

Use of biological invasions and their control to study the dynamics of interacting populations

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INTRODUCTION

One of the difficulties of conservation biology is the general lack of experimental approaches. Because it is often unethical, or simply because this new discipline deals with small and/or fragile populations, experiments on those populations are not always feasible. As a result, the knowledge on population dynamics, when not dealing with laboratory populations of caged invertebrates, has often come from theoretical studies, with notable exceptions such as those based on of some populations isolated on particular islands (e.g., (Clutton-Brock and Coulson, 2002; Grenfell *et al.*, 1998). However, one aspect that is often lacking from theoretical studies, as well as from natural isolated populations, is the interspecific dimension: in the above cases, it is rather exceptional to take into account more than two interacting populations. Yet, as we hope to show in this chapter, direct and indirect “complex” interspecific relationships may be the major ecological forces in some communities. They can thus be crucial for applied ecology as well

as represent heuristic tools for students, and intellectual candies for functional ecologists.

However, there is an enormous set of ecological events that can be viewed as natural, large-scale experiments: biological invasions. Several aspects make biological invasions an interesting tool for the study of interspecific interactions: they are of various types, involve many different organisms, and happen in contrasted ecosystems. Biological invasions are often a very rich source of information for the understanding of ecosystem functioning, as they originate from introductions that are generally relatively well documented. In addition, in many cases, the invaded ecosystem is an island, with all the advantages that insular ecosystems provide for fundamental research: closed ecosystems, with limited size and of relatively simple and non-redundant trophic webs. In the same way that the physiology of an individual may be better understood during illness, the disfunctioning of an ecosystem may help gain knowledge about its normal functioning. In this regard, the changes generated by the simple modifications that are species introductions and their consecutive spread provide many different types of information. Thus, biological introductions represent simple experiments of species addition into a new trophic web. Such experiments can benefit from controls and replicas in the case of archipelagoes.

Similarly, species deletions can be studied in large-scale experiments that are even more accessible to population or community biologists, as they can be designed by them: the control or eradication of the alien species. With this new tool of species addition and deletion from the comparatively simple island ecosystems, one may gain more knowledge of basic processes such as colonization, dispersion, spatial spread, as well as the dynamics of interacting populations. We will here focus on this latter aspect, restricting our analysis on three- and four-species interactions, and shamelessly basing it on our previous studies.

In this chapter, we will present a number of mathematically simple models that depict some “complex” interspecific relationships, with the aim of showing how the study of biological invasions and their control can be useful for the study of fundamental ecological processes that are more problematical to understand in other contexts. Here, complex relationships are defined as interactions within trophic webs that encompass more than two populations (with possible indirect processes), and that may not be really complex in a biological sense, but that are more demanding to study analytically. We also use ‘control’ in a somewhat lenient style. This term can have two meanings: it can be a general term of action against an alien species ranging from simple reduction up to eradication, and it can more specifically mean reduction of the population size down to acceptable levels, in ecological or economic terms. The latter is called ‘mitigation’ or ‘reduction’ and is opposed to ‘eradication’. In this Chapter, we will use ‘mitigation’ for partial population removal, ‘eradication’ when removal is total, and ‘control’ as a general term. We will articulate our presentation in two parts; the first part depicts systems where species are added to a trophic web (the biological invasions), and the second part depicts systems where species are removed (con-

servation programs), focusing on the possible associated indirect processes in each case. A secondary objective of this chapter is to convince the readers, be they students in biology or conservation managers, that mathematical modeling is a powerful tool to understand, and in some case to predict, ecosystem functioning and reactions. Yet for pedagogic purposes, we will present our analyses based on the description of several concrete examples with little or no emphasis on the technical aspects of the mathematical models. We provide references for more details about the models and their analysis.

All the models presented here are deterministic coupled differential equations based on classical Lotka-Volterra predation or competition models. Each population is described by a simple logistic equation, modified to take into account its relationship with the other population(s). Although biologically simple, the models presented here can show a relatively high mathematical complexity when it comes to, for example, determining equilibrium points. Confident that the simplest models are the most useful (Ginzburg and Jensen, 2004), we systematically refrained from unduly adding complexity to our equations, which results in a lack of predictive power. These models are therefore not aimed at providing precise values of population trends or of control measures in the field; neither the nature of the models, nor the state of current knowledge in the field would allow useful quantitative predictions. Rather, the aim of this exercise is to emphasize the link between species, the importance of indirect interactions, and the unexpected outcome of control actions if they are not thoroughly taken into account. We believe that the qualitative information provided by our mechanistic models is suitable to offer the information we seek in this context. Also, while parameterising models to reproduce field results is a very useful way of identifying plausible mechanisms of trophic interaction, it does not (in and of itself) provide a direct test of the importance of those plausible mechanisms. The information they generate should always be completed by information coming from empirical and experimental studies. In this Chapter, we will only deal with the modeling part.

In order to render the reading of this chapter less tedious, we will describe in detail the process leading to the model for the first example only, and will only give the model for the other examples. Although some will differ in details, all models are based on similar principles. Apart from the more complete description of the first case, all examples will be presented in a similar way, to allow easy comparisons between cases.

NATURAL ECOSYSTEM EXPERIMENTS: ADDITIONS AND DELETIONS
OF SPECIES**Biological invasions as a species addition experiment***The hyperpredation process: three-species interactions**a - the case*

Introduced species are notorious for their deleterious impact on invaded communities and their direct effects on trophic systems, such as decrease of prey (or competitor) populations. While they represent catastrophic events in terms of biodiversity conservation, those effects are not of major interest to theoretical ecology. For this reason, we will focus on less obvious effects, starting with an example concerning the extinction of an endemic parrot caused by the introduction of rabbits to an insular system.

The rabbit is one of the most documented introduced mammal species, often associated with a dramatic impact on endemic plant species. To date, this herbivore has been introduced (most of the time purposefully) to more than 800 islands (Flux and Fullagar, 1992). Rabbits have a high ecological adaptability, and as such easily succeed when introduced in to ecosystems where indigenous grazers are much less numerous and competitive (Flux, 1993). The very rapid increase of their populations can lead to a dramatic quantitative and qualitative impoverishment of the vegetation (Chapuis *et al.*, 1994; Selkirk *et al.*, 1983), resulting in dramatic denudation of the soil (Scott, 1988) and have an impact on animal species which depend on the vegetation (Gillham, 1963).

Effects of rabbits on indigenous vertebrate species can also be more complex. These mammals are preyed upon by other introduced vertebrates, in particular by feral domestic cats. Cats, for example, are opportunistic predators which switch prey according to relative spatial and/or temporal availability (Fitzgerald, 1988). When rabbits are abundant, domestic cats are known to prey largely upon them. However, rabbits can constitute a smaller part of the cat diet when birds, reptiles or other mammals are relatively more abundant. In several sub-Antarctic islands, rabbits are only a secondary prey item in months when seabirds are present, but appear to enable cats to subsist over winter when seabirds are absent (Chapuis, 1995a, b). A similar effect is documented in the spatial dimension: rabbits often enable cats to reach remote colonies or populations of indigenous prey in islands with heterogeneous indigenous prey distribution (Brothers and Copson, 1988). In these cases, the presence of rabbits has an indirect effect on other prey species used by introduced cats.

Predation by cats introduced to Macquarie Island caused the decline of burrow-nesting petrels (Brothers, 1984) and the extinction of an endemic parakeet and a banded rail (Taylor, 1979). Cats were introduced to the island 60 years before the introduction of rabbits, however the cat driven extinction of birds dates back

to just 10 years following the introduction of rabbits (Taylor, 1979). Rabbits were not observed as having any direct effects on the land birds. In fact, it is believed that the rabbit population allowed a significant increase in the cat population, resulting in an increased predation pressure on the land bird species. This process, related to the more general “apparent competition” (e.g., (Abrams, 1987; Abrams *et al.*, 1998; Holt, 1977) has been termed hyperpredation (Courchamp *et al.*, 2000; Smith and Quin, 1996).

It is generally assumed that life history traits and behavior of the introduced prey make it resistant to high levels of predation pressure. A higher reproductive rate, high density and efficient anti-predator responses (which are often lacking in the indigenous species) exhibited by the introduced prey could enable an increase in the predator population without a large decrease in the introduced prey population. Furthermore, the lack of serious competitors and the relatively few parasites typically found in introduced populations can also increase their potential for dramatic population growth (the enemy release hypothesis: (Keane and Crawley, 2002)). These features imply the ability to sustain high predation pressure, as cats are supposed to remove only the individuals with low survival (dispersing young, sick and dead, (Smith and Quin, 1996)). The resulting increased population of predators cannot be sustained by the indigenous prey species which, compared with the introduced prey species, has inferior (less well adapted) reproductive and anti-predator characteristics. The conjunction of a low adaptation to predation and an artificially high predation pressure can lead to a dramatic decrease in an indigenous prey population, up to total extirpation.

b - the model

We will thus present a simple model of hyperpredation to illustrate how the extinction of the bird population on Macquarie Island can be explained by an indirect effect of the introduced rabbits. For heuristic purposes, we first present a two-species model, and then modify it into a three-species model. We hope that this will help the understanding of this model and of the other sets of equations in this chapter (which are all based on the same principle). We use the example of bird (local prey), rabbit (introduced prey) and cat (introduced predator), and will refer to these species for the sake of simplicity, but other species can present similar relationships.

The bird-cat model can be given the following form:

$$\left\{ \begin{array}{l} \frac{dB}{dt} = r_b B \left[1 - \frac{B}{K_b} \right] - \mu_b CB \\ \frac{dC}{dt} = \lambda_b \mu_b BC - \nu C \end{array} \right. ,$$

where the number of individuals at time t in the bird, rabbit and cat populations are B , R and C , respectively. The rabbit-cat model is the same. The intrinsic growth rates of the bird and the rabbit populations are r_b and r_r , respectively. The predation rate is μ_b on the bird population and μ_r on the rabbit population. The carrying capacity of the environment for the bird population is K_b and the carrying capacity of the environment for the rabbit is K_r . The rate at which eaten prey are turned into new predators is λ_b for birds and λ_r for rabbits, and v is the predator mortality rate. In a more general manner, the same parameters will be used for the next models, with indexes corresponding to the first letter of the species considered.

If two prey species are to be considered simultaneously, the formulation of the predation rates and of the growth rate of the predator must be changed accordingly: instead of $\mu_b C$ and $\mu_r C$, the predation rates are given the form

$$\frac{B}{B+R} \mu_b C \quad \text{and} \quad \frac{R}{B+R} \mu_r C$$

for the bird and the rabbit predation rates respectively, so that the predation rate is still a function of the availability of the prey but varies with relative prey proportions. The adaptation of the introduced prey in terms of an anti-predator behavioral response is given by a preference of the predator for the indigenous prey (which is more easily detected and/or caught) over the introduced prey. This preference is a ratio (α) with a simple biological meaning: given equal availability, the predator will prey upon the indigenous prey α times more often than on the introduced prey. We assume that $\alpha \geq 1$, and that one rabbit and one bird prey items are energetically equally valuable to the cat. The predation terms are now given by

$$\frac{\alpha B}{\alpha B + R} \mu_b C \quad \text{and} \quad \frac{R}{\alpha B + R} \mu_r C$$

on the indigenous and introduced prey respectively. This change is reflected in a similar way in the predator growth rate:

$$\lambda_b B \left[\frac{\alpha B}{\alpha B + R} \right] \mu_b C + \lambda_r R \left[\frac{R}{\alpha B + R} \right] \mu_r C :$$

it depends on both the numbers and the proportion of prey. We have now the following system:

$$\left\{ \begin{array}{l} \frac{dB}{dt} = r_b B \left[1 - \frac{B}{K_b} \right] - \frac{\alpha B}{\alpha B + R} \mu_b CB \\ \frac{dR}{dt} = r_r R \left[1 - \frac{R}{K_r} \right] - \frac{R}{\alpha B + R} \mu_r CR \\ \frac{dC}{dt} = \frac{(\lambda_b \mu_b \alpha B^2 + \lambda_r \mu_r B^2)C}{\alpha B + R} - \nu C \end{array} \right.$$

Note that similar formulations of the model could be used and that the aforementioned choices are arbitrary. In particular, we used a predation term proportional to the number of prey. We did so to keep the formulation of the original paper (Courchamp *et al.*, 2000) but alternative models can reproduce the hyperpredation process. Also, like for the rest of the models presented in this chapter, we do not take into account the further risks encountered by populations when at small sizes (environmental and demographic stochasticity, Allee effects etc.). Most of those would anyway only strengthen our point. The classical compartmental representation of the model is presented in Fig. 1A, the corresponding set of equations is shown in Fig. 1B, and a selected representation of the population trends with time is given in Fig. 1C. The other examples will be illustrated with figures following the same format.

The study of this set of equations (both analytically and numerically, see (Courchamp *et al.*, 2000) shows that the indirect effect of the introduced prey may be very important. Indeed, according to the values of the parameters, the increase of the predator population triggered by the presence of the introduced prey can drive the indigenous prey to very low numbers and potentially to extinction. The effect of hyperpredation is the strongest for species with low intrinsic growth rate and low environmental carrying capacity. This model also illustrates that the hyperpredation process may be due to a combination of well-adapted life history traits and efficient behavioral response of prey, but that the “better-adapted” behavioral response may have more importance than “better-adapted” life history traits, at least for the cases considered (Courchamp *et al.*, 2000). Thus, a prey species introduced into an environment in which a predator has also been introduced is likely to allow so high an increase of this predator, that local prey, less adapted to high levels of predation, could suffer a population decline and possibly even extinction. Such a process has consequences when it comes to management actions.

c - Conservation consequences

Historically, conservation programs for many islands have been processed case by case. Until recently, introduced species were always considered separately, with, at best, separate programs for each species, and timings depending mostly on funding and logistics, or, more frequently, one single program for the visibly

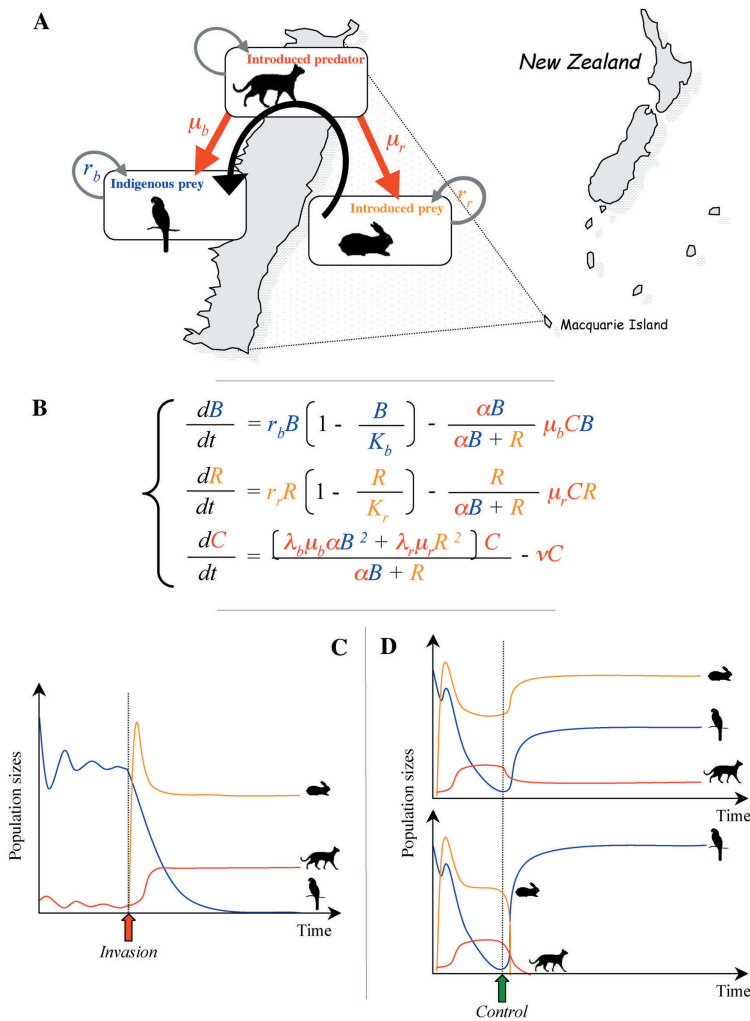


Fig. 1 Representation of the hyperpredation model, with the introduced prey, indigenous prey and introduced predator being illustrated by rabbits (R), birds (B) and cats (C), respectively. (A): compartmental representation and illustration of the island from where the example is taken, here Macquarie Island, off New Zealand. Each box represents a population, and the arrows represent fluxes between them. The large, curved arrow represents an indirect effect. Each species is illustrated in a color that is also used for the set of equations (B) and for the drawings that represent the population dynamics of the interacting species after introduction of a species (C) or control of an introduced species (D). In this example, following the cat introduction (red arrow), the increase of the cat population allowed by the large population of rabbits leads to bird extinction (C). Following control (green arrow in D), the bird population only partially recovers if only the cat is controlled (top panel of D). However, the same cat control level leads to cat eradication and full recovery of birds if both the rabbits and the cat are controlled (bottom panel of D).

most devastating species. As a result, when a conservation program involved an island such as the one we just mentioned, with a hyperpredation process taking place, the key role of the introduced prey was not systematically obvious. Predators are often perceived as having the most important deleterious effects on invaded ecosystems, and consequently control programs were more often directed at them, sometimes neglecting the introduced prey. Yet, we have just seen that in the presence of introduced predators, introduced prey could have an indirect impact on indigenous prey. Basing our efforts on the model presented in the previous section of this chapter, we studied the relative efficiency of control programs aiming either at the predator only, or at the introduced prey and predator simultaneously. The model on which we based this has been published in (Courchamp *et al.*, 1999), and this model is only slightly different from the associated model without control (Courchamp *et al.*, 2000). We will not reproduce the model here, as the interest lies not in the details of the equations. The only important point is the addition of a control effort on either the alien prey or the alien predator (or both). This control is added to the corresponding equation by a simple linear term. We emphasize the fact that, in the model, the introduced prey (rabbit) still has no direct effect on the local prey (bird).

Some possible population trends of the system in presence of control are shown in Fig. 1D. The study of this model shows that control of rabbits can facilitate the eradication of cats. Indeed, when no control is undertaken, the cat population stays large, mainly because of the presence of rabbits, and can eliminate the birds in the long term. When cats only are controlled, the presence of rabbits can preclude cat eradication, and the bird population recovery is only partial. In contrast, for the same cat control effort, eradication of rabbits allows eradication of cats and total recovery of birds. Actually, if the control of introduced prey is not sufficient, the indigenous prey will be destroyed, even if the predator population is being controlled.

Obviously we argue here, that even in absence of visible direct effect, introduced prey should be controlled when a predator has been introduced, in order to prevent an artificial predator population increase. In addition, removing an introduced predator population without controlling the introduced prey may be difficult to achieve since they constitute a constant source of food to the predator. Also, it would not be an appropriate solution because removing the predation pressure would increase the difficulties of later coping with introduced prey, which are often characterized by high reproductive rates. On the other hand, controlling only the introduced prey is unsatisfactory in the long term because predators could report high predation pressure on the indigenous prey. Combined control of both species seems here to be the best restoration strategy. In addition, starting both control programs together would also result in advantages due to synergetic effects: costs may be reduced (if costs related to transportation, or hunting and trapping can be shared by the two programs) and efficiency might be increased (e.g., through the additive effects of primary and secondary poisoning of predators) (Flux, 1993; Rammell *et al.*, 1984; Robertson *et al.*, 1994).

To conclude, it is worth reiterating that the higher efficiency of dual control is not due to direct effects of rabbits on birds (habitat destruction and competition for food and shelter), since they are not taken into account here. Nor is the predicted success of dual control due to the preference of the predator, since this preference is set in favor of the indigenous prey in the model. This success is due to the addressing of the hyperpredation process.

The hyperpredation process: four-species interactions

a - the case

The cat is a well-known predator of both insular birds and small introduced mammals, so the example above should be relatively easy to spot. Whenever a local population is threatened by an introduced predator, a diet study of the predator in question should be conducted in order to assess the importance of the impact on the local population, but also potential hyperpredation processes. However, there are cases where this strategy is not obvious, because the cause of a prey population decline may not be spotted as easily. An interesting illustration of this is the severe decline of the insular fox on the Channel Islands in the 1990's.

The Channel Islands group is made up of eight small islands off the Californian coast, USA. The island grey fox (*Urocyon littoralis*) is a small carnivore that arrived on the first island 16,500 years ago. The fox now inhabits the six largest islands and has evolved on each of these in isolation, resulting in six populations representing six different subspecies, all endemic to these islands. On the three northern islands, the insular foxes and their main competitor, the endemic spotted skunks (*Spilogale gracilis amphiala*), were the two terrestrial top-predators of the Channel Islands. In the early 1990's, a study conducted on the home range of the foxes witnessed a considerable decline in the three northern island populations (Roemer, 1999). This severe decline had no obvious cause at first, and many classical ecological forces were investigated: lack of sufficient resource, competition with the spotted skunk and diseases. To no success. Predation was also investigated, although the insular fox was the top terrestrial predator of these ecosystems. Suspicion that foxes were killed by golden eagles led to a new effort of research in this direction. Golden eagles have historically been seen visiting the islands, but they never stayed long enough to constitute a threat to the local prey. A study combining metabolic and energetic approaches with population modeling demonstrated that the local prey were too few to allow a pair of dispersing eagles to breed on and colonize the islands. Yet it became obvious that eagles were killing foxes as well as spotted skunks. On one of these islands, Santa Cruz, field workers eventually discovered a golden eagle nest, in which fox remains attested for the suspected predation on this species. But the problem remained. How would the eagle threaten fox survival through predation, if there was not enough local prey on the island to allow the continuous presence of the eagles? The discovery of the nest provided the answer: remains of piglets were also found in the nest.

Feral pigs (*Sus scrofa*) were introduced on to the three northern islands where the foxes are declining (it was also present on two of the southern islands, but has already been or is almost eradicated there). In addition to the direct damages that introduced pigs are known to cause to the flora and fauna they invade ((Hone, 1995)), this alien species also threatened some local species through an indirect process. By producing piglets all year round, they provided visiting eagles with enough resources for them to colonize the islands. Eagles also irregularly depredated other local prey such as foxes or skunks. However, even this low predation rate on a species that is ill-adapted to avian predation, behaviorally as well as at the population level, was sufficient to drive the fox population towards extinction. The decline was all the more dramatic that the breeding eagle population rapidly grew in numbers, thereby increasing the pressure on the fox population. In the mean time the nocturnal skunks benefited from the arrival of the eagle because they benefited from the release of competition pressure from the declining fox populations while also being killed less often than them. The hypothesis was thus that the arrival of pigs had allowed visiting eagles to stay and breed, and thereby they attracted a common predator to insular prey. Pigs are well adapted to predation — they produce numerous piglets that can escape eagle predation once they reach three months of age. Therefore, there were less consequences for the pig population than the local prey due to the arrival of the eagle (Roemer *et al.*, 2001).

b - the model

To test this hypothesis, a model of the population dynamics of the interacting species was constructed and parameterized with data obtained from the field. The model was based on a simple combination of two classical Lotka-Volterra models: one of competition and one of predation. The skunk and the fox population dynamics were described by a competition model, the pig and the eagle population dynamics were described by a predation model, and a predation term of the eagle was added on both fox and skunk populations. Using a correction term for proportions and preference coefficients (ϕ and σ respectively) as in the previous example, we end up with a system of four equations, one predator and its three prey, two of which are competitors. The system and illustrations of population trends are shown in Fig. 2. More details can be found in Roemer *et al.* (2002).

Simple simulations show that in absence of the pigs (if the system is run with an initial number of pigs set at zero), any introduction of eagles, however large, will eventually lead to colonization failure and fox population persistence. However when pigs are present, a single pair of eagles will be able to colonize the island and build a population that is so large that foxes will go extinct while pigs will remain at moderate densities.

It is also interesting to note that the decline in fox numbers, consecutive to the hyperpredation process triggered by the introduction of pigs, is concomitant with an increase of the endemic skunk. In fact, the arrival of eagles reversed the

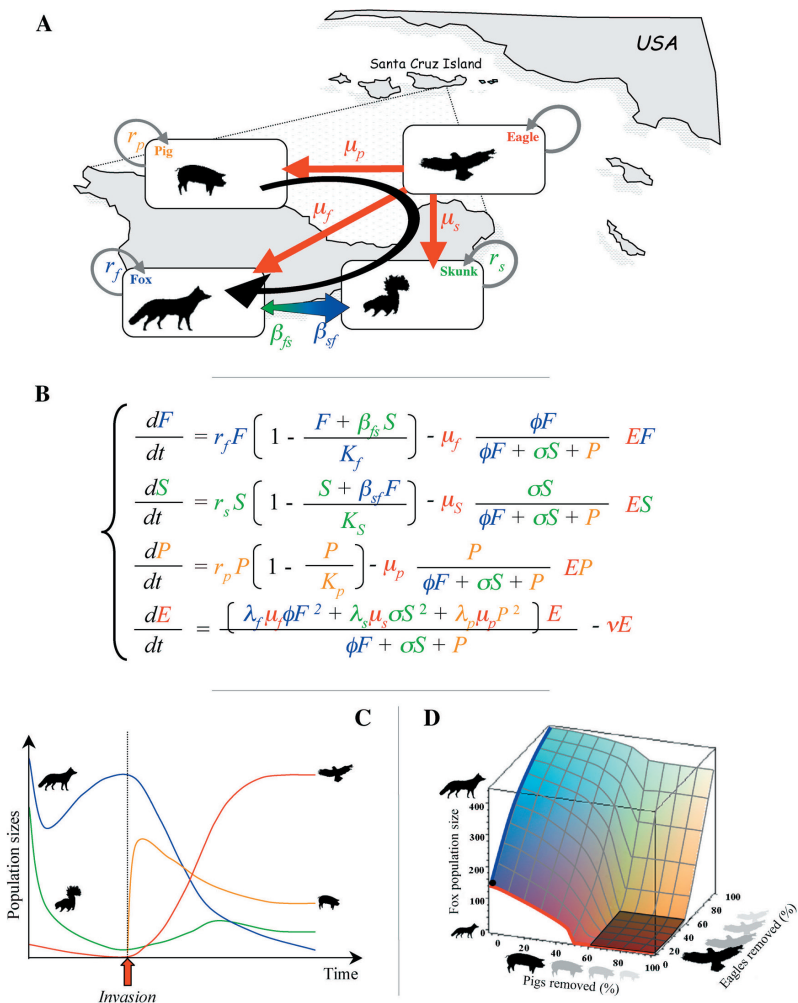


Fig. 2 Representation of the hyperpredation model example with four species: fox (F, blue), skunk (S, green), pig (P, yellow) and eagle (E, red). As in Fig. 1: (A) is the compartmental representation, (B) is the resulting set of equations, (C) is the illustration of populations trends given by (B) following pig introduction and eagle colonization, and (D) is the populations trends following pig and/or eagle control. The parameters are the same than previously, with ϕ and σ being the preference parameters of the eagle for the fox and the skunk over the pig, respectively (same as α in Fig. 1). The control strategy (D) is represented in three dimensions. To help visualize the 3D effect, the colors do not refer to species, but to different population sizes. This graph shows that the population size of foxes is proportional to eagle control, but inversely proportional to pig control. As a result, foxes will decline following pig control only if eagles are not controlled simultaneously. In absence of significant eagle mitigation, high levels of pig mitigation can result in fox extinction (grey area).

competitive outcome between the two top terrestrial predators, shifting forces from direct competition in favor of the fox to apparent competition in favor of the skunk. This second apparent competition process, embedded in the first one, renders any conservation strategy at the least complicated, as the insular spotted skunk is endemic from the northern Channel Islands and are currently benefiting from the fox decline.

c - Conservation consequences

Foxes are now extinct in the wild on two of the three northern islands, with the population on the third island, Santa Cruz, on the verge of extinction (62 individuals in the wild at the end of 2004). Our modeling exercise suggests that the extinction of two populations of the top predator in two insular ecosystems is likely due to an indirect process: a process where an introduced prey attracted a common predator and eliminated an endemic prey through apparent competition only.

Obviously, the solution to this problem lies with the pigs. The most evident plan of action was to remove the pigs from the northern islands. This would have the double advantage of stopping their direct deleterious effects on the local flora and fauna, as well as eliminating the prey basis for the eagles, leading them with little more choice than starvation or emigration. In fact, several conservation strategies were implemented simultaneously. Among them, eagle live-trapping was quite successful, with less than ten individuals proving impossible to trap or that kept coming back from the translocation area. However, it was easy to see that as long as pigs remained, eagles would start breeding on the island again and thus start a new population. The solution therefore seemed to be the complete removal of pigs from Santa Cruz Island. Yet, the study of a model based on the previous one showed once more that indirect interactions may lead to counter-intuitive results (Courchamp *et al.*, 2003b). As for the previous example, the basic model shown in Fig. 2B was changed simply by adding a linear control term to the pig and to the eagle equations.

By varying the control rate of pigs and eagles from zero (no control) to one (eradication), we can mimic different control strategies (control of pigs only, of eagles only or of both species, with different strength) and compare their relative efficiency with no risk to the local populations. Doing so revealed that mitigation of pigs would in fact lead to a decrease in the fox population (Fig. 2D). Eradication of pigs, the intended course of action on Santa Cruz, would lead to fox extinction. Due to the low fox population and the large eagle population, the foxes would be entirely destroyed before the eagles died or emigrated. In theory, the solution is thus simple: remove both the eagles and the pigs. However in practice, the removal of such a large pig population is logistically difficult. In addition, the removal of the eagle would be impossible through live trapping only, and ethically and legally challenging, because golden eagles are protected species in the USA and therefore cannot be killed.

To conclude this part, it may be interesting to note that when more species and more interactions are taken into account, new processes may be unveiled that could not be perceived with only two-species studies. Yet, if better understanding a system is undoubtedly useful for conservation managers, it is not always sufficient for them to be able to know how to act. In the present case, a study taking all species into account revealed that a seemingly obvious line of action (pig removal) would indeed likely achieve results opposite to those desired, and poses a difficult decision to make: remove a protected population in order to save an endangered subspecies. If it is obviously not trivial to make conservation choices, even in the simplest situations, it can sometimes become a challenging dilemma theoretically, logistically, legally and morally. In the present case, the only remaining populations of several fox subspecies were threatened with imminent extinction. However, the proximate cause of this threat is the presence of a protected bird. Furthermore, the decline of the fox benefits the only populations of an endemic skunk. As we have seen, when a (difficult) choice is made, the opposite outcome may well arise. Furthermore, all this is without considering species outside this simplistic system. One could also consider the question under a wider angle, for example including the San Clemente loggerhead shrike, *Lanius ludovicianus mearnsi*, a critically endangered bird, to which the insular fox is the main predator. On San Clemente Island, the fox population has been, ironically, adversely impacted by a US Navy program to protect this bird: attempting to thwart any predation of shrikes, fox were initially trapped and shipped off island or euthanized during the shrike-nesting season (95 foxes removed in 1999, 46 of which permanently). But this is another story...

Along the same line of this conservation riddle, the next part of this chapter investigates the importance of direct interactions in control programs, with the aim of showing that the removal of the primary cause of an ecosystem disfunction will not always help restore the initial conditions. In some cases, not taking into account indirect interaction may lead to even further damage, to the point that it may be wiser to advocate not to remove populations that are known to cause direct negative impacts on invaded communities, at least until adequate knowledge is gained and relevant control strategies are inferred.

Control of invaders as a species removal experiment

Release from introduced herbivores

One concept that is relatively new in the study of invading species, and that has been the core principle of our own studies, is that even if a species is proven to be inflicting important damages to a community it invades, the mere removal of that species may not systematically be the solution to restoring the community. As we have shown with the California Channel Islands example, unconsidered control may even lead to the opposite outcome, that is, further damage, including possible extinction of the species intended to be protected. This fact highlights

the need to have a clear and complete view of the relationships among species that are connected directly or indirectly with the introduced species that is subject to control. It nowadays sounds trivial to state that all the species that interact with a population for which removal is planned, are likely to be affected in diverse ways by any such actions. Thus, the success of an eradication program is measured not only by the complete removal of the controlled species, but also by the absence of further dysfunction. Yet, such errors still occur regularly during conservation programs, sometimes simply because conservation programs have insufficient funds to allow thorough pre-control studies of the invaded community, as well as long term post-control monitoring. Sometimes, simply because conservation action is urgently needed and there is no time for such pre-control study.

The importance of knowing the relationships between invading species and those in the invaded community is well illustrated by the goat and pig eradication on the Sarigan Island. This island is part of the Commonwealth of the Northern Mariana Island, in the Pacific Ocean. Introduced pigs and goats threatened the local flora and fauna, triggering a conservation program consisting mainly of goat and pig eradication (Kessler, 2001). As the island is isolated, and hence difficult to access, the program designed included only a minimal pre-eradication study. The program was considered a full success in terms of removing the introduced mammals, however it failed in its ability to detect that the island had also been colonized by an introduced vine, *Oerculina ventricosa*, which appeared to be a preferential food item for the goats. It is perhaps not surprising that this vine was not found in the pre-control study as it was likely to have been at a low density due to selective grazing by goats. Even a very thorough study might have failed to see it. Yet, it may be valuable to point out that, when possible, simple fenced exclosure studies prior to eradications can often help land managers see if unwanted results will arise after an eradication of herbivores. If so, then appropriate control of non-native plants can be planned along with the herbivore removal. Unfortunately, this was not done and the control program, which aimed at releasing plant species from goat grazing, had a different impact on the overall plant community than the one expected. As the pressure of grazing was removed from all grazed plants, introduced plants were able to fully express their competitive superiority with regards to native plants, resulting in the rapid invasion of the community. Fig. 3 shows how, within only two years, the removal of an exotic grazer led to a complete invasion of the island community by an exotic plant that appears to have a competitive superiority over local plants. As most of the Sarigan Island ecosystem is now covered by vines, one can easily imagine how the indirect effect of having removed goats is now deleterious for the local plants as well as animals that depend upon them.

The mesopredator release effect

The process we have seen with the release of an exotic plant maintained at low density by a browser can be generalized to releases from almost any other type of



Fig. 3 Evolution of the landscape of Sarigan Island, following the eradication of goats. As this introduced herbivore no longer held in check the expansion of the introduced vine, a favored food item, the vine rapidly increased, covering most of the insular plant communities within two years. This illustrates how an exotic grazer affected the competition relationships between local and introduced plants, and how its removal can lead to dramatic and unexpected outcome for the communities which protection was aimed at.

natural enemy. We will illustrate this with the next two examples. This is, however, not to be mistaken with the enemy release hypothesis (Keane and Crawley, 2002), which proposes that invading species are so successful partly because they are released in the invaded habitat from the pressure of their natural enemies (rarely introduced with them).

On Stewart Island, New Zealand, a population of introduced cats was threatening one of the last populations of kakapo (*Strigops habroptilus*), an endemic flightless parrot. A diet study revealed kakapo remains in 5.1% of 118 collected cat scats (Karl and Best, 1982). This seemingly low predation pressure can have a dramatic effect on insular populations which evolved in the absence of such predators and are therefore not adapted to even low levels of predation. Moreover, the kakapo population was already small and fragile, adding to the weight that introduced cats could have on its fate. This could have been sufficient to trigger a program of cat control on the island.

However, rats (known to be important bird predators) had also been introduced on Stewart Island. In the same diet study (Karl and Best, 1982), rat remains were found in 93.0% of these cat faeces. This shows the indirect role cats might play in preserving native fauna, through reduction of rat predation pressure on kakapo. In fact it is easy to see that in some cases the indirect positive effect of cat predation on rats is more beneficial for the local prey than the direct negative effects of cat predation on the prey themselves. In such cases, the elimination of the feral cat population could lead to a more severe negative impact on the local species through an increase in the rodent population as a consequence of the removal of their predators. The attempted reduction of the cat population on Amsterdam Island has been abandoned as it is alleged to have caused a compensating rise in the number of rats and mice (Holdgate and Wace, 1961). This process, termed "mesopredator release", has been described in fragmented insular ecosystems (Soulé *et al.*, 1988) and applies well to many insular food webs (e.g., (Schoener and Spiller, 1999).

Conversely, the eradication of rodents first (which has now proven feasible, even on relatively large islands) might induce cats to switch prey, resulting in a brutal increase in predation pressure on the threatened indigenous species, as experienced for stoats and rats in New Zealand (Murphy and Bradfield, 1992). This is a similar process to the one described above for the pig control in presence of eagles on Santa Cruz Island. As the optimal control strategy is neither simple to find, nor intuitive, it is convenient to study it through the analysis of a mathematical model which mimics the dynamics of the three species in this system. The main results of such a study (Courchamp *et al.*, 1999a) are reproduced below to illustrate how the control of an invading species can provide an ideal opportunity to progress the understanding of the numerous and often complex interactions among populations.

For the sake of clarity, we will not present the model equation in any detail. Suffice to say that the system is described by a set of three coupled equations: one prey (parrot), its predator (the rat, in this case a mesopredator) and one

superpredator (cat) which eats both the prey and the mesopredator. The model, and the resulting population trends are represented in Fig. 4.

The study of the above system leads to the quite obvious conclusion that both predators should be eradicated at the same time. However, not only is such a strategy challenging from a logistical point of view, but in addition it may not always be the best solution, especially if the system includes more introduced predators. Indeed, the prey-mesopredator-superpredator system that we have just described can be further complicated. There are cases where the presence of a third predator can render the eradication of the mesopredator problematic if it also acts as a predator to this third predator (and thus at the same time as a mesopredator and a superpredator). Being aware of the potential dangers of removing a superpredator when a mesopredator is present, the managers of the conservation program of Bird Island, Seychelles, decided, rightly, to simultaneously remove introduced cats and rats in order to protect the local bird colonies. They had, however, overlooked the presence of the introduced crazy ant (*Anoplolepis longipes*), which were present in very low numbers on the island (Feare, 1999). The larvae of these ants seem to have been an important prey item of the introduced rodents, such that the rat eradication led to a demographic explosion of the ants. This resulted in the ants covering a large part of the island, with a heavy impact on land crabs and bird colonies. In fact, this problem of chain reaction following the removal of an introduced species, also called surprise effect or Sysiphus effect (Mack and Lonsdale, 2002), can be generalized to other natural enemies such as herbivores or competitors.

The competitor release effect

The control of an invader has the potential to release any species interacting with the controlled invaders from its pressure, be it exploitation or interference. Therefore, one can imagine very similar processes with a browser or a competitor. Let us consider, as a final example, a “competitor release effect”. Let us set the scene: an island, invaded by, say, a rat species. The island is north of New Caledonia, in the Entrecasteaux Reef. Let us call it Surprise Island, which suits very well a study on surprise effects. A thorough study of the invaded ecosystem, completed to characterize the impact of introduced rats on that island, revealed the presence of a small isolated population of introduced domestic mice. The population seems small and restricted, so that their impact on the ecosystem is likely to be negligible. In fact, in similar situations, they have been in the past neglected, partly because mouse populations are difficult to eradicate, partly because such small populations were not viewed as a threat, and partly because the conservation program concerned another species and funds and protocols were not available to deal with mice. As an example, the rat and rabbit control of Saint Paul Island, in the Antarctic ocean, has been very successful in eradicating these two introduced mammals (it was even at the time the greatest area ever cleaned up from introduced rabbits), but the program did not focus on the small

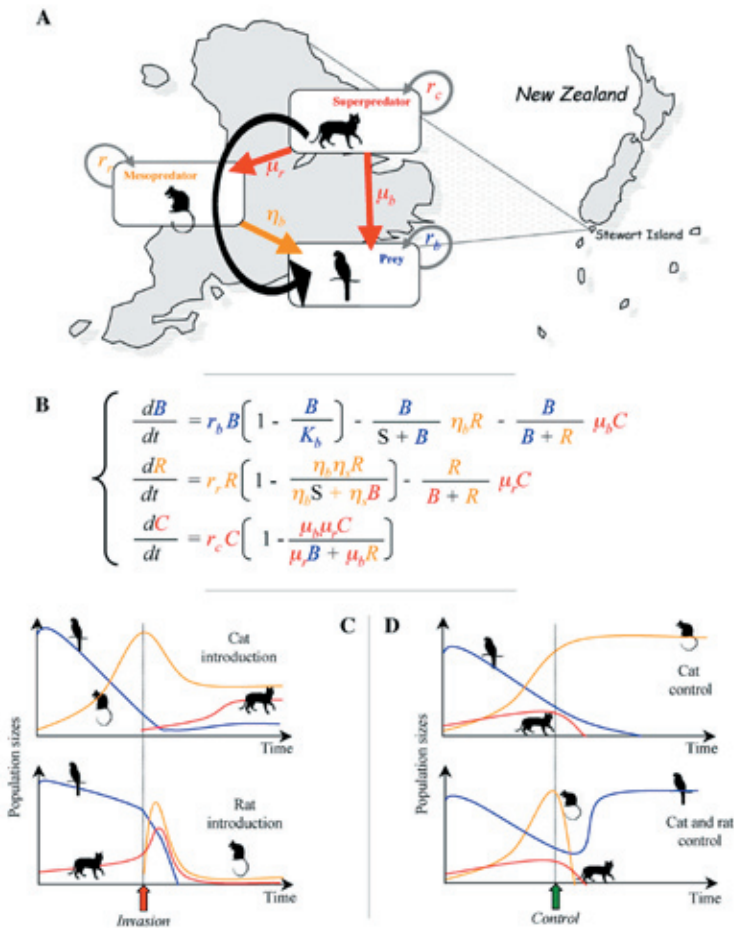


Fig. 4 Representation of the mesopredator release process, with the introduced superpredator being the cat (C, red), the introduced mesopredator being the rat (R, yellow), and the indigenous prey being the bird (B, blue). As in Fig. 1, (A) is the compartmental representation, the example coming from Stewart Island, off the New Zealand mainland, (B) is the resulting set of equations, and the two following panels are typical population trends following introductions (of the superpredator, (C) top and of the mesopredator, (C) bottom) or control (of the superpredator only, (D) top and of both the superpredator and the mesopredator, (D) bottom). Panel (C) shows that in some cases, a superpredator introduction will decrease the predation pressure on local prey, via its predation on the mesopredator (top), while a mesopredator introduction will allow an increase of the superpredator (process similar to the hyperpredation), leading to a further decrease of the prey, via a combination of increased predation of the increased superpredator population, and additional predation from the newly introduced mesopredator (bottom). Panel (D) shows that control of both introduced predator needs to be done to protect the prey (bottom), as the control of only the superpredator can trigger a mesopredator release, which eventually leads to the local prey extinction (top).

mouse population that was known to occur on the island (Micol and Jouventin, 2002).

The study of the Surprise ecosystem suggests that resources are abundant enough for the introduced mice to develop a larger population than they have done. This suggests that the mouse population is restricted by a natural enemy, and it comes naturally to mind that it is the competing rat that restricted them from further expanding their range. Although it is quite difficult to unambiguously demonstrate such competition relationships, field specialists seem unanimous in the view that rats are strong competitors of mice, to the point of often excluding them when common resources are few. It seems then quite predictable, especially after having read the previous examples of “surprise effects” in this chapter, that the planned eradication of the introduced rats on Surprise Island is likely to release the mice from rat competition, and thus to allow them to increase in numbers. Such an outcome is not only intuitively logical, it is also very easy to demonstrate through the analysis of a basic Lotka-Volterra competition model, to which a control term is added to one of the competitors. For the sake of simplicity, we study this three-species system (one prey and two competing predators) through only a two competitors model: the shared prey is ignored here, which also allows a generalization of the system to non-predator competitors.

Analysis of this system clearly shows that the mitigation of the higher competitor (the rat), will lead to an increase of the lower competitor as pressure from competition is lifted. The higher the mitigation, the larger the mouse population. A sudden, complete removal of the rat population is likely to result in a demographic explosion of the mouse population. This was the case on Saint Paul Island following the removal of rats in 2000 (Micol and Jouventin, 2002): released from their competitors, mice numbers increased dramatically, to such a point that for a time they far exceeded the carrying capacity of the habitat. Obviously, mice are less harmful than rats, and thus in some cases the end benefit of the rat removal is positive, even if the mouse population increases. Yet, mouse outbreaks can be very problematic, as mice have been shown to be active predators of invertebrates, reptiles and even birds that can be 300 times their weight (Campos and Granadeiro, 1999; Cuthbert and Hilton, 2004; Fitzgerald *et al.*, 1996; Le Roux *et al.*, 2002; Newman, 1994; Smith *et al.*, 2002).

But this competitor release effect is in fact neither surprising nor very interesting for the study of interspecific relationships. The obvious approach to such situations seems simply to apply a simultaneous control to both competitors. And it is all the better that we are dealing with competing rodents, as a simultaneous control is easily feasible with a common rodenticide, for example. End of story, or so it seems. In fact, just to make sure no more surprises are going to emerge from the system, it is possible to complete the model by adding a simultaneous control term to the inferior competitor as well (see Figs 5A and 5B). It seems logical to link the two control rates, for they will often be (at least in the case of rodents) controlled in the same program. For example, one can have $\omega_r/\delta = \omega_m$, with ω_m being the control rate of the mice, the lower competitor (the mouse) and δ the control

specificity. A value of, say, 2 for δ means that superior competitors are controlled twice as much as inferior competitors. This is very likely if, for example, baits are accessible in priority to higher competitors, or if the trapping design is aimed at the higher competitor, but they also allow to trap the lower competitor, although with a lower efficiency (the program aim is to remove the rats, but rat traps also can catch mice). Studying this very simple system reveals in fact a subtler and less expected competitor release effect. As shown in Fig. 5C, the simultaneous mitigation of both competitors can lead to a release of the lower competitor. In some cases, this release can amount to actual population explosions. It is possible that aiming at controlling, say an introduced rodent, a control program will lead to a dramatic increase of another rodent, even if that one is controlled too.

Moreover, Fig. 5D shows that the competitor release is directly proportional to the control rate. This means that the more the targeted species is controlled, the more important the competitor release effect will be. This is not so obvious to predict, as it implies that the inferior competitor is controlled too, with a control effort that increases at the same rate as that of the superior competitor. In other words, the more rodents are controlled, the more mice appear. Even if mice are actually caught in traps, and killed by poison, the more we kill them, the more their population will increase. Quite the opposite of an expected outcome.

Although this process may be less intuitive and therefore less often foreseen, it is *a posteriori* quite easy to understand. This is likely to occur as soon as the lower competitor benefits from the differential effect of the simultaneous control of both competitors; when its indirect positive effect (the removal of their competitors) exceeds its direct negative effect (their own removal).

Obviously, such a process can be interesting if the lower competitor is a local species, which survival was threatened by the controlled population. In this case, the dramatic increase of its population following competition release is nothing less than the program objectives. This can be considered in cases where an introduced species is to be removed because it threatens a local population through competition, but where control programs were not implemented for fear of damage to non-target species. In those cases, any unintended non-target death should be more than balanced by the death of the introduced competitors. There is no happy ending, however, if the lower competitor appears to be another introduced species, which increase can inflict further damages to the invaded ecosystem, especially if that increase is dramatic. Again, in many conservation situations, managers have to make trade-off choices, and it may appear that a competitor release be eventually less detrimental than allowing the presence of the introduced predator. Yet, dramatic increases of alien species are often very harmful to ecosystems, and this eventually should always be assessed.

There is much more that could be said about such a system, even as simple as it is, and about the case studies in which the overlooking of an enemy release led to surprise effects that eventually caused further damages to invaded ecosystems. However, being that the aim of this chapter is to convince the reader that biological invasions and their control can provide an excellent model system for

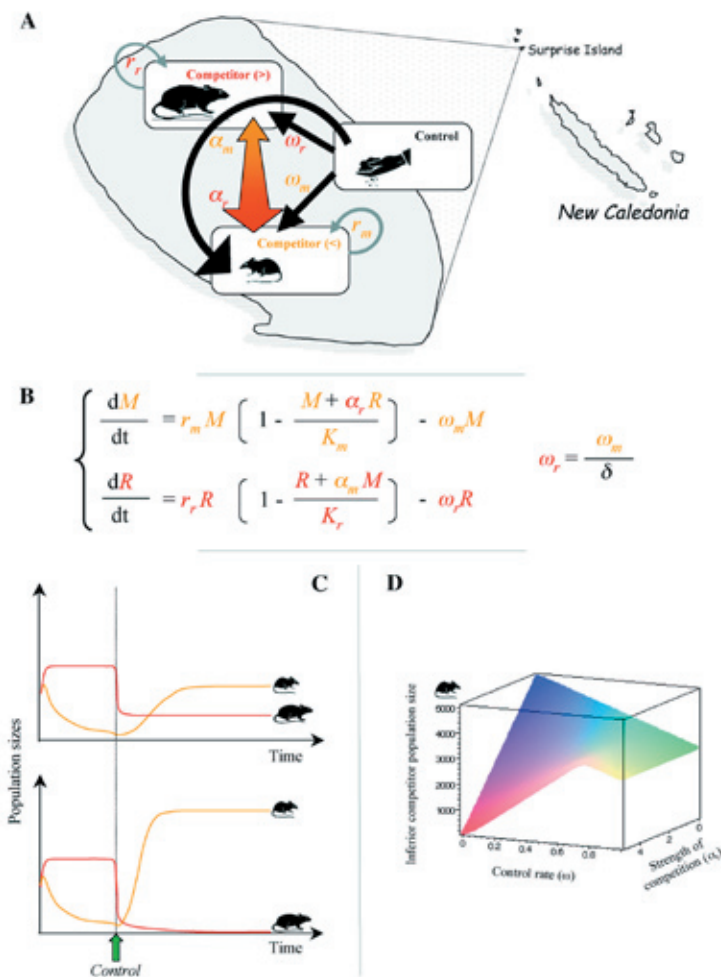


Fig. 5 Illustration of the competitor release effect. Panel (A) shows the compartmental representation of the example taken from Surprise Island, off New Caledonia, where two rodents are competitors: rats (R, red) being a superior competitor over the mice (M, yellow). The equation set in the presence of simultaneous control is given in panel (B). Here, both (C) and (D) represent population trends following control. Panel (C) shows the population trends of the two competitors as a function of time, for two different combinations of control effort and control specificity (see text). In both cases, the rodent control can lead to the demographic explosion of one of the rodent populations. Panel (D) shows the population trends of the lower competitor, as a function of the control effort and the control efficiency. As in Fig. 2, the colors are given here to facilitate the 3D effect. This panel shows that if the competition is strong, the demographic explosion of the lower competitor is proportional to its control. As the competition pressure from the superior competitor is lifted by the control, the resulting gain in population growth is compensating the losses occurred by the control, resulting in a larger population than in absence of control.

the study of interspecific relationships, we will only close this example by an obvious, if overlooked, statement. In some cases, the direct negative impact of a species can hide an indirect positive effect on the same community, sometimes on the very same species. In a classical system where species addition or removal is not the rule, such interactions can remain hidden. In the case of invaded communities and of associated conservation programs, species removal can highlight these undetected relationships. Such highlight is however done in the form of further damage in the system, with a risk of biodiversity loss, and should therefore be anticipated. If indirect positive effects are greater than the direct negative effects, one must be extremely cautious in any restoration action intended to protect the affected species.

CONCLUSION

Biological invasions are primarily considered for their harmful effects on biodiversity in invaded ecosystems, especially on islands. This is far from surprising as islands are places of major biological diversity (and are often included in ecological hotspots, [Myers *et al.*, 2000; Reid, 1998]) and of high probability of exotic species introduction. For example, 644 mammal introductions have been documented on islands (Ebenhard, 1988), while Gargominy *et al.* recorded more than 800 exotic species of flowering plants in the wild in New Caledonia alone (Gargominy *et al.*, 1996). These figures have undoubtedly increased nowadays. The number of species that went extinct as a result of these invasions is imposing too. Consequently, the number of control programs has been on the rise this last decade, and here again there are a great number of documented examples, with, for example, over 150 eradication programs just for exotic mammals in New Zealand (C.R. Veitch, pers. comm.).

We have so far insisted much on caution and planning in any mitigation/eradication effort in management programs. We feel it is nevertheless essential to start our conclusion by rewording the obvious: the best response to biological invasion is almost always mitigate, and when possible eradicate, the alien population. In many cases a hesitancy to proceed with this has caused more damage to biodiversity than have the unexpected results of poorly planned or simply unlucky eradications.

However, the aim of this chapter was to take a different point of view regarding biological invasions, and to show that such events, however not systematic, can be viewed as opportunities to increase fundamental knowledge in ecology. Additions and deletions of species in trophic webs that are comparatively much simpler than usual should greatly enhance our ability to discern intrinsic dynamical processes as well as direct and indirect interactions between species (and here we view population dynamics as good markers of such mechanisms). This approach also has the dual advantage of addressing mechanisms on a real-scale (something impossible in laboratory based studies) and of encompassing

all the charming constraints of biological reality (something missing in purely theoretical ecology).

It is, of course, not our purpose to minimize the contribution of theory in this regard. Despite their indubitable advantage in this domain, field-based studies that use invasions as an experiment have much to gain from a synergy with concomitant laboratory and theoretical approaches. We even urge conservation biologists and biodiversity managers to use theoretical-based results to found their conservation program design, and to look into historical cases in order not to endlessly repeat mistakes of the past. An idea associated to this is the need for conservationists as well as biodiversity managers to know when to stop a program and rethink the strategy (Courchamp *et al.*, 2003a). To know when we are starting to play the witch's sorcerer and when to stop is an essential, yet difficult faculty. History has shown us that often more harm is generated when trial and error processes are used indiscriminately. One good example of this is given by the attempted mitigation of rats in sugarcane fields in Jamaica. There, cane growers introduced ants (*Formica omnivora*), which did not reduce rat numbers but soon became a problem themselves. To remove rats and ants together, it was then decided to introduce toads (*Bufo marinus*). But toads still did not control rats, and became a pest themselves. Finally, small Indian mongooses were introduced to control rats and toads. Mongooses failed to control either, and began preying on native birds, posing new threats to wildlife (Silverstein and Silverstein, 1974).

We recognize that there has been much to gain from these kinds of historical mistakes and that these hard-won lessons might even turn out to be globally beneficial for the biodiversity in the long run. However, we believe the trial-and-error approach time has now passed, and biodiversity managers should persevere in the current trend of basing restoration strategies on sound scientific grounds. This can only be done in developing specific studies on populations interacting in invaded communities as well as those that use such invasions as a didactic tool to understand basic processes in population ecology.

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