56 are globally extinct [9]. Introduced bird species contributed to this hecatomb through disease transmission [112] and possibly through competition [29]. Remarkably, 53 non-native bird species are now established on the islands [65], approximately “balancing” the extinctions. However, almost all of the introduced birds are common in their native ranges, and many have been introduced to other sites. They can hardly be said to “compensate” for the global extinction of the native birds.

Certain introduced species in specific circumstances increase biodiversity very locally by providing a resource for native species that would otherwise be more sparsely distributed in the region. For instance, in Argentina the kelp *Undaria pinnatifida*, native to cold temperate regions of the Pacific northwest, constitutes a new structural habitat that increases the local richness of native animal species [36]. As with the introduced species claimed to aid conservation, discussed above, it is important in each case to tally the long-term net benefits and debits to regional ecosystems.

(iii) Are actions against introduced species xenophobic?

A persistent claim, originally from scholars in the social sciences and humanities (references in [72]), is that antipathy towards introduced species is simply displaced xenophobia. This suggestion is rarely expressed by scientists working on invasions, but the burst of recent criticism at least hints at this charge: consider the title of Davis et al. [20]: “Don’t judge species on their origins.” A full examination of this allegation is beyond the scope of this article; I have treated it fully elsewhere [72,79]. This view of invasion biology amounts to a classic social construction of science [10], in which the development of a field is ascribed to the psychological states and power relationships among the participants rather than to increasing knowledge of the subject of study.

An excellent example is the work of the American historian Philip J. Pauly [54], who saw the approximate synchrony of the first American laws restricting human immigration and the earliest statutes attempting to prevent harmful biological invasions as proof of his thesis. The increasingly strict immigration laws are widely acknowledged to have reflected a growing nativism in early 20th century America [33,95]; so, in Pauly’s view, the anti-invasion regu-

lations could only reflect the same xenophobic sentiment: “attitudes towards foreign pests merged with ethnic prejudices: the gypsy moth and the oriental chestnut blight both took on and contributed to characteristics ascribed to their presumed human compatriots” [54]. In fact, the invasions of both the gypsy moth *Lymantria dispar* [90] and the chestnut blight *Cryphonectria parasitica* [30] were devastating and widely lamented by the contemporary public and politicians. The discussions in Congress and the federal agencies that led to early regulations of species introductions referred heavily to these impacts [72]. This is not to say that nativists of the period did not occasionally deplore non-native species, but the scientists of that era and modern invasion biologists focused, in fact, on impacts, not origins [15]. Absent from analyses such as Pauly’s is a consideration of the impacts of introduced species, much less sophisticated insights such as those of Aldo Leopold, who recognized that the absence of co-evolution with native species led to far greater risks of damage from introduced species than from native ones [42].

(iv) Whatever their impacts, is it futile to fight invaders?

Several critics of the effort to stem invasions concede that at least some of them do wreak substantial damage, but they argue that, in the face of growing trade and travel, the effort is largely hopeless and we should not waste precious resources trying to stop them. This sentiment was captured vividly by Mark Gardener (in [103]), a signatory to the Comment by Davis et al. [20], as he neared the end of his tenure as director of the Charles Darwin Research Station in the Galapagos: “It’s time to embrace the aliens. Blackberries now cover more than 30,000 ha here, and our studies show that island biodiversity is reduced by at least 50 % when it’s present. But as far as I’m concerned, it’s now a Galapagos native, and it’s time we accepted it as such.”

In fact, such pessimism is not warranted, particularly in light of the relative youth of modern invasion biology and the tremendous recent strides in management technologies [76]. Of course, the best approach is to have sufficiently stringent regulations and inspection such that few invaders enter in the first place; as in medicine, an ounce of prevention is worth a pound of cure. The experience of New Zealand in the wake of its Biosecurity Act of 1993 shows that such measures are both feasible and effective [85]. The impediments to putting such measures in place are mostly political, although the expense of establishing adequate inspection has played a role [81]. If an introduced population nevertheless becomes established, the next step would be to find it quickly and try to eradicate it. Nowhere in the world are there adequate monitoring programs to find such incipient invasions, even though engaging citizen scientists is a cost-effective way to greatly improve monitoring and it has led to several remarkable eradications of populations that almost certainly

would otherwise have become devastating invasions [81,82].

It is often argued that eradication of a long-established, widespread invader is impossible (e.g., [18,60]), and there is little doubt that is far more difficult than eliminating a limited, narrowly distributed population. However, several very widely established invaders have nevertheless been eliminated, such as the pasture weed *Kochia scoparia* in Western Australia [58] and the melon fly *Bactrocera cucurbitae* in the entire Ryukyu Archipelago [37,39]. Recently, the viral pathogen of ungulates, rinderpest, which devastated Africa in the 20th century, was eradicated from the face of the Earth [50]. These successes are not to say that eradication is straightforward, only that it is often technologically feasible and that recent advances (see, e.g., [12,98]) have made possible many eradication efforts that would have seemed hopeless only one or two decades ago.

If eradication fails, there are several technologies that can maintain invasive populations at levels that are not problematic. Traditional maintenance management approaches are physical control, mechanical control, chemical control, and biological control. Each has achieved major success, and each has failed in other circumstances [76,83]. The important point is that the technologies associated with all of these methods have evolved (e.g., [14,21,55,97,109]).

In addition, novel approaches to maintenance management (and in some cases possibly eradication) of particular invaders arise occasionally. The essence of creativity is that we cannot predict exactly when it will arise and from what direction, only that new ideas will occur with some frequency. This is certainly proving true for the management of invasive species, as interest in and publicity about the problem increase. For instance, invasive sea lampreys (*Petromyzon marinus*) in the North American Laurentian Great Lakes—long controlled somewhat successfully with lampricides and dams but at great expense and with some non-target impacts—can now be managed in many circumstances by exploiting a pheromone emitted by larval lampreys to attract adult lampreys to particular streams to breed [88,89]. Invasive zebra mussels (*Dreissena polymorpha*), long intractable to chemical control because they are acutely sensitive to the presence of toxins in the water and shut their valves in response to them, can now be managed at municipal and industrial water facilities where non-target native mollusks are not a concern. This is achieved by “BioBullets,” minute beads of toxic potassium chloride that the mussels cannot sense because they are coated with a masking fatty substance that dissolves after they have been filtered out of the water by the mussels [1]. Autocidal methods that manipulate an invasive species’ genetics in such a way as to lower its population size were proposed in the 1960s and 1970s (e.g., [32]), but the necessary technologies were lacking. Today, in an era of transgenes and ge-

netic modification, such methods are again being researched and have reached the testing state in both fishes (e.g., [6]) and dipterans (e.g., [59]).

(v) Animal rights objections to the management and eradication of vertebrates.

Attempts to eradicate or even simply to manage mammals and birds often generate heated opposition from animal rights and animal welfare organizations, such as People for the Ethical Treatment of Animals and The Fund for Animals (PETA) [80,83]. Perhaps the best known example is the spread of the North American gray squirrel in Italy. As noted above, in Great Britain the gray squirrel has greatly reduced native European red squirrel populations, by spreading squirrel pox and by competition [110]. An escaped population in central Italy led to a well-planned eradication campaign, because of the feared threat to mainland European red squirrels [8]. However, a lawsuit by animal rights advocates, sustained by Italian courts, stopped the campaign in its tracks [7] and the gray squirrel has, accordingly, continued to spread; it is currently nearing France [22]. Even rats threatening seabird populations have elicited enough sympathy to inspire attempts to impede eradication campaigns [34,80].

This issue usually boils down to whether one considers collective entities, such as species or populations, to be worthy of moral consideration, if that moral consideration confers rights on such entities (say, a population of an endangered seabird), and whether such rights trump the rights to continued life of individuals of some other species, introduced by humans, that may threaten them (e.g., introduced rats) [80]. Philosophers are divided on this issue, so it is not surprising that so is the public. Animal rights advocates generally come down on the side of the rights of individual sentient animals to continued life. Clearly, all sides of this debate

favor humane ways of killing invasive sentient individuals if such individuals are to be killed, but even if a completely painless management or eradication method were to be devised, certain advocates of animal rights would object to it.

Discussion

Controversies over the urgency and scope of the problems posed by invasions, the real impact of invasions on biodiversity, the charge of xenophobia, and the argument that opposing invasions is largely futile are not likely to ever go away, but they will be less divisive with continued research and especially education of the public about the results of that research. As more people learn more about the impacts of invasions and the developing technologies for managing them, they will be increasingly inclined to support management activities. Policymakers, reflecting the will of the public, will follow suit. However, the controversy revolving around animal rights is of a different type. It reflects deep-seated differences in worldview and an almost religious zeal in certain individuals on either side of the issue. Such profound underlying differences will not quickly yield to better education about the negative impacts and the promising management possibilities. In such cases, society as a whole will have to reach a decision, as scientists are simply citizens among many others in society. Perhaps the early engagement of social scientists in attempting to understand the differing viewpoints and to adjudicate among them would aid in generating good outcomes. The ability of a segment of the Italian population to determine the fate of a species and, consequently, various ecosystems throughout Europe suggests that better methods are needed to allow all stakeholders to have input into decisions that are urgent, irrevocable, and of great consequence. ■



Daniel Simberloff is the Nancy Gore Hunger Professor of Environmental Studies at the University of Tennessee at Knoxville. At Harvard University, he received his A.B in mathematics (1964) and obtained his doctoral thesis under Prof. E.O. Wilson (1969). He worked at Florida State University from 1968 to 1997, when he became the Nancy Gore Hunger Professor of Environmental Studies at the University of Tennessee, where he directs the Institute for Biological Invasions. His research focuses on ecology, evolution, conservation biology, biogeography, and statistical ecology, with specific topics including invasion biology, community composition and structure, and community morphological structure; he is considered to be a world leader in the study of invasive species. In 1971 he shared with E.O. Wilson the Mercer Award of the Ecological Society of America. Other awards include the 2006 Eminent Ecologist Award of the Ecological Society of America, and the 2012 Ramon Margalef Award for Ecology. He is a fellow of several academies including the American Academy of Arts and Sciences, and the US National Academy of Sciences. (Image courtesy of Generalitat de Catalunya).



Professor Daniel Simberloff, recipient of the Ramon Margalef Award for Ecology 2012, delivered the lecture entitled "Biological invasions: much progress, plus several controversies" on 31 October 2012 at the University of Barcelona.

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Scientists awarded the Ramon Margalef Prize for Ecology (2005–2012)

The Autonomous Government of Catalonia created the Ramon Margalef Award for Ecology to honor the memory of the Catalan scientist Ramon Margalef (1919–2004), one of the main thinkers and scholars of ecology as a holistic science. His contributions were decisive to the creation of modern ecology. This international award recognizes those people around the world who have also made outstanding contributions to the development of the science of ecology. More information can be obtained at: www.gencat.cat/premiramonmargalef.

Year	Winner	Main topic of research	Country
2005	Paul Dayton	Population and community ecology, mostly in benthic environments.	USA
2006	John Lawton	Dynamics of populations and communities, impact of global changes in organism populations and communities.	UK
2007	Harold A. Mooney	Plant physiological ecology and phenomena affecting global changes, such as ecological invasions, the loss of diversity and the degradation of ecosystems.	USA
2008	Daniel Pauly	Study of the decline of fish stocks and the ecosystems' response to human pressure.	France
2009	Paul R. Ehrlich	Population and human over-population.	USA
2010	Simon A. Levin	Mathematical modelling and empirical studies in the understanding of macroscopic patterns of ecosystems and biological diversities.	USA
2011	Juan Carlos Castilla	Marine ecology, mostly rocky ecosystems and their sustainability.	Chile
2012	Daniel Simberloff	Invasive species and their impact in the loss of diversity.	USA