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IBAR Course

Chapter 1 : Invasive species - insects and islands

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Invasive species - insects and islands

This chapter of the IBAR course (Invasive species: insects and island environment) is the first of three entitled “INVASIVE SPECIES - BIOLOGICAL CONTROL - AGROECOLOGICAL CASE STUDY”, and is based on recent scientific papers on biological invasions in a changing context, from the globalization of transport to degraded habitats. In this chapter, you will acquire basic knowledge and a critical look at different ideas, beyond Chapters 2, "Biological control, introduction and acclimatization of auxiliary insects" and 3 (Agroecolological management of fruit flies on Reunion Island).

Summary

Chapter 1, **Invasive species - insects and islands, will guide you across the** definition of biological invasions, the Williamson's tens rule, anthropogenic arrivals and their quantification (case study on the island of Gough), and the important transition between establishment and invasion. The vulnerability of islands to biological invasions, as well as the main factors involved, will be seen. The main effects and costs of insect invasions will be shown in natural as well as in cultivated areas. Finally, you will have a glimpse at science and society aspects, of the perception of the role of species invasions.

A. DEFINITION OF BIOLOGICAL INVASIONS

What does the term 'invasive species' mean to you? Exactly what is a biological invasion, and why is it an interesting topic? These are the questions we asked national park researchers and managers at a summer school on biological invasions held by the University of Reunion Island in June 2013. You'll be watching the interviews, answering some questions and hearing the first definitions of invasive species. The interviews were conducted by David Josserond, a scientific journalist.

In order of appearance on the screen:

Christoph Kueffer, Institute of Integrative Biology, Zurich, Switzerland.

"The definition of an "invasive" species: first, this species is not from Reunion, it was introduced by man, and then it creates problems. Many exotic introduced species pose no problems, while others increase in numbers very fast, are very competitive, and this can be a problem for native and endemic (found nowhere else on earth, editor's note) vegetation"

Stéphane BARET, National Reunion Park, France. "We talk about invasive alien species or invasive species; this is an exotic species (although here we are in the tropics!) that comes from elsewhere, which was introduced in a place (for Reunion, on the island) voluntarily or not by man. Voluntarily: we can bring fruit trees for agriculture. As involuntarily introductions we often cite rats, which arrive in the hold of a boat and are then propagated naturally, but this remains an involuntary introduction by man. Thus all species, introduced voluntarily or unvolontarily by man, are considered as exotic"

Mathieu ROUGET, Department of Plant Sciences, University of Pretoria, South Africa. "What interests people most on the issue of invasive plants is: the loss of biodiversity that invasive species can cause"

Vincent FLORENS, Biosciences Department, Faculty of Science, University of Mauritius, Republic of Mauritius. "There are very few efforts to prevent the arrival of these species. They often have perceived benefits in the short term, which take precedence over any damage they may cause. But the country loses out in the end. We do not take into account the invasions caused which will disturb many things – species go extinct, the hydrological cycle will be completely disrupted, etc ..."

QUIZ

Is it possible for a species considered to be an invasive species at a given location, to be a native of the same location?

Explanation: No .... if a species is introduced by man in a geographic region in which it doesn't occur naturally, it is considered to be an exotic species in that area. If it is able to establish in its new environment, expand its range across its native habitat and become abundant, then it is considered to be an invasive species. In one of his recent publications, C. Kueffer mentioned that some native species have been considered as invasive by certain authors, but not everyone agrees on this issue! (Humair et al., 2014). On rare occasions, a native species can indeed appear to invade a native environment, but is not considered as invasive, since it is not exotic. There exists a term in French for species in this category: "envahissante". We will stick to the definition given above and consider invasive species as a subset of introduced (i.e. exotic) species.

Reading the French language GEIR website (Group of Invasive Species of La Reunion island, http://www.especesinvasives.re/especes-invasives/especes-invasives-a-la-reunion/), we learn that among more than 2,000 introduced plant species, 151 are considered as invasive (with 848 known native species). Concerning fauna (but not including insects and mollusks), 48 native and 70 introduced species have been described in Reunion Island, including 11 invasive species. EU Regulation No 1143/2014 published by the European Parliament and the Council on October 22, 2014, on the prevention and management of the introduction and spread of invasive alien species, states (Article 6) that by January 2, 2017, each Member State with outermost regions shall adopt for each of those regions a list of invasive alien species of concern, in consultation with those regions. To fulfill these requirements, a preliminary list was drawn up for Reunion Island in concertation with different government and local stakeholders.

How many alien plant species of concern do you think there are on the proposed list for Reunion Island? 80? 800?

Explanation: The answer is approximately 800 (the exact number will be released in 2017). About half the species are already present on the island, whilst the other half is still absent.

Which sentences and/or words do the interviewees use to define an invasive species? (More than one answer)

exotic, non-native
native

introduced by humans
competitive compared to native species

cause disruption or damage

Explanation: The only wrong answer is "native". Invasive species are not native: they have been moved or have moved out of their original range. The ISSG (Invasive Species Specialist Group) of IUCN, founded in 1994, provides a definition of invasive species which approximates that heard in our interviews, and which has a negative connotation (http://www.issg.org/is_what_are_they.htm). The invasion is anthropogenic (voluntary or involuntary), and moves the invasive species outside its native range. Note that pioneering work by Elton (1958), who began research in invasion ecology, and later Williamson (1996a), dissociated the phenomenon of invasion and its consequences, and did not limit the use of the term "invasion" to only man made, i.e. anthropogenic, invasions.

The invasive species is a disturbance agent that harms biodiversity. According to ISSG, these species are “animals, plants or other organisms introduced by man into places out of their natural range of distribution, where they become established and disperse, generating a negative impact on the local ecosystem and species", according to Sax, Stachovicz and Gaines, 2005, « invasive refers to those species that are known to cause ecological or economic damage » , according to Lockwood, Hoopes and Marchetti, 2007, « ... how non-native species interact with human society, and how we can use ecological knowledge to prevent the influx and impact of invaders ».

However, sometimes the data or criteria that would be needed to distinguish between natural or anthropogenic processes are missing (if we consider that climate change has an effect on species' geographic distributions, is this species' modified geographic distribution of natural or anthropogenic origin?), as well as also to understand the nature and impact of non-native species (Pascal, Lorvelec and Vine, 2006).

A particular word is used in combination with the plants in the interviews, it can also be used in connection with rats. What is it? (it has four letters)

Explanation: The answer is PEST; invasive plants are often called plant pests. The negative connotation of the word PEST has its origins in the bubonic plague (which was called "pest" in English in the 1550s, and is still called "la peste" in French), and which ravaged human populations up to the 17th and 18th century. The black rat *Rattus rattus* was responsible for transmitting fleas infected with the bacillus *Yersinia pestis* to humans. Did you know that the eradication of plague was partly due to competition between *Rattus rattus* and the Norwegian rat *Rattus norvegicus,* which was immunized against the disease and arrived in Europe in the 18th century? In this case, one invasive species came into competition with another, which had a positive impact on human health (Barbault & Atramentowicz, 2010; Monecke et al., 2009). Unfortunately, the negative impacts of *R. norvegicus*, *R. rattus* as well as *R. exulans* on a range of threatened species and on ecosystem functioning are well documented, and represent a far more common situation, in particular in insular environments. From 1983, these three species of rats were introduced in more than 80% of the world's island groups (in Russel and Holmes, 2015).

B. THE WILLIAMSON'S TENS RULE

When a species arrives in a non-native environment, it does not ultimately become established. Williamson was one of the first scientists to study and evaluate different transitions, which were named :

Importation/Introduction/Establishment/Pest

The term « pest » may be replaced by « invasive ». His first studies in Great Britain concerned releases of genetically modified organisms, as well as a detailed flora of British gymnosperms and angiosperms (Ecological Flora Database (Fitter & Peat, 1994)).

In the Williamson's tens rule (Williamson & Fitter, 1996a, 1996b) three stages of invasion are distinguished : escaping (transition from imported to introduced), establishing, becoming a pest. The transition from imported to introduced, which can be called escaping, has a probability of around 10% in many cases, and the probability of establishing is also often about 10%. Thus in the tens rule, each transition has a probability of around 10% (between 5 and 20%). In other words, the probability for one imported species to become a pest is around 1/1000. In the particular case of predators and parasitoids, released intentionally and thus considered as introduced, their rates of establishment and becoming a pest will be discussed hereafter.

QUIZ

If we accept that the "10% rule" applies to all 20 species present on a boat that transports them out of their original range, what is the probability that one of these species becomes invasive once it has arrived at its destination?

1/1000 to 2/10

1/10000 to 2/100

or 1/100000 to 2/1000

Explanation: The correct answer is 1/1000 to 2/10. With about 20 different species on the boat, between 5% and 20% of species are retained at each barrier (see 3 barriers below)

Import/Introduction

Introduction/establishment

Establishment/invasion

The probability for each plant species transported to become a pest ranges between $(5\%)^3 = 1.25/10^4$ and $(20\%)^3 = 8/10^3$

The probability that one of the 20 species transported by boat becomes a pest is therefore $20 * 1.25 / 10^4 = 2.5 / 10^3$ to $20 * 8/10^3 = 1.6 / 10$

We have just reviewed the Williamson rule. For some species, this rule is confirmed (e.g. for vertebrates, insects, pathogens). However, there are also exceptions, including insects intentionally introduced for the purpose of biological control, which we will be looking at in chapter 2. Following Williamson's rule step by step, we will consider some instructive examples, first man's effect on the numbers of species introduced in a non-native territory.

C. ANTHROPOGENIC ARRIVALS AND THEIR QUANTIFICATION: A CASE STUDY ON THE ISLAND OF GOUGH

Transported by humans, species arriving in a non-native territory often travel with traded goods (e.g. insects on ornamental plants), or directly via transport networks (e.g. rats transported by ships). We present a case study of Gough, an island covering 25 square miles (65 km^2), located in the South Atlantic. Access to the island is difficult, it takes 7 days by boat from the city of Cape Town, South Africa. Entomological studies have been regularly conducted on Gough island, which is home to a weather station. A quantitative estimate of exotic insects (i.e. whose arrival was assisted by man since his arrival on the island in the 16th century) and natives has been made, as we will now see.

The case of Gough illustrates how the influence of humans (whether or not arriving by boat) has accelerated the arrival of insects beyond the way they arrive naturally transported by the wind or currents. Although this case study does not take into account the different stages of the invasion process, it serves as an inventory of the arrival of such species in an environment otherwise little disturbed by man.

The small (6500 hectares) mountainous island of Gough is located in the middle of the South Atlantic (40°17'-40°22' South, 52°9'-10°01' West) 217 miles (350 km) SSE of Tristan da Cunha and 1622 miles (2610 km) from South Africa. The island belongs to the territory of Tristan da Cunha (a British dependency). Tristan da Cunha is composed of 5 islands. The first arrival of man is dated to 1675. This was followed by scientific and cartographic expeditions, commercial and whaling (as well as seal hunting) in the 19th century, followed since 1956 by only one trip a year to renew the team at the weather station, the only building on the island. In fact, the low levels of human impact since man's arrival has allowed Gough to remain one of the best preserved of all temperate oceanic islands, which was awarded the status of UNESCO World Heritage site.

A research project to assess the current state of endemic biodiversity / exotic invertebrates on this island was funded by the Darwin Initiative Survival of Species, conducted by the Universities of Sheffield (UK) and Pretoria (South Africa), the Administration of Tristan da Cunha (responsible for the conservation of biodiversity on the island), and the South African Department of Environmental Affairs and Tourism (DEAT) (which manages the meteorological station and ensures the UK management plan is respected).

After a 7 day boat trip (departing from Cape Town), researchers evaluated the invertebrate fauna between September 1999 and September 2001. Ninety sites were delimited on an altitudinal gradient, and were sampled at different intervals; species of invertebrates were identified in the UK, or, in the case of uncertainty, by other experts. The identified species belong to the order Pterygota, and were grouped according to their status. The status included species endemic to the island of Gough or to the Tristan da Cunha islands, native, and exotic (Gaston et al, 2002; 2003).

Before the first man stepped onto Gough island (in 1675), the rate of insect arrivals is estimated to have been one species every 95,000 years, and after 1675, at one species every 5 years.

The cartoon seen in IBAR illustrates the arrival rate of insects before 1675. Then an exerciser uses the Chi2 square test to analyze, according to different insect orders: "Anthropogenic arrivals and their quantification: a case study from the island of Gough". You will have to make sure you know the **Chi-square Test for Independence**. You may for example visit this tutorial : http://www.ling.upenn.edu/~clight/chisquared.htm. The conclusion of the exerciser reads as follows: according to our data and the Chi2 test, the repartition of indigenous/introduced species is dependent on the insect order. For the order of Blattoptera, whose species do not easily fly, we can imagine that arrivals are rare naturally (winds, currents, birds ...) and are facilitated by human transportation means such as ships. Accordingly, Bishop Museum's program of trapping at sea from 1957 to 1967 mentioned the capture of most insect orders in the Pacific Ocean, at miles away from coasts, with the exception of Blattoptera (Holzapfel et Harrell, 1968). However, remember that the data we used are fictive: the real data (which are not enough to perform a Chi2 test) were multiplied by 3 for making a Chi2 analysis possible (80% of the cell values of the table should at least reach the value 5).

QUIZ

If you see a new species on an island at time t, to what stage of the Williamson rule can it be ascribed?

Transport
Introduction
Establishment
Invasion

Explanation: If one observes some insects at a time t, with no further information, it's impossible to distinguish between the three stages: introduction, establishment or invasion. To deduce more, additional information is needed on the number of individuals and their distribution over time.

Two researchers recently reviewed the possible causes of unsuccessful establishments or invasions following the transport of species (Zenni and Nunez, 2013). They analyzed 76 publications (studies) on intra-specific *differences (failure or success) based on locations of introduction (mostly deliberate). In your opinion, how many of these studies suggest and then test the likely causes of the failure of the introduction of a transported species?*

virtually all
nearly 50%
less than 25%

Explanation: No hypothesis was proposed for the species failure to establish or invade in more than half of the studies cited (48 studies). Only 11 studies suggested and tested possible causes. The authors of the review thus underline the absence of research on these subjects. To publish negative results is not always encouraging, but combined results on the same species at different locations can advance our understanding of the process of invasion, when it occurs. And this is why journals like the "Journal of Negative Results" exist! In all, five possible causes of failure are mentioned: Insufficient number of gametes or transported propagules able to survive and subsequently reproduce; unfavorable biotic factors (competition, predation of resident species) and/or abiotic factors (soil composition, climate, rate of water flow, etc.) prevent survival to sexual maturity; loss of the mutualistic partner required for survival (mycorrhizal fungi, pollinators, etc.); low genetic diversity.

D. TRANSITION BETWEEN ESTABLISHMENT AND INVASION

For an introduced species, the question you've just seen concerned the transition between introduction and establishment. The establishment of a species (ability to breed and maintain itself), may depend on environmental characteristics (climate, habitat, resources, etc.), propagule pressure (the frequency of introductions and number of individuals concerned) and biotic interactions (e.g., between native and introduced species). The transition between introduction and establishment was studied specifically in the case of intentionally introduced species, so their establishment was desired! We will return to these cases in chapter 2 (biological control).

To come back to biological invasions, we now look at the transition from establishment to invasion. To better predict biological invasions, it is essential to identify the characteristics of the invasive species: below you will now see examples of how researchers undertook these investigations.

How can an introduced and established species become invasive?

The “enemy loss” hypothesis was mainly based on studies of plants since the 1990s. A given species’ specialist enemies (pathogens, parasites, predators) do not necessarily travel with it under the same conditions, and consequently may be "lost". In the new area where the species is introduced, often there are no natural enemies of the introduced species. In addition, enemies present in the area of introduction are often not effective against the new species, to which they are not adapted. Thus, the enemies that are already present often do not change host or prey, and consequently do not affect the exotic species, and the generalist enemies that are present, continue to prefer native species.

Thus, the introduced species is at an advantage over competing native species present in its introduced range. Although the "loss of enemy" hypothesis can be used to explain examples of successful invasive species, it is neither necessary nor sufficient for most biological invasions, and other parameters (inherent to the species itself or the area of introduction) play a role. A species can become invasive despite the presence of specialized enemies. Similarly, a species may be unable to overcome the hurdle of becoming established or invasive despite the loss of enemies (Keane and Crawley, 2002; Colautti et al., 2004). Finally, other mechanisms may come into play during the invasion process and have been described in some studies in which enemy species are not even mentioned. Below are some examples:

- One way of checking whether “loss of enemy” contributes to the success of invasive species is to look at whether the enemies found in the area where an invasive species has been introduced are less effective on the latter than on native species of the same type. Out of a total 14 studies of this kind, only four have actually reached this conclusion. A recent study focuses on the parasitoid *Dinocampus coccinellae*: native ladybirds from Europe and America serve as a host for the development of its eggs, which it lays in the ladybirds' bodies (photo), eventually killing them. However, in the invasive ladybird species *Harmonia axyridis*, deliberately introduced from Asia for biological control (see below and Chapter 2), this form of parasitism exists but is less effective. In this context, *H.axyridis* develops a competitive edge over other ladybird species. However, we are not yet aware of all the enemies of *H.axyridis* in its native territories and areas of introduction: here, "loss of enemy" is a notion to be handled with precaution! References: Colautti et al., 2004; Roy et Wajnberg, 2008; Comont et al., 2013.

- Other studies compare the enemies of invasive species in their native territory and their area of introduction: out of 12 studies of this type, ten conclude with the notion of "loss of enemy" in the area of introduction; only four confirm an enemy effect on the host. For example, in a set of 26 species (molluscs, crustaceans, mammals, fish, birds, amphibians and reptiles) hosting 16 different species of parasite, it has been demonstrated that this set only hosted seven species in their area of introduction. One example is the green crab (Europe and North Africa), introduced into America, Australia and South Africa (marine transport, ballast water, etc.): its success has been aided by a fall in parasitism. The voracious *Carcinus maenas* is listed in the GISD "Top 100" invasive species and has caused the decline of other crab and bivalve species, and has a negative impact on fish farming (through predation, competition and by modifying habitats). On the poster opposite, the crab is "Wanted" and the description reads, "five spines; flat rear legs, up to 7.62 cm wide, rear shell, variable in colour: black, marbled, often green or orange". References: GISD, Colautti et al., 2004, Torchin et al., 2003.

- *Fallopia japonica* is an invasive plant originally from Japan and East Asia and introduced for ornamental purposes. It has expanded beyond the gardens and is now seen as invasive, especially in Europe. Its characteristics have been compared in its native and non-native territories. Several characteristics have been observed in the non-native territory: fewer generalist plant-eating enemies found, better growth rates, impact on the related plant communities, octoploid (twice as many chromosomes as certain native *F. japonica*, which are tetraploid). In fact, it has been demonstrated that all the European *F. japonica* originated from the same octoploid clone, introduced in the Netherlands in the

19th century by Siebold, a Bavarian doctor and naturalist. The role of this octoploidy remains unknown. As such, “loss of enemy” probably contributes to the success of the species in non-native territories, but cannot be dissociated from other parameters in the study. Reference: Maurel et al., 2013. Photo source: MdE (licence Wikimedia Commons, CC-BY-SA 3.0 German).

- While *F. japonica* only needed introducing into Europe once, multiple introductions can facilitate the invasive process, as was the case for the perennial herb *Phalaris arundinacea*, a significant threat in humid environments and introduced in North America in the 19th century. Analysis of the genetic diversity of this herbaceous plant in its native territory (Europe) and area of introduction (North America) has confirmed that there was a series of introductions. Intrapopulational genetic diversity is higher in the area of introduction than in the native territory, and new combinations of alleles are found: these data indicate that individuals that are not found together in Europe grew alongside one another in North America, leading to hybridisation and recombination. Finally, invasive genotypes (mainly recombinant) have shown better performance (better development speed, aptitude for dispersion, growth, etc.), probably explained by greater genetic variability and an aptitude for natural selection. References: GISD, Lavergne & Molovsky, 2007.

- *Bufo marinus*: An even more striking evolution in invasive character has been observed since the introduction of the *Bufo marinus* toad in Australia in 1936: its expansion has increased from a rate of 10 km/year in 1940 to 50 km/year today. It was introduced with the aim of controlling insect pests but *B. marinus* is now ranked among the ISSG “Top 100” invasive species. Researchers from Sydney University have characterised the toad’s migration front: it comprises the fastest individuals with the longest legs. In addition, correlation between the toad’s generation and leg length indicates that this feature evolves with crossbreeding. Hence, based on spatial segregation, rapid individuals crossbreed with one another at the migration front, which leads to the emergence of recombinant phenotypes, and they are faster again. To date (28 April 2014), individuals had been observed on the west coast of Australia. References : Shine et al., 2011; Phillips et al., 2006; Atlas of living Australia, http://www.ala.org.au/

Predicting whether a species can become invasive requires knowledge of changes in its distribution. Such knowledge is acquired from biodiversity surveys in particular. For example, in a biodiversity monitoring network in Europe (for France: program Vigie Nature, http://vigienature.mnhn.fr/) used by naturalists and volunteer observers, the movements of 9,490 bird communities and 2,130 butterfly communities were analyzed by scientists. Differential northwards movements by the two communities due to global warming was identified: the butterfly (the prey of birds) migration front exceeded the bird migration front by 77 km, and a 135 km lag was identified between changes in temperature, implying significant changes in interactions, both between these groups (butterflies on the migration front lost one of their enemies, the birds!) and their environment (Devictor et al., 2012). In this particular case, it should be noted that the change in the natural distribution of two species is due to environmental change, not a species being introduced outside its native range: the impact on biotic interactions is possibly more gradual, and may decrease over time.

Meta-analysis and differential gene expression now allow researchers to use a global approach to understand which elements characterize a species' invasive potential. Such research mainly concerns plants. One example is the search for genes involved in the invasion process in populations of the invasive herbaceous annual *Ambrosia artemisiifolia* (5 native populations, 6 introduced populations), in which the expression of 45,000 genes was quantified thanks to collaboration between botanists and bioinformaticians). In three different environmental conditions, significant differences in expression were shown for 180 genes. Two categories of genes were identified: those responding to blue light, and those involved in the response to stress, likely indicators of the performance of invasive plant growth and adaptation to a new environment (Prentis and Pavasovic, 2013; Hodgins et al., 2013)

A second example is the meta-analysis of 117 studies that compare 125 and 196 invasive plants and native plants at the same native site. The authors tested various performance indicators (resource use efficiency, leaf area, growth rate, size "fitness", etc.). Most were found to differ significantly between invasive and native plants (not invasive elsewhere). For "growth", the observed difference was even greater in the tropics. Among the introduced plants, whether invasive or non-invasive, the indicators "size" and "fitness" were significantly higher in invasive plants (Van Kleunen et al., 2010).

Question: Did Van Kleunen's study at a given location reveal any differences between non-native invasive plants and plants native to the location, known to be invasive elsewhere ?

The answer is no. Concerning the indicators mentioned **at a given location,** no significant **differences were observed between non-native invasive plants and plants native of this location (known to be invasive elsewhere). These results suggest that invasive plants share characteristics, whether in their location of origin, or in their new location** (Van Kleunen et al., 2010)**.**

A similar study focused on the Séneçon du Cap (*Senecio inaequidens*, Asteraceae), in native (South Africa) and non-native (Europe) territories. Séneçon has been introduced several times since the 19th century, and has since disseminated. Results suggest some populations have an invasive potential that pre-existed in their area of origin; this hypothesis is an alternative to the adaptive evolution of species, under which the species become invasive once they reach the location in which they are introduced (Bossdorf, 2008).

If invasive plants display similar characters at their location of origin and at their destination, what about the locations?

To answer the question of whether niche shifts are a common or unusual phenomenon among alien invasive species, changes in niches between native and invaded ranges were assessed in major plant invaders between North America (NA) and Eurasia (EU), in both directions (50 plants, ranging from trees to herbs). The reciprocal comparison of EU and NA invaders was an important test of niche conservatism, because EU and NA are the only pair of two large, separated land masses with a largely overlapping climate space and a long history of reciprocal anthropogenic exchanges of floras. Pluviometry and temperature were the main parameters taken into account. Although levels of niche overlap among species ranged from 17% to 64%, niche conservatism was observed in 46% of species between the native and invaded range in EU and NA (similarity test with a significance level ≤ 0.05). Only 14% of the species studied showed more than 10% expansion, and one outlier species showed >50% expansion (possibly resulting from ecological and/or evolutionary changes, or from limited dispersal in the native range). Among the plant species in the sample that had reached Australia, Holarctic invasive species were found to remain in Holarctic climates and were rarely found in new climates. In other words, when considering the available climate in the invaded range, species colonize climatic conditions close to the ones they colonized in their native range. Shifts in climatic niche are thus rare among terrestrial plant invaders between their native and introduced ranges (Petitpierre et al., 2012).

Concerning the recent invasion by the tropical ant *Wasmannia auropunctata* (one of the "worst 100" invasives, ISSG) in a Mediterranean region (Israel), which is subject to cold temperatures, an integrative study combining experimental, genetic and SDM (species distribution models) approaches showed that adaptation to cold occurred at the southern limit of the native range (i.e. northern Argentina) before their dispersal to Israel (Rey et al., 2012).

Such "prior adaptation" scenarios have also been linked to habitats altered by humans (Hufbauer et al., 2012). One likely example is *Leptinotarsa decemlineata*, the Colorado potato beetle, which is a pest of many solanaceous crops and also considered to be one of the "100 worst" invasives (ISSG). In this particular case, the human alteration of habitat took the form of potato farming. The original geographic distribution of the *L.decemlineata* beetle included Mexico and some parts of western and central USA, and its original host range is thought to span only three non-cultivated species of the genus *Solanum*, *Solanum rostratum*, *S.angustifolium*, and *S.elaeagnifolium*. *L.decemlineata* started to use the potato, *Solanum tuberosum*, introduced from South America into North America and Europe for intensive cropping in the 18th century, as a host in the 1830s and 1840s within its native range (central USA). Subsequently, the beetle spread throughout both North America and Europe as a major pest. Evidence suggests that adaptation was involved in the use of potato as a host plant. After the inclusion of potato in its diet, the beetle was able to spread far beyond its original geographic range, both to contiguous areas and to other continents where potatoes are grown, notably Europe, via human-aided long-distance dispersal (Hufbauer et al., 2012 and references herein).

We have seen that if the habitat of introduction resembles that of their native habitat, the expansion of species may be facilitated by pre-adaptation in their native range. Island habitats, which are particularly sensitive to invasions, are now presented.

E. VULNERABILITY OF ISLANDS TO BIOLOGICAL INVASIONS

"A tale of invasive species" (University of Minnesota, College of Design), from Ellen Schofield and David Andow, was the winner of the Teaching/Instruction category of the 2012 Ecological Society of America.

Video transcript: A TALE OF INVASIVE SPECIES

Meet Oliver and Frank. They live in two very different places

Frank lives in a BIG city. Oliver lives far away on a small island

Oliver only eats the nectar of the rare pink orchid. Frank will eat anything

Oliver slowly raises a small family. Frank raises a HUGE family

They are both nice guys

But, if one accidentally gets picked up and moved to the other's territory

It can be a problem. Frank quickly eats all of the island's rare orchids

And his large family tramples the tiny island. This SQUEEZES Oliver out of his only habitat. When an organism gets moved from its natural habitat it becomes an invasive species. Moving from one habitat to a new one used to be a slow process.... But with modern transportation, species can be transported around the glbe faster than ever. Faster travel means more opportunity for accidental introductions of exotic species. Most die, but more introductions means a greater chance of introducing an invasive species. Protect Minnesota's native species by not transporting foreign organisms

Interview with Stéphane Baret, Reunion Island National Park, by David Josserond, a scientific journalist, during the summer school on biological invasions organized by the University of Reunion Island in June 2013.

English transcript of the video:

"We are on an island where there were no human beings during the last 3 million years. The species which arrived there naturally, evolved in their natural environment, without any human impact or influence. For example, on an island (oceanic island, note of the editor) there are no large herbivores (terrestrial herbivores, note of the editor). After the introduction of a large herbivore, there may be negative impacts on the flora. In islands such as Hawaii, we can find some brambles which : in the absence of herbivores, have not maintained their thorns. In the island of La Reunion, we have a similar example, where the insular bramble species has reduced thorns, compared to its continental equivalent. As there are no herbivores, there is no energy to waste to be protected from them. There are numerous examples of this type: exotic species are introduced in a different environment, where native plants have lost some of their functions".

QUIZ: biological invasions in an insular environment

What are the main messages delivered by the videos?

Message delivered by both the video and the interview: Insular (endemic) species are vulnerable when faced with introduced (exotic) species

Description of the interactions between introduced (exotic) and insular (endemic) species in the video: the introduced (exotic) species feeds on the rare food source of the insular (endemic) species

Description of the interactions between introduced (exotic) and insular (endemic) species in the interview: the introduced (exotic) species may feed on the insular (endemic) species, which did not maintain its defenses since its arrival on the island.

Explanations

The vulnerability of insular endemic species faced with introduced exotic species, is highlighted in both the video and the interview.

In (Myers et al., 2000), among the 25 defined biodiversity hotspots ("where exceptional concentrations of endemic species are undergoing exceptional loss of habitat. As many as 44% of all species of vascular plants and 35% of all species in four vertebrate groups are confined to 25 hotspots comprising only 1.4% of Earth's land surface"), 9 are islands.

In the meantime, the number of biodiversity hotspots has been expanded to 35 (2.3% of the Earth's land surface) by Conservation International (http://www.conservation.org/how/pages/hotspots.aspx).

According to (Kier et al., 2009), 180,000 of the world's islands host more than 20% of its biodiversity, and whose endemic species' richness (plants, vertebrates) is more than 10 fold that of the continents.

Most of the extinctions attributed to biological invasions are described as happening on islands (Vitoussek et al., 1977; Sax et al., 2008). Loss of an endemic insular species is definitive, since it exists nowhere else.

Ben Warren describes an unquantified case from his former research at the joint University of Reunion Island-CIRAD research unit UMR PVBMT, France (ANR Project BIOTAS):

"The island of Reunion is a good example of species' extinctions due to invasion of non-native species. Following the arrival of humans in 1640 it has experienced the extinction of 64% of its native land vertebrate fauna (endemic species, found nowhere else on earth) including numerous species of birds, two flying foxes, a tortoise and two skinks. These extinctions are implicated in the unprecedentedly low rates of seed dispersal recorded on Reunion, and associated low rates at which woody species from lowland rainforest remnants recolonize the landscape following forest fragmentation (Thébaud and Strasberg 1997). Other than hunting, non-native predators are likely causes of decline of many such species (Cheke & Hume 2008).

It is often assumed or hoped that such high rates of extinction are a thing of the past. However, there are reasons to believe that extinctions continue at this high rate today, but concern species that are less conspicuous and poorly known. In a project focused on surveying genetic diversity of terrestrial invertebrates in the Mascarenes (BIOTAS, 2007-2013), we relied heavily on records generated by naturalists specialized on the Mascarene invertebrate fauna. To our dismay we found that many invertebrates that could easily be located as recently as the early 1990s (some having even being recorded as common) could no longer be found by the same specialists despite surveying that was far more intensive than in the 1990s. For example, on La Reunion island, three species of terrestrial mollusks that were easily located in the early 1990s (e.g. in two cases, after half an hour of searching within 100 m of the car park at Mare Longue) could not be found in the six year period from 2007-2013, despite more than 20 days of intensive searching (involving the same people) throughout the native forest of the humid east. An important line of future research would be to investigate the causes of such declines. At this stage, circumstantial evidence makes us suspect invasions by non-native species to be among the most important factors".

The video shows that the introduced (exotic) species feeds on the rare food source of the insular (endemic) species, and is thus responsible for the extinction of the insular (endemic) species. For example, one of the causes of extinction of Haast's eagle (*Hieraaetus moorei*, weighing up to 30 pounds, only one young per year), living on New Zealand South Island, is indeed the extinction of its flightless prey, the moa (55-550 pounds, only 1 to 2 chicks per brood) and *Aptornis* (22-26 pounds, a ground-breeding bird). The *Aptornis* eggs and chicks have been an easy prey for the introduced Polynesian rat *Rattus exulans*, and altogether Haast's eagle, the moa and *Aptornis* predated the arrival of humans, from their arrival (year 1000) onwards. The estimated years of extinction for moas, *Aptornis* and Haast's eagle are 1000-1200, 1200-1780 and 1200-1780 respectively (Holdaway, 1989).

The insular environment, with its fewer species and its disharmony (no competing predation for the resources of insular predators), is thus particularly vulnerable: flightless and ground-breeding birds are easy prey for introduced mammalian predators. Moreover, the endemic insular species are also more fragile because of their low population numbers. Other causes of extinction may be direct predation (humans, rats, cats, dogs, pigs etc.), habitat degradation (mainly due to humans), or transmission of pathogenic microorganisms via introduced species (Milberg and Tyrberg, 1993; Whittaker, 1998; Le Guyader, 2008).

In his interview, Stéphane Baret cites the example of introduced (exotic) species, feeding easily on an insular (endemic) species (which has not maintained its defenses since its arrival on the island). The hypothesis that insular endemic plants evolved in the absence of large mammalian herbivores may lack defenses against herbivory, was tested by comparing plants endemic to the island of Santa Cruz (15 million years old, lacking herbivorous predators) with those on the nearby California mainland. Six pairs of shrub species, each represented in the two areas (insular and mainland) were analyzed (chemical defenses such as phenols and tannins, number and length of leaf spines, leaf size, as well as being subjected to feeding trials by foraging sheep). Chemical and morphological defenses were found to be significantly reduced in each of the island species, and sheep preferred to feed on the island species in each of the three pairs analyzed. Taken together, these results "support the hypothesis that insular endemic plants lack defenses against exotic herbivores, and also support the hypothesis that the introduction of exotic species in island ecosystems is a major cause of extinction" (Bowen and Van Vuren, 1997).

F. MAIN FACTORS INVOLVED IN THE VULNERABILITY OF INSULAR ENVIRONMENTS TO BIOLOGICAL INVASIONS

In the case of terrestrial islands surrounded by water, two groups can be considered: first oceanic islands that were devoid of life when they were formed as they are of volcanic or tectonic origin, and second continental islands that were formed by fragmentation of existing landmasses. Using the size of New Guinea (303,380 square miles) as an arbitrary limit, the surface area covered by islands represents 3% of the total surface of the Earth (Mielke, 1989, p7).

When conceiving their island biogeography theory more than 50 years ago, MacArthur and Wilson used islands as model systems to develop a conceptual framework for their field (The theory of island biogeography, 1967). Based on their assumptions, two main predictions can be made: first, near islands (located closer to a continent) have more species than remote islands; second, large islands have more species than small islands. Molecular tools and increasing data acquisition now enable the re-assessment of some fundamental issues that interested MacArthur and Wilson. These include the formation of ecological networks, species abundance distributions, and the contribution of evolution to community assembly (Warren et al., 2015).

Oceanic islands host a high proportion of the world's endemic species, contributing the most to Earth's biodiversity. Island factors that have been shown to interact to provide the conditions necessary for in situ speciation include isolation, age and size of the region concerned, as well as variables often associated with area, such as topographic complexity and elevation (Warren et al., 2015). Many such species are at risk of extinction owing to habitat degradation and loss, biological invasions and other threats.

Four main factors, two of which we have already seen, may explain an island's vulnerability to invasive species:

1) As partially seen in the video, the low number of endemic insular species, as well as remaining open niches on the most remote islands, will provide a low competitive environment for newly introduced species, who may more successfully exploit available resources, and who may not encounter an enemy similar to the one they left behind (loss of enemy hypothesis).

2) As already seen in the interview, specialization of insular species to local environments, which might increase fitness on the generational timescale at which selection acts, may nevertheless reduce tolerance to changes arising over longer time-scales, such as that of new arrivals (in Warren et al., 2015).
3) The colonial history of certain islands (in the Atlantic Ocean, in the Caribbean region, etc.), as well as their role as transit ports along commercial maritime routes, accelerated introductions of diverse exotic species (organisms in the ballast water, rats, micro-organisms and insects together with plants, etc.)
4) Population density is another detrimental factor. Among some biodiversity hotspots, e.g. Polynesia, Micronesia, New Zealand and the Caribbean Region, the population density is higher than Earth's average, while natural reserves occupy correlatively less space (Luck, 2007).

Using the completely revised Global Invasive Species Database and revisiting the IUCN Red List, Bellard and collaborators (Bellard et al., 2016) provided new maps of the vulnerability of threatened vertebrates: centers of Invasive Alien Species-threatened vertebrates are concentrated in the Americas, India, Indonesia, Australia and New Zealand, especially on islands. They found that the threat posed by invasive alien species in relation to other threats (i.e. habitat loss, pollution, overexploitation, climate change) is greater on islands than mainland areas, except in South America.

You can read more about invasive species on islands at:

http://ibis.fos.auckland.ac.nz, where you'll find the Island Biodiversity and Invasive Species Database (IBIS). IBIS records and provides information on the occurrence, biological status and impacts of invasive alien species on native species on islands, with a focus on those classified as ‘threatened’ in the IUCN Red List of Threatened Species.

You can search for data concerning invasive species in Hawaii at: https://www.invasivespeciesinfo.gov/unitedstates/hi.shtml#thr (United States Department of Agriculture, National Invasive Species Information Center).

A synthesis article (Dealing with invasive alien species in the French overseas territories: results and benefits of a 7-year Initiative, Soubeyran et al., 2015) is also of interest: invasive alien species (IAS) are one of the most serious threats to the rich and unique biodiversity of the 13 French overseas territories scattered across three oceans and two continents. With the exception of French Guiana in South America, most of these territories are islands,. They host more endemic species than the whole of continental Europe, and 11 out of these 13 territories are located in 5 of the 25 global biodiversity hotspots defined in (Myers et al. 2000), namely Polynesia–Micronesia, Madagascar and the Indian Ocean Islands, Caribbean Islands, New Caledonia and Mesoamerica.

G. EFFECTS OF INSECT INVASIONS

Invasive insects, whose effects are described hereafter for six of them (*Dacus ciliatus, Bemisia tabaci, Harmonia axyridis, Aedes albopictus, Adelges tsugae, Dendroctonus ponderosae*) will also be introduced (and invade) chapters 2 and 3 ! One insect even depreciates wine quality ...

Dacus ciliatus: this fly, which belongs to the *Tephritidae* family, (you'll meet it again in chapters 2 and 3), is a major pest of a wide range of *Cucurbitaceae* in Africa, Asia and the Middle East. Adult flight (helped by wind currents) and the transport of fruit (fruits are hosts to *D. ciliatus* larvae) are major means of dispersal. It can also have an indirect economic impact on exports. It is an EPPO A1 quarantine pest (European and Mediterranean Plant Protection Organization; A1 pests are absent from the EPPO region), and is also of quarantine significance to CPPC (Caribbean Plant Protection Commission). The adult measures 0.24-0.28 inches (7-8 mm) in length. (CABI)

Bemisia tabaci: the adult whitefly is about 0.04 inches (1mm) in length. A female lays 80 to 300 eggs during its lifetime, and 10 to 15 generations of B. tabaci can undergo are possible per year. The B. tabaci species complex contains at least 20 "cryptic" species. MED (Mediterranean) species are effective vectors of many different plant viruses which, combined with its high level of polyphagy, make it extremely problematic in agricultural regions where crops (tobacco, tomato, sweet potato, cotton, cassava, ornamental plants, etc.) may be susceptible to viruses acquired from indigenous plants. Crop yield losses can reach 100%, due to direct effects and/or viral transmission. Although *Bemisia* is generally a tropical/sub-tropical whitefly species, MED species can easily be transported to temperate regions of the world on plants. In these cooler regions, MED species can survive in a protected environment and could feasibly spread virus diseases to new locations (http://www.cabi.org/isc/datasheet/112682, and references herein).

Harmonia axyridis: the harlequin ladybird can reach 0.2-0.3 inches (5-8 mm) in length. It can survive temperatures < 32°F (0°C) and > 104°F (40°C), females lay up to 4,000 eggs during the 3 months of their reproductive activity. Of Asian origin, *H.axyridis* was used in classical, augmentative and conservation biological control programs against aphids worldwide, from 1916 to at least 2001. After the first releases in North America (1916), *H.axyridis* ladybirds were found in the wild in 1988, rapidly invaded most of North America and Europe, and are now spreading in South America and South Africa. The invasion of *H.axyridis* is a threat for the populations of native ladybirds and other aphidophagous insects, both due to intraguild predation and competition for resources. It is also regarded as a grape and wine pest, and as a human nuisance because it aggregates in buildings when seeking overwintering sites in the fall (http://www.cabi.org/isc/datasheet/26515).

Aedes albopictus: this Asian tiger mosquito is about 0.07 inches (1.7 mm) in length and is mainly transported in tires stored in the open-air containing standing water (ideal for the development of *A.albopictus* larvae). Originally from Southeast Asia, it has spread to Europe, the Americas, the Caribbean, Africa and the Middle East. More than 22 RNA viruses can be transmitted to humans by this vector, including Zika, West Nile, Japanese encephalitis, Chikungunya and Dengue viruses. Few vaccines have been successfully developed to date, and in some patients, infections have had fatal outcomes. In the same subgenus *Stegomyia*, the yellow fever mosquito *Aedes aegypti* (the most prevalent species in the tropics and subtropics) has a similar black and white pattern, spreads similar viral diseases and is thus also a threat for human health (DAISIE, GISD).

Adelges tsugae: Considered as native in China, Japan and possibly western North America, the hemlock woolly adelgid (*Adelges tsugae*) is a small, aphid-like insect that has become a serious pest of eastern and Carolina hemlock (*Tsuga canadensis* and *Tsuga caroliniana*) in the USA and Canada.

Transportation is via wind, vehicles, humans, animals and trade in plants. Signs of infestation are the presence of white, woolly egg masses on the underside of hemlock needles: the photo shows the nymph stage (0.12 inches (3 mm) in diameter). Infested *Tsuga* defoliate prematurely and will eventually die if left untreated. *A. tsugae* is difficult to control, as the white waxy secretion protects it from pesticides. It is dispersed to new habitats through the nursery trade and locally by wind, birds, mammals and humans. The 3.2 million acres (1.3 million hectares) of *Tsuga* forests in North America are threatened in the next 15 to 25 years, with severe adverse ecological impacts because hemlock trees provide important habitats for many wildlife species.
(http://www.cabi.org/isc/datasheet/3270 and references herein; ISSG; Aukema et al., 2010).

Dendroctonus ponderosae: this insect is about 0.22 inches (5.5 mm) long and has not yet appeared outside its geographic range (western USA, British Columbia and southwestern Alberta, Canada, and Baja California, Mexico). It is dispersed by direct flight (adults may travel up to 1.9 miles (3 km)), wind or the transport of untreated wood (containing larvae). The mountain pine beetle has been at outbreak levels in western North America ever since foresters and forest entomologists began monitoring damaging pests. The mountain pine beetle can attack any species of *Pinus* within its geographic range. Trees attacked by the mountain pine beetle are usually killed by a single generation of beetles.

QUIZ - Two databases (http://www.issg.org/database/welcome/, GISD (Global Invasive Species Database) and http://www.europe-aliens.org/, DAISIE (Delivering Alien Invasive Species Inventories for Europe)) provide a «top 100» list of the worst invasive species. GISD only includes one species per genus, to ensure the inclusion of a wide range of examples. Although it is very difficult to identify 100 invasive species from around the world that really are "worse" than any others, species were selected for the list according to two criteria: the seriousness of their impact on biological diversity and/or human activities, and their illustration of important issues surrounding biological invasion. In DAISIE, the «100 of the worst» invasive aliens in Europe identified cover a broad spectrum of life forms and represent some of the worst species in terms of their impact on biodiversity, economy and health. Additional and regularly updated information (datasheets on more than 9,000 invasive species) can be obtained from the Invasive Species Compendium, hosted by CABI (Centre for Agricultural Bioscience International) at http://www.cabi.org/isc/.

Which of the insects mentioned below are among the "top 100" in any of the databases? Choose the worst ones, click on the pictures below, then read the explanations !

Explanations: *Bemisia tabaci* and *Aedes albopictus* are listed by both ISSG and DAISIE as being among the «top 100» worst invasive species. *Harmonia axyridis* is among the «top 100» worst invasive species only according to DAISIE. *Adelges tsugae* is not listed among the «worst 100» invasive species. *Dacus ciliatus* is not listed in any of these databases, but *Ceratitis capitata*, another fly of the *Tephritidae* family, is ranked among the «top 100» invasive species by DAISIE. *Dendroctonus ponderosae* has not yet appeared outside its geographic range (western USA, British Columbia and southwestern Alberta, Canada, and Baja California, Mexico), and can therefore only be considered as potentially invasive (http://www.cabi.org/isc/datasheet/18354, last modified June 2015).

H. COST OF BIOLOGICAL INVASIONS; CONTRIBUTION FROM INSECTS

Assessing the cost/benefit of invasive species is one way of raising awareness of prevention and control methods among the various stakeholders in society. In order to do so, economists and ecologists were required to work together, something that proved quite difficult at the outset, since their two specialities differ so much.

One of the first people to tackle this question was David Pimentel, now Professor Emeritus (entomology, ecology and evolutionary biology) at Cornell University (US). In one of his most recent publication (Pimentel, 2005), he assesses the costs related to invasive species in the United States, compiling the known costs of crop protection, the damaged suffered, invasive species rates, and so on.

QUIZ: *90% of the total cost identified is linked to plants, arthropods (mainly insects), micro-organisms and invasive mammals. What are the annual costs? How many species are taken into consideration?*

What is the annual cost and the number of invasive species represented by mammals, plants, arthropods and micro-organisms? Drag one label per category. But make sure you read the general explanation right after!

Answers:

25000 invasive species, annual cost 34.5 billion US $: Plants

20 invasive species, annual cost 37 billion US $: Mammals

20000 invasive species, annual cost 47 billion US $: Micro-organisms

4500 invasive species, annual cost 18 billion US $: Panarthropods (mostly, arthropods; see glossary)

Explanation: Plants (an estimated 25,000 invasive species in the United States), and micro-organisms (an estimated 20,000 invasive species in the United States) are the richest set in terms of number of invasive species counted in the United States. Most plants were imported for their fibres, for ornamental purposes or for food. An estimated 5,000 imported plant species have established themselves in the natural environment. The estimated annual cost is mainly accounted for by "weeds" in aquatic environments, pastureland, lawns and crops, and by other invasive plants (e.g. purple loosestrife and *Melaleuca* genus trees). More than 90% of the total cost concerns crop losses ($24 billion) and weed control in crops and pastureland ($8 billion).

For 20 mammal species introduced into the United States – usually deliberately (except for the rat, a stowaway in the hold of ships) – the total cost (due to damage and losses) has been estimated at close to $37 billion a year. The largest share is attributed to rats (50% of the total cost) and cats (45% of the total), taking into account agricultural stocks consumed (and the related damaged) by rats, and small mammals, birds, reptiles, amphibians killed by cats. Mammals register the highest cost per species.

Let us turn our attention to invasive micro-organisms: 80% of the cost is made up of crop losses. Most of these species were introduced unintentionally via hosts or contaminated elements (plants, insects, mammals, soil, etc.). Certain animal or plant viruses are closely linked to the host insects that carry them. The cost could therefore be assigned to arthropods instead. For example, healthcare costs and the drop in productivity attributable to the West Nile virus, transmitted to humans by the *Aedes albopictus* mosquito (example referred to earlier), have resulted in an annual cost of $56 million over the last 14 years (Barrett, 2014).

The invasive arthropods recorded in the United States (4,500 species) are mainly insects, introduced unintentionally by boat (ballast water, host plants, soil, etc.) or plane. Others were introduced deliberately (as part of biological control programmes, see the example of *Harmonia axyridis*). Again, nearly 80% of the cost assignable to invasive arthropods is due to crop damage, mainly caused by plant-eating insects. Other costs include forestry product losses ($2.1 billion) and damage caused by the red ant, *Solenopsis invicta* ($1 billion).

More than half (52.5%) of the estimated total cost concerns agricultural losses/costs. For every $5 of losses/costs, approximately $1 can be assigned to arthropods. Nonetheless, the author recalls that fact that crops and livestock farming are also based on imported species (poultry, cattle, rice, corn, wheat, etc.) and cover 98% of the United States food requirements (Pimentel, 2005).

QUIZ

How does the estimated value of agricultural output coming from imported exotic species in the United States compare to the estimated annual cost of invasive species in agriculture in 2005 ($80 billion)? Is it 10 ten times more? 100 times more? 500 times more?

Explanation: the value of agricultural output from imported exotic species in the United States is estimated at $800 billion, i.e. ten times more than the estimated value of costs and losses attributable to invasive species.

Impact of insects in natural environments (forests)

Pimentel states that, in natural environments, the invasive species mentioned are directly responsible for significant biodiversity loss. However, the cost linked to the decline or loss of endemic species is more difficult to quantify.

Generally speaking, it is estimated that economic data is known for just 1–2% of invasive species (quoted in Aukema et al., 2011). The figures are no better for insects: in 1999, out of 139 impact studies concerning invasive species in the natural environment (freshwater fish and invertebrates, marine invertebrates, plants, insects and terrestrial invertebrates), only 21 concerned terrestrial invertebrates and insects, proving that research is scarce in this field (Parker, 1999). The cost of these impacts is difficult to assess in farmed environments: a forest, for example, provides various ecosystem services (recreational and cultural value, a support for biodiversity, derived products, carbon sequestration, water purification, controlling erosion, etc.).

New methods have been developed to better assess these costs, as described by (Aukema et al., 2011) for example. Using an exhaustive database including 455 invasive insect species, 62 of which have an impact (Aukema et al., 2010), the costs have been estimated according to two criteria: i) stakeholders suffering losses or incurring expenses (federal or regional government, private landowners or forest owners), and ii) the insects' feeding method (sap-sucking insects (weakening, necrosis, deformation, disease transmission, etc.), leaf feeders (leave destroyed, delayed growth or death), stem and wood borers (wood consumed or depreciated, introduction of pathogens, etc.). For each category of insect and cost, the data was compiled and the uncertainty estimated.

A QUIZ is then commented as follows:

The breakdown of total annual cost/damage, concerning specifically lost wood production from forests, totals $2.1 billion a year in Pimentel's paper (information taken from publications from 1994 and 2001) and comes to an annual total (upper range) of $175 million in Aukema's paper (the period in question was 2000 to 2009). The difference is around a factor of 10. In fact, Pimentel's estimate appears to be broader: it is based on an estimate of the total depreciation of wood production due to insects ($7 billion a year) and considers that the proportion of invasive insects (30%) would have a financial weighting also equal to 30% of the losses caused (i.e. $2.1 billion). On the other hand, Aukema used specific data on invasive species and we may therefore consider his estimate to be more accurate.

The total value of damage caused by invasive insects in forests can not be compared from the two papers: while the upper range of the cost assignable to all invasive insects in trees is estimated at $5.3 billion in the United States for the period 2000–2009, the only value indicated in Pimentel's paper is assigned to the loss of forest wood production ($2.1 billion, estimate from publications from 1994 and 2001 and based solely on the loss of wood produced).

Concerning the breakdown of losses and costs per stakeholder, the total sums (upper range) paid out/lost by private landowners and municipal funds are respectively close to 53% and 43%, which shows the weighting of these stakeholders compared to wood producers, who account for a lower proportion.

As for costs assigned to borer insects, they account for 71% of the total costs (upper range) and are a cause for concern. The proportion of borers in invasive insects has risen over the last 30 years, especially with the use of wooden packaging in trade. According to the model developed by Aukema and his partners, there is a more than 3% likelihood of a new borer species causing at least as much damage over the next ten years as the harmful species already present.

I. PERCEPTION OF THE ROLE OF SPECIES INVASIONS: THE EXAMPLE OF A GARRY OAK SAVANNAH NATURAL RESERVE

Are invasive species the drivers or passengers of change in degraded ecosystems? This question is the title of a paper by MacDougall and Turkington, published in 2005 and addressing the issue of the real impact of invasive species on native species in a context of degraded habitats. We will look at this in this chapter.

In the early 2000s, MacDougall and Turkington embarked on a study in the Cowichan Garry Oak Reserve (Garry oak – *Quercus garryana*) in British Columbia (Canada). The region's plant community is rich in native species (454 taxons) and naturalised exotic species (144 taxons), some of which are deemed invasive. Taking extracts from two specific websites concerning the reserve, let's analyse the impact attributed to invasive species on the native species:

http://www.natureconservancy.ca/en/where-we-work/british-columbia/featured-projects/cgop/

Threats

The intact Garry oak meadows (les prairies à chêne de Garry) of the Cowichan Valley are found in an area where development is active and widespread. Vancouver Island's warmest climate creates an ideal location for vineyards and pastures, and attracts ongoing residential building. Introduced invasive species frequently out-compete the more fragile native plants.

http://www.cowichanlandtrust.ca/projects/cowichan-garry-oak-preserve

A History of Degradation and Loss

During the last 150 years, agricultural and urban development have overtaken (supplanté) most Garry Oak ecosystems. Construction has damaged roots, causing tree fatalities. Fire suppression has opened Garry oak regions to invading species. Overgrazing by domestic and feral livestock has impaired Garry oak regeneration and enabled non-native plant species to take over. As a consequence, unaltered Garry oak meadow is difficult to find in British

Columbia today. Much of what remains has been strongly modified or corrupted by invasive species

Among the ideas presented for these two sites, the actions directly attributed to invasive species are: i) taking over native species, or ii) significantly altering/modifying natural spaces. For example, as the invasive plant competes with natives for limited nutritional resources, it will win, to the detriment of the native species.

Perception of species invasions: are invasive species drivers or passengers?

To go back to MacDougall and Turkington, the questions that they raise are directly related to the statements that we have just seen. Are the interactive processes forced by invasive species responsible for the decline of native plants? Or is the presence of invasive species merely the indirect consequence of habitat degradation that facilitates their implantation? To answer to these questions, experiments were conducted on a herbaceous cover comprising exotic and native species; the invasive species concerned were graminoids, *Poa pratensis* (you can search for this species on http://www.issg.org/database/welcome) and *Dactylis glomerata* (you can search for this species on http://www.cal-ipc.org). The other species present include native graminoids and herbaceous species (or forbs: morphologically and functionally different from graminoids).

The alien (or exotic) plants, *Poa* and *Dactylis*, both graminoids, were dominant (50–80% of the total cover on the plots studied at the Cowichan Garry Oak Reserve) and were subsequently removed over a three-year period by the people running the experiment, to see what then happens on these plots. The other native graminoids (marked by a white flower here) and herbaceous species (forbs) (marked by a mauve flower here) are in the minority.

QUIZ: *What was the main result attained at the end of this three-year period (several possible answers)?*

Top bubble: Has another exotic invasive species replaced the exotic graminoids that were removed?

Middle bubble: did the native graminoids "make the most" of the disappearance of the exotic species on the plots to become dominant?

Bottom bubble: Have other native species, already found on the plots, replaced the exotic graminoids that were removed?

Explanation:

The top and bottom "bubbles" both occurred: firstly (top bubble), a species of bush (*Cytisus scoparius*), deemed invasive in this region (http://www.issg.org/database/species/ecology.asp?si=441), quickly spread on the plot. This was due to contamination from seeds used in other experiments (not described here). The presence of this bush (only on the plots where the exotic graminoids were removed) suggests that grasses – exotic or native – preserve the savannah status of the site and help maintain its balance. However, the bush was removed as and when it grew over the three years, because the goal of the study only covered herbaceous (forbs) and graminoid species. In addition (bottom bubble), other native herbaceous species (forbs), already present replaced the exotic graminoids removed. Implantation in the available space was therefore facilitated for these species, which are functionally different from graminoids; on the other hand, the expected recruitment of native graminoids did not occur. Native graminoids, probably due to their low dispersive and development capacity in disturbed habitats, did not gain the upper hand despite the lack of exotic graminoids. In other words, the middle "bubble" did not occur: native graminoids did not benefit from the removal of exotic graminoids to dominate the plots. As a result, the authors rejected the assumption of the direct role of exotic species on native species development.

To sum up, we can reiterate the fact that invasive species do not always have a direct effect on native species. Causes found further upstream in the process, such as the modification of habitats i) facilitate the presence of invasive species, although the latter themselves are not always fatal to native species, and ii) are detrimental, either alone or through interaction with other factors, to native species. The invasive species is therefore a passenger and not a driver. What can we say about the passengers at the time of departure? It is now suggested that the harmonisation of degraded habitats across the world would encourage the arrival of adapted species, which would then cross the borders and spread, moving into “familiar territory”. Habitat degradation (caused by humans) therefore appears to be a decisive factor in the emergence of invasive species.

References: MacDougall A.S. & Turkington R. (2005). Didham R.K., , Tylianakis J.M., Hutchison M.A., Ewers R.M. and Gemmell N.J. (2005). Barbault R. et Atramentowicz M. (2010).

J. PERCEPTION OF INVASIONS – SCIENTIFIC AND SOCIETY ASPECTS

The attitudes of the various stakeholders (non-specialist public, users of recreational spaces, managers of natural spaces, hunters, fishers, farmers, etc.) do not only depend on the scientific information shared but also on social context, the species in question, possible conflicts of interest and the role assigned to humans in species introduction (for example, Humair et al., 2014, and the references included).

With the exception, for example, of ornamental plants not known for their invasive nature and inappropriately planted in parks and gardens, the public’s perception of invasive species is often described in somewhat derogatory terms. The negative perception of invasive species is practically a knee-jerk reaction, regardless of the species in question and the effects it might have.

In media reports as early as the 1920s, we could read things like “a gentleman thief, amusing and disconcerting, an accomplished athlete, the Arsene Lupin of cetaceans” (*La Dépêche de Brest* newspaper, 1926) in a description of a species of cetacean causing havoc in schools of sardine in France’s Finistère region (Dalla Bernardina, *Les invasions biologiques sous le regard des sciences de l’homme*, in Barbault R. and Atramentowicz M. (2010)). Anthropomorphisation of the species sometimes means that the ecological phenomena related to the invasive species are no longer reported and the public is misled.

The use of warlike terminology to describe an invasive species (attacked, armed, etc.), as seen in the pioneering work by Elton published in 1958 (i.e. after the Second World War), is equally off-putting! (Larson, 2005). Later on, we will look at the adverse effects of using this type of vocabulary when we focus on biological control and its perception in Chapter 2.

As we saw earlier in this chapter, the term ‘invasive’ is often associated with negative impacts in scientific literature; for example, invasive species are ranked according to their “moderate” to “severe” impact, while species translocations are described as "biological pollution”, and invasion as a "problem”. Out of 120 scientific papers published in the major journals between 1998 and 2003, only 33% were devoted to research into the facilitator effects (considered as positive) between exotic and native species (Fuller, 1991; Middleton, 1999; Myers & Bazely, 2003, Bruno, 2005; quoted in Goodenough’s review, 2010).

Among the negative effects below, students have to drag (with mouse or trackpad) the examples that they have already seen (one example per negative effect):

VECTORS FOR PARASITES/DISEASE, POISONING

Aedes albopictus

INTRAGUILD PREDATION

Harmonia axyridis

COMPETITION WITH NATIVE AMPHIBIANS

Bufo marinus

Explanations: These general explanations cover the three examples in the question but go further, listing the different kinds of negative effects.

PREDATION/CONSUMPTION

Santa Cruz sheep: the native vegetation on Santa Cruz island suffered severe damage after the introduction of sheep that later became established as a feral population, with density of 2–3/hectare. They were eradicated in 1980.

Harmonia axyridis, one of the “Top 100” invasive species in Europe, can reduce the biodiversity of other aphid predators through competition for resources and intraguild predation (predation of other aphid predators)(DAISIE).

COMPETITION

Harmonia axyridis, as seen above, as well as *Bufo marinus*: initially introduced to control insect pests, *B. marinus* is now one of the “Top 100” invasive species (ISSG). It competes with native amphibians for resources and habitat.

HYBRIDISATION WITH NATIVE SPECIES

We have not yet seen an example of this. When similar species hybridise and produce fertile offspring, we can observe the introgressive movement of the exotic species’ genes to a native species, to the expense of the genetic integrity of that native species, or causing a disadvantage for purely-native populations (known as inbreeding depression). In Germany, the genetic analysis of 75 hybrid plants led to the identification of seven native plants that were particularly under threat (Bleeker et al., 2007).

VECTORS OF PARASITES/DISEASES, POISONING

Bufo marinus, which can poison domesticated animals and reptiles (through its skin), and *Aedes albopictus*, one of the "Top 100" invasive species; the female is capable of transmitting more than 22 RNA viruses to humans, such as Dengue fever, the West Nile virus, Chikungunya and Japanese encephalitis. More often than not, there are no vaccinations against these diseases, which can be fatal to certain subjects (modified according to DAISIE, ISSG).

PHYSICAL MODIFICATION OF THE HABITAT

We have not yet seen an example of this. This type of modification (soil erosion, water cycle, nitrogen cycle, etc.) can benefit the exotic species, reinforcing the invasive process, but may be detrimental to the native species. For example, the spread of exotic graminoid species *Melinis minutiflora* in Hawaii between 1988 and 1998 was linked to an acceleration of the soil nitrogen cycle, with nitrogen mineralisation (making it absorbable) rates that were twice as high, to the expense of the native *Metrosideros polymorpha* tree. Yelenik and D’Antonio (2013) were the first to demonstrate the reversibility of this phenomenon, when they measured rates that had returned to normal 17 years later, while *Melinis* dominance dwindled at the same time. In an experiment to reduce competition from *Melinis*, the authors showed that two nitrogen-fixing trees, *Acacia* (native) and *Morella* (exotic), were able to benefit from this. However, it was the exotic *Morella* species that was observed in the field, probably due to its superior dispersive ability. These results are similar to those of MacDougall and Turkington in 2005, confirming the difficulty in restoring degraded habitats (Yelenik & D’Antonio, 2013).

Some positive effects described for biological invasions are all followed by an example: others can be found in scientific literature.

Parasite hosts: the transmission of parasite trematodes is mitigated by the presence of the cupped oyster *Crassostrea gigas* and the common slipper shell *Crepidula fornicata*, introduced to European coasts, reducing the parasite load of the native blue mussel *Mytilus edulis* (Thieltges et al., 2009).

Food source: Californian butterflies (most of them native) depend on exotic plants to feed their larvae and lay their eggs (35% and 40% respectively) (Shapiro, 2002).

Pollination/seed dispersion: introduced bee species *Apis mellifera* pollinates native Australian plant, *Dillwynia juniperina* (Gross, 2001). The marsupial *Trichosurus vulpecula*, introduced into New Zealand, has been active in spreading the seeds of native plants since the decline of the native frugivorous pigeon *Hemiphaga novaeseelandiae* (Duncan et al., 2002).

Modification with causes outside the ecosystem: the exotic Australian pines (*Casuarina equisetifolia*) that line the beaches of Florida provide protection from human-generated light sources at night, with a positive effect on the sea turtle (*Caretta caretta*) egg-laying process (Salmon et al., 1995)

Apart from Thieltges et al., 2009, all the references above are mentioned in Goodenough (2010). Some positive effects of introduced species on biological conservation have thus been described, and are source of discussion in scientific literature (references quoted by Humair et al., 2014).

We musn't forget that biological invasions were identified as one of the main causes of biodiversity loss (alongside the climate, land cover, nitrogen deposits and atmospheric CO_2; see, for example, Sala et. al., 2002), and most species extinctions occurred in an insular environment (Groombridge (1992) and Steadman (1997), quoted in Whittaker (1998)).

As we saw in the paper by MacDougall and Turkington, the extent of the role of invasive species among the other causes of biodiversity loss is difficult to assess independently. Over the years to come, we hope that you will take an interest in the profuse expansion of knowledge and ideas about invasive species. While some invasive species control programmes apply what we call biological control, certain organisms used in biological control have become invasive species! Move on to Chapter 2 if you want to find out more.

H. REFERENCES AND LINKS

Aukema JE, McCullough DG, Von Holle B, Liebhold AM, Britton KO, et al. (2010) Historical accumulation of nonindigenous forest pests in the continental US BioScience 60: 886-897.

Aukema JE, Leung B, Kovacs K, Chivers C, Britton KO, Englin J, Frankel SJ, Haight RG, Holmes TP, Liebhold AM, McCullough DG, Von Holle B (2011). Economic Impacts of Non-Native Forest Insects in the Continental United States, PLoS ONE, 6(9): e24587. doi:10.1371/journal.pone.0024587

Barbault R. et Atramentowicz M. (2010; coordination éditoriale) Les invasions biologiques, une question de natures et de sociétés. Quae.

Barrett, A. D. (2014). Economic burden of West Nile virus in the United States. The American journal of tropical medicine and hygiene, 90(3), 389-390.

Bellard, C., T. Blackburn, P. Genovesi, P. Cassey & J.M. Jeschke 2016. Global patterns in extinction and threats to vertebrates by biological invasions in islands. Pp. 12 in: R. Gabriel, R.B. Elias, I.R. Amorim & P.A.V. Borges (Eds). Conference program and abstracts of the 2nd International Conference on Island Evolution, Ecology and Conservation: Island Biology 2016, 18-22 July 2016, Angra do Heroísmo, Azores, Portugal. Arquipelago. Life and Marine Sciences. Supplement 9.

Bleeker W., Schmitz U., Ristow M.(2007). Interspecific hybridisation between alien and native plant species in Germany and its consequences for native biodiversity, Biological Conservation, Volume 137, Issue 2, Pages 248-253.

Boeuf G., Allain Y-M. et Bouvier M. (2012) Rapport remis à la Ministre de l'Ecologie, Janvier 2012; L'apport des sciences participatives dans la connaissance de la biodiversité.http://www.developpement-durable.gouv.fr/IMG/pdf/Rapport_Sciences_participatives_2012.pdf

Bossdorf O., Lipowsky A. and Prati D. (2008). Selection of preadapted populations allowed Senecio inaequidens to invade Central Europe. Diversity and Distributions 14, 676-685.

Bowen, L., & Vuren, D. V. (1997). Insular endemic plants lack defenses against herbivores. Conservation Biology, 11(5), 1249-1254.

Cheke, A. S., & Hume, J. P. (2008). Lost land of the Dodo: the ecological history of the Mascarene Islands. T and AD Poyser, London.

Cincotta R.P., Wisnewski J. & Engelman R.(2000). Human population in the biodiversity hotspots. Nature 404 (990-991)

Colautti R.I.Ricciardi A., Grigorovich I.A. and MacIsaac H.J. (2004). Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 721-733

Colautti, R. I., & Richardson, D. M. (2009). Subjectivity and flexibility in invasion terminology: too much of a good thing? Biological Invasions, 11(6), 1225-1229.

Comont, R. F., Purse, B. V., Phillips, W., Kunin, W. E., Hanson, M., Lewis, O. T., Harrington, R., Shortall, C. R., Rondoni, G., Roy, H. E. (2013), Escape from parasitism by the invasive alien ladybird, Harmonia axyridis. Insect Conservation and Diversity. doi: 10.1111/icad.12060

Devictor V. , et al. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. Nature Climate Change (2), 121-124.

Didham R.K., , Tylianakis J.M., Hutchison M.A., Ewers R.M. and Gemmell N.J. (2005). Are invasive species the drivers of ecological change? Trends in Ecology and Evolution, 20(9), 470-474.

Dungan, R. J., O'Cain, M. J., Lopez, M. L., & Norton, D. A. (2002). Contribution by possums to seed rain and subsequent seed germination in successional vegetation, Canterbury, New Zealand. New Zealand Journal of Ecology, 26(2), 121-128.

Elton, C.S. (1958). The ecology of invasions by animals and plants. London: Methuen

Fitter A.H. & Peat H.J. (1994). The Ecological Flora Database. Ecology 82, 415-425.

Gaston K.J. , Chown S.L. & Bradley P. (2002). Final Project Report, Darwin Initiative for the Survival of Species, 7th round. Invertebrate diversity and endemism at Gough Island and threats from introduced species.

Gaston K.J., Jones A.G., Hänel C. and Chown S.L. (2003). Rates of species introduction to a remote oceanic island. Proceedings of the Royal Society of London B 270, 1091-1098.

Goodenough, A. E. (2010). Are the ecological impacts of alien species misrepresented? A review of the “native good, alien bad” philosophy. Community Ecology, 11(1), 13-21.

Gross, C. L. (2001). The effect of introduced honeybees on native bee visitation and fruit-set in Dillwynia juniperina (Fabaceae) in a fragmented ecosystem. Biological Conservation, 102(1), 89-95.

Haila, Y. (1990). Toward an ecological definition of an island: a northwest European perspective. Journal of Biogeography, 561-568.

Helen E. Roy, E. Wajnberg, éditions Springer, 2008. From Biological Control to Invasion: the Ladybird Harmonia axyridis as a model species.

Hodgins K.A., Lai Z., Nurkowski K., Huang J. et Rieseberg L.H. (2013). The molecular basis of invasiveness: differences in gene expression of native and introduced common ragweed (Ambrosia artemisiifolia) in stressful and benign environments. Molecular Ecology 22, 2496-2510.

Holdaway, R. N. (1989). New Zealand's pre-human avifauna and its vulnerability. New Zealand journal of ecology, 12(supplement), 11-25.

Holzapfel P. et Harrell J.C. (1968). Transoceanic dispersal studies of insects. Pacific insects 10(1):115-153.

Hufbauer R.A., Facon B., Ravigné V., Turgeon J., Foucaud J., Lee C.E., Olivier Rey O. et Arnaud Estoup A. (2012). Anthropogenically induced adaptation to invade (AIAI): contemporary adaptation to human-altered habitats within the native range can promote invasions. Evolutionary Applications 5(1) 89-101.

Humair F., Edwards P.J., Siegrist M., Kueffer C. (2014). Understanding misunderstandings in invasion science: why experts don't agree on common concepts and risk assessments. NeoBiota 20: 1-30.

Kier G., Kreft H., Lee T.M., Jetz W., Ibisch P.L., Nowicki C., Mutke J. and Barthlott W. (2009). A global assessment of endemism and species richness across island and mainland regions. Proc Natl Acad Sci U S A. Jun 9; 106(23): 9322-9327.

Larson BMH (2005) The war of the roses: demilitarizing invasion biology. Front Ecol Environ 3(9):495-500

Lavergne S. et Molovsky J. (2007). Increased genetic variation and evolutionary potential drive the success of an invasive grass. PNAS 104(10), 3883-3888

Le Guyader (2008). La biodiversité : un concept flou ou une réalité scientifique ? Courrier de l'environnement de l'INRA N°55, 7-26.

Lecointre, G.; Le Guyader, H., Visset, D. (2006). La classification phylogénétique du vivant, Belin, 3eme édition.

Lockwood J.L., Hoopes M.F. & Marchetti M.P. (2007). Invasion Ecology, Blackwell Publishing, Oxford, UK.

Luck G.W. (2007). A review of the relationships between humanpopulation density and biodiversity Biol. Rev. , 82 (607-645).

Mac Arthur, R. H., et Wilson, E. O. (1967). The theory of island biogeography. Monographs in Population Biology, 8, vol. 1.

MacDougall A.S. & Turkington R. (2005). Are invasive species the drivers or passengers of change in degraded ecosystems ? Ecology 86 (1), 42-55.

Mark Van Kleunen, Ewald Weber et Markus Fischer (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13(2), 235-245.

Maurel N., Fujiyoshi M., Muratet A., Porcher E., Motard E., Gargominy O. et Machon N. (2013). Biogeographic comparisons of herbivore attack, growth and impact of Japanese knotweed between Japan and France. Journal of Ecology 2013, 101, 118-127

Mielke, H.W. (1989). Patterns of life: biogeography of a changing world. Unwin Hyman, Boston.

Milberg, P., & Tyrberg, T. (1993). Naïve birds and noble savages-a review of man-caused prehistoric extinctions of island birds. Ecography, 16(3), 229-250.

Monecke S., Monecke H. & Monecke J. (2009). Modelling the black death. A historical case study and implications for the epidemiology of bubonic plague. International Journal of Medical Microbiology 299, 582-593.

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. et Kent J. (2000). Biodiversity hotspots for conservation priorities. Nature 403, 853-858.

Parker, I. M., Simberloff, D., Lonsdale, W. M., Goodell, K., Wonham, M., Kareiva, P. M., Williamson B., Von HolleP.B., MoyleJ.E. Byers & Goldwasser, L. (1999). Impact: toward a framework for understanding the ecological effects of invaders. *Biological invasions*, *1*(1), 3-19.

Pascal M., Lorvelec O. & Vigne J.D. (2006). Invasions biologiques et extinctions. 11.000 ans d'histoire des vertébrés en France. Belin/Quae.

Petitpierre B., Kueffer C., Broennimann O., Randin C., Daehler C. et Guisan A. (2012). Climatic Niche Shifts Are Rare Among Terrestrial Plant Invaders. Science 335(6074), 1344-48.

Phillips B.L., Gregory P. Brown G.P.,Webb J.K., Shine R.(2006). Invasion and the evolution of speed in toads. Nature 439, 803.

Pimentel, D., Zuniga, R., Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological economics, 52(3), 273-288.

Prentis P.J. & Pavasovic A. (2013). Understanding the genetic basis of invasiveness. Molecular Ecology 22, 2366-2368

Rey O., Estoup A.,Vonshak M., Loiseau A., Blanchet S., Calcaterra L., Chifflet L., Rossi J.P., Kergoat G.J., Foucaud J.,Orivel J., Leponce M.,Schultz T. & Facon B. (2012).Where do adaptive shifts occur during invasion? A multidisciplinary approach to unravelling cold adaptation in a tropical ant species invading the Mediterranean area. Ecology Letters 15: 1266-1275.

Russell, J. C., & Holmes, N. D. (2015). Tropical island conservation: rat eradication for species recovery. Biological Conservation, 185, 1-7.

Ryan M. Keane and Michael J. Crawley, TRENDS in Ecology & Evolution Vol.17 No.4 April 2002

Salmon, M., Reiners, R., Lavin, C., & Wyneken, J. (1995). Behavior of loggerhead sea turtles on an urban beach. I. Correlates of nest placement. Journal of Herpetology, 560-567.

Sax D.F., Stachovicz J.J. & Gaines S.D. (2005). Species invasions: insights into ecology, evolution, and biogeography. Sinauer Associates Inc, Sunderland.

Sax, D. F., & Gaines, S. D. (2008). Species invasions and extinction: the future of native biodiversity on islands. Proceedings of the National Academy of Sciences, 105(Supplement 1), 11490-11497.

Shapiro, A. M. (2002). The Californian urban butterfly fauna is dependent on alien plants. Diversity and Distributions, 8(1), 31-40.

Shine R., Brown G.P., and Phillips B.L.(2011). An evolutionary process that assembles phenotypes through space rather than through time. PNAS 108(14), 5708-5711.

Thebaud, C., & Strasberg, D. (1997). Plant dispersal in fragmented landscapes: a field study of woody colonization in rainforest remnants of the Mascarene Archipelago. Tropical forest remnants: Ecology, management, and conservation of fragmented communities, 321-332.

Thieltges D.W., Reise K., Prinz K. et Jensen K.T. (2009). Invaders interfere with native parasite-host interactions. Biol Invasions 11:1421-1429.

Torchin, M. E., Lafferty, K. D., Dobson, A. P., McKenzie, V. J., & Kuris, A. M. (2003). Introduced species and their missing parasites. Nature, 421(6923), 628-630.

Vincent Devictor, Chris van Swaay, Tom Brereton, Lluís Brotons, Dan Chamberlain, Janne Heliölä, Sergi Herrando, Romain Julliard, Mikko Kuussaari, Åke Lindström, Ji˘rí Reif, David B. Roy, Oliver Schweiger, Josef Settele, Constantí Stefanescu, Arco Van Strien, Chris Van Turnhout, Zden˘ek Vermouzek, Michiel Wallis DeVries, Irma Wynhoff and Frédéric Jiguet (2012). Differences in the climatic debts of birds and butterflies at a continental scale. Nature Climate Change (2), 121-124.

Vitousek PM., D'Antonio CM., Loope LL., Rejmanek M. et Westbrooks R. (1997). Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21(1):1-16).

Whittaker, R. J. (1998). Island biogeography: ecology, evolution and conservation. Oxford University Press.

Williamson, M. & Fitter, A. (1996a), The varying success of invaders. Ecology, 77(6).

Williamson, M. & Fitter, A. (1996b), The characters of successfull invaders. Biological Conservation 78, 163-170

Yelenik S.G. & D'Antonio C.M. (2013). Self-reinforcing impacts of plant invasions change over time. Nature (503), 517-520

Zenni R.D. et Nunez M.A. (2013). The elephant in the room: the role of failed invasions in understanding invasion biology Oikos 122 (6), 801-815.

Atlas of living Australia: http://www.ala.org.au/

BIO&AGRI,information portal about biodiversity in the Indian Ocean (in French): http://www.agriculture-biodiversite-oi.org

CABI Centre for Agriculture and Biosciences International : www.cabi.org

California Invasive Plant Council: http://www.cal-ipc.org/

DAISIE (Delivering Alien Invasive Species Inventories for Europe): http://www.europe-aliens.org/

GISD (Global Invasive Species Database): http://www.issg.org/database/welcome/

Global Invasive Species Database: http://www.issg.org/database/welcome/

IBIS (Island Biodiversity and Invasive Species): http://ibis.fos.auckland.ac.nz/

IUCN/SSC Invasive Species Specialist Group (ISSG) http://www.issg.org