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Importance of microorganisms to macroorganisms invasions — Is the essential invisible to the eye? (The Little Prince, A. de Saint--Exupéry, 1943)

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ABSTRACT

("*Life would not long remain possible in the absence of microbes*"; Louis Pasteur).

Microorganisms comprise the majority of earth's biodiversity and are integral to biosphere processes. Biological invasions are no exception to this trend. The success of introduced macroorganisms can be deeply influenced by diverse microorganisms (bacteria, virus, fungus and protozoa) occupying the whole range of species interaction outcomes, from parasitism to obligate mutualism. These large range of interactions, often coupled with complex historical and introduction events, can result in a wide variety of ecological dynamics. In this chapter, we review different situations in which microorganisms impact biological invasions. First, we consider outcomes of microorganism loss during the introduction of alien species. Second, we discuss positive effects of microorganisms on the invasiveness of their exotic hosts. Third, we

examine the influence of microorganisms hosted by native species on the success of introduced species. Finally, in an applied perspective, we envisage how microorganisms can be used (i) to better decipher invasion processes, and (ii) as biological control agents.

1.   INTRODUCTION

Throughout history, humans have changed their environment by introducing plants and animals into newly colonized habitats. The anthropogenic range extension of organisms can be expanded beyond plants and domesticated animals used for nutrition, to include the release of ornamental plants and animals as game, and the introduction of agents for biological pest control. More generally, human activities can also contribute to unintentionally spread other exotic species (Banks et al., 2015; Blackburn & Ewen, 2016; Wilson et al., 2009). Thousands of species have been transported by humans from their native range to new habitats. Non-indigenous species that expand their range in their newly introduced habitats are considered invasive if they deeply modify the structure and population dynamics of the recipient community. For example, invasive species can lead to a decrease in recipient community species diversity, blocking of successional stages, changes in food webs and flows of matter, and thus can have a negative impact on the area of introduction (Simberloff et al., 2013). Research in invasion biology seeks to understand why some species become successful invaders while others do not, even if they are closely phylogenetically related.

Invasive populations are generally founded by relatively few individuals that are likely infected with only a subset of all possible microorganisms from the native range source population (Blackburn et al., 2015; Colautti et al., 2004). In addition, abiotic (e.g. climate) and biotic (e.g. occurrence of alternative hosts) differences between source and arrival environments can disrupt the life cycles of some microorganisms, leading to further microorganism loss in the arrival ranges (MacLeod et al., 2010). Furthermore, introduced macroorganisms also have to cope with increasing numbers of novel parasites during their range expansion. The loss of either antagonist or mutualist species of microbial symbionts can have strong ecological and evolutionary consequences for host organisms, and is at the core of prominent hypotheses to explain invasion success or failure.

To keep the discussion simple, hereafter we will use terms such as "microorganism" and "parasite" not in it their strict biological signification, but more for their ecological significance. We intend "microorganism" to include all uni- or multicellular microscopic organisms such as fungi, bacteria and protozoan, but also viruses. Similarly, "parasite" will encompass viral, bacterial, or fungal pathogens.

Microbial symbionts co-introduced with invasive species can play critical roles in the colonization of new habitats. In fact, recent evidence suggests that microorganisms can have broader ranging impacts on community interactions during biological invasions processes than that was previously acknowledged (Brown et al., 2014; Rizzo et al., 2016; van Elsas et al., 2012). Aside from viral, bacterial or fungal pathogens, more than 40% of all animals display a parasitic lifestyle (including macroparasites), providing at least a crude estimate of their emerging role in invasion biology (Dobson et al., 2008). Pathogens do not walk alone, since other passengers, such as commensals and mutualistic symbionts, are also common. Most remarkable examples are found in terrestrial arthropods: recent surveys estimated that >40% of insect species harbour maternally inherited endosymbionts, such as *Wolbachia* which is among the most abundant intracellular bacteria so far discovered, infecting thousands of insect species (Duron et al., 2008; Zug and Hammerstein, 2012). In some cases, these endosymbionts have evolved towards mutualism by performing key metabolic functions required to support normal host development: these endosymbionts have become obligate, meaning that both partners entirely depend on each other for survival and achieve their life cycle (Moran et al., 2008). Furthermore, in most cases, there are secondary (e.g. facultative) symbionts as well, which can exert a variety of effects: increasing host survival and reproductive success, conferring advantages under certain environmental conditions, facilitating resource acquisition, protecting against natural enemies, interfering with the replication and transmission of parasites or subtly manipulating host reproduction (Bonfante and Genre, 2010; Brownlie et al., 2009; Dion et al., 2011; Moran et al., 2008; Oliver et al., 2010; Simon et al., 2011). As arthropods vary in the numbers and types of harboured endosymbionts, this provides heritable and functionally important variations within host populations – which in turn will influence their invasiveness (Ferrari and Vavre, 2011; Oliver et al., 2010).

A number of hypotheses link detrimental microbial symbionts to ecological outcomes in biological invasions. First, the Enemy Release Hypothesis posits that invasive species can be more competitive in invaded habitats because they have left a significant fraction of their natural enemies in their native range (Mitchell and Power, 2003).

Second, the Novel Weapons Theory posits that invasive species carry traits that provide increased competitive ability, such as chemical weapons that provide a selective advantage over naive competitors (Callaway and Ridenour, 2004). This theory can be expanded beyond chemical factors that benefit the invader to include co-invading parasites. Indeed, parasites tolerated by the invasive carrier, but which can harm native competitors in newly colonized habitats, can be considered as biological weapons (Strauss et al., 2012; Vilcinskas, 2015). This phenomenon described as "spill-over" (Power and Mitchell 2004) is based on the expectation of a lower virulence of parasites in hosts that have coevolved with them, but a higher virulence in new phylogenetically-closed hosts because of a lack of evolved immunological resistance (Schmid-Hempel, 2011).

In the same vein, the Biotic Resistance Hypothesis claims that the success of some exotic invaders can be dampened due to novel parasites invaders encountered in newly colonized habitats. These parasites can display higher virulence on invaders than on native species because they lack a co-evolutionary history with the invader (Schmid-Hempel, 2011). However, invasive species can also function as novel reservoirs for native pathogens normally hosted by native species closely related to invaders. Indeed, they can act as vectors of infection towards native species in the area of introduction, amplifying the detrimental effect of invasion and increasing native pathogen loads. This may be explained for instance by immune traits of the invader population that allow it to overcome native parasites within the colonized areas (Lee and Klasing, 2004). This phenomenon of apparent competition mediated by native pathogens is known as "spill-back" (Kelly et al., 2009), and is related to the 'Accumulation of Native Pathogens Hypothesis' (Eppinga et al., 2006; Strauss et al., 2012). In our approach to deciphering the roles played by microorganisms in the invasive success of their hosts in newly colonized habitats, this chapter will be structured around two major points. First, we will review literature studies focused on microorganisms in order to evaluate current evidence for the hypotheses we have presented. Second, we will explore the potential to use microorganisms as practical tools to manage invasions either by (i) using co-introduced species to retrace invasion histories and routes, or (ii) using microorganisms present in the native range as biocontrol agents to manage invasive species.

2. IMPACT OF MICROORGANISM LOSSES ON BIOLOGICAL INVASIONS

2.1 The Enemy Release Hypothesis

The Enemy Release Hypothesis (ERH; Fig. 1) predicts that in newly colonized areas, invasive species will escape a portion of the pathogens that are present in their native range. As a consequence, this release from enemies will have negative effects for native species in the recipient community (Colautti et al., 2004; Keane and Crawley, 2002; Torchin et al., 2003). Numerous reviews have explored the complexity of the ERH (Colautti et al., 2004; Heger and Jeschke, 2014; Jeschke et al., 2012; Prior et al., 2015). A key condition of the ERH is that "enemy loss" occurs. This pattern is expected because introduced populations are likely to harbour only a subset of the parasites of their parental population(s) (Torchin et al., 2003), either because of sampling effect (introduced hosts were by chance not infected) or because of the absence of conditions required for parasite persistence in the introduction area (e.g., absence of a host species or a small host population size) (MacLeod et al., 2010). Parasite loss may be accentuated further if the process of introduction favours healthy individuals or particular individual stages (e.g., juveniles) that are free of parasitic infections (Perkins et al. 2008). Evaluating enemy loss has been the subject of numerous studies focusing on microorganisms, as shown below (see also Blackburn and Ewen, 2016). Another key condition of the ERH is that enemy loss has positive consequences on the performance of the introduced host (Colautti et al., 2004; Prior et al., 2015), allowing the host to reallocate resources from immunity to invasiveness-related traits, such as rapid reproduction, dispersal ability or the ability to cope with challenging environmental factors. However, we will see below that this condition of the ERH often remains untested.

2.1.1 Is there any loss of pathogenic microorganisms by invasive species?

Several empirical studies on microorganisms support the idea that successfully invading hosts frequently lose microbial enemies as they colonize new areas. Introduced plants commonly leave behind many viruses and fungal pathogens from their native ranges (Mitchell and Power, 2003; Rúa et al., 2011; van Kleunen and Fischer, 2009). In insects, the loss of *Wolbachia* — an intracellular bacterium manipulating host reproduction — is commonly observed, such as in invasive populations of ants (Reuter et al., 2005; Rey et al., 2013; Schoemaker et al., 2000; Tsutsui et al., 2003; Yang et al., 2010), and *Citrus* thrips (Nguyen et al.,

2016). In crustaceans, the absence of microsporidian parasites in British invasive populations of the amphipod *Dikerogammarus villosus* compared to continental European ones suggested enemy loss (Arundell et al., 2015). In vertebrate hosts, the prevalence and diversity of avian malaria infections were shown to be lower in introduced than in native populations of the house sparrow *Passer domesticus* (Marzal et al., 2011), the barred owl *Strix varia* (Lewicki et al., 2015), and the New Zealand bell-bird *Anthornis melanura* (Baillie et al., 2012). A comparison on seven non-native freshwater fishes introduced into England and Wales also showed evidence of enemy release from the native parasite fauna, which only a part was present in their introduced populations in England and Wales (Sheath et al., 2015)

However, the loss of microorganism enemies is not ubiquitous across successful invaders. For example, the total number of microbial taxa was found to be similar between native and invaded ranges of the common wasp *Vespa vulgaris*, though regionally distinct pathogen communities could indicate that some pathogens are missing in the area of introduction (Lester et al., 2015). Moreover, wasps are highly susceptible to honey bee pathogens, and can have rapidly acquired some of them during their spread (Lester et al., 2015). No evidence for enemy loss was found for microsporidian parasites in invasive populations of the amphipod *Crangonyx pseudogracilis* (Slothouber Galbreath et al., 2010), or for haemosporidian infections in the range expanding populations of the house sparrow *Passer domesticus* in Kenya (Coon and Martin, 2014). In the latter case, one possible explanation was that the important period of invasion relative to this pattern was outdated (Coon and Martin, 2014).

Understanding how enemy pressure varies over the time course of an invasion and how this relates to the invasion dynamics is important in the context of the ERH (Colautti et al., 2004). Microorganism loss can persist for a long time in invasive populations. For instance, populations of the alfalfa weevil *Hypera postica*, an invasive pest of various leguminous crops, were still free of their original endosymbiotic *Wolbachia* twenty years after their introduction into Japan, though they were occasionally infected (1.43% infection prevalence in Japan, compared to 100% in the European source area) by an exotic new strain from an independent origin (Iwase et al., 2015). Several lines of evidence suggest that microorganism loss can be a transitory situation (Gendron et al., 2012; Hawkes, 2007). First, new host-microorganism associations can form over time in the invaded range, leading microorganisms to be progressively recruited by introduced hosts. For example, the diversity and frequency of local endophytes were shown to increase with time since introduction of the weed *Ageratina adenophora* in China (Mei et al., 2014). Similarly, an experimental study on 12 introduced plants species in New Zealand showed negative soil feedbacks increase with time since their establishment, suggesting an accumulating effect of

below-ground native microorganism enemies over time (Diez et al., 2010). The rapid accumulation of enemies from the local fauna can therefore eventually result in similar enemy loads for invasive and native host species within the invaded range. The rapid acquisition of local trypanosome and microsporidian pathogens from native hosts can underlie high parasite loads in invasive populations of the bumblebee *Bombus hypnorum* (Jones and Brown, 2014). Furthermore, the pace of enemy accumulation for invasive species can depend on their phylogenetic novelty in a recipient community because more phylogenetically novel introduced species experience a stronger escape from local pathogens (Parker et al., 2015). In addition, microorganism loss can be transient if co-invading microorganism enemies experience a lag time for population growth in the invaded range, related for example to an Allee effect (Liebhold and Bascompte, 2003). This was the case for two specific pathogens of the invasive forest defoliator *Lymantria dispar*, the entomophthoralean fungus *Entomophaga maimaiga* and a baculovirus, which were shown to catch up with their host in its introduction area in only a few years (Hajek and Tobin, 2011), and for a microsporidian parasite of the freshwater amphipod, *Dikerogammarus villosus* (Wattier et al., 2007). It is possible that the empty niche space freed up by a transient loss of microorganism enemies for invasive populations can facilitate the emergence of novel native or invasive pathogen communities: this idea was suggested by the surprisingly diverse assemblage of undescribed foliar pathogens across the invasive range of the grass *Microstegium vimineum* one century after its introduction (Stricker et al., 2016).

2.1.2 Is there any effect of pathogenic microorganism loss on introduced hosts?

Enemy loss does not necessarily mean enemy release (Colautti et al., 2004; Prior et al., 2015). For many invasions, there is little convincing evidence that enemy loss is a determinant of invasion success in natural populations (Blackburn and Ewen, 2016). For instance, enemy release does not appear to be the main driver of the invasion success of the barred owl in North America, as only rare lineages of their *Haemoproteus* enemies were lost in invasive populations (Lewicki et al., 2015). However, there are also cases supporting a role for enemy loss in invasion success. For example, invasive house sparrows exhibit a loss of virulent avian malaria lineages (Marzal et al., 2011). Partial support for effective enemy release has also been reported by correlative studies at intra or inter-specific levels. Invasive plants are often less damaged by pathogenic microbes in their invaded range as compared to in their native range, and they often suffer lower impacts of pathogen in the invaded range s than do native species (reviewed in Mitchell et al., 2006). For example, plant species introduced to the US from Europe are infected

by 84% fewer fungi and 24% fewer virus species in the naturalized range, and the greater the release from pathogens the more invasive these species tend to be (Mitchell and Power, 2003). The latter pattern was however shown to be reversed for 140 North American plants that have spread in Europe (van Kleunen and Fisher, 2009). As stated in this more recent study, these contrasting results remain difficult to explain. A greater post-fire reduction in pathogen damage for native grassland plants, as compared to invasive ones, is consistent with the ERH, as fire eliminates litter and thus eggs and spores of native parasites, (Roy et al., 2014). Also, the diversity of avian malarian lineages was shown to be negatively related to body condition during winter in reintroduced populations of the New Zealand passerine *Anthornis melanura* (Baillie et al., 2012).

Experimental studies are more convincing concerning effective enemy release. The only experimental study found in animals suggested that the escape from the protozoan gut parasite *Ascogregarina taiwanensis* can explain the competitive advantage of the mosquito *Aedes albopictus* in its introduction range (Aliabadi and Juliano, 2002). Otherwise, experimental studies are still largely restricted to plants since plant ecologists have long recognized the insufficiency of observational evidence to unequivocally assess the ERH (Keane and Crawley, 2002). Common garden experiments on taxonomically paired plants have shown that introduced plants species were subject to less negative soil microbial feedbacks compared to native ones (Agrawal et al., 2005; van Grunsven et al., 2007). Cross-inoculations have more precisely demonstrated a more negative effect of local soil microbiota on plant growth for native plants than for invasive ones (Callaway and Ridenour, 2004; Gundale et al., 2014; Maron et al., 2014). However, some other experimental studies show contrasting results concerning the ERH. As an illustration, fungicide treatments had a greater negative impact on fungal pathogens affecting the survival of seeds of native compared to exotic herbaceous plants (Dostal, 2010). Also, pesticide treatments had no effect on the survival of the neotropical shrub *Clidemia hirta* in its native or introduced range (deWalt et al., 2004). Similar results were obtained by inoculation/sterilisation experiments on the invasive forb *Centaurea solstitialis* (Andonian et al., 2012), or by plant-soil feedbacks measurements on the leguminous tree *Robinia pseudoacacia* (Callaway et al., 2011) or the forb *Solidago gigantea* (Maron et al., 2015). Soil feedbacks were, however, found to be variable in time and/or space, suggesting a biogeographic mosaic of interaction strengths related to invasion success (Agrawal et al., 2005; Andonian et al., 2012; deWalt et al., 2004; Maron et al., 2014).

Fungal endophytes can allow invasive plants to escape enemies (Keane and Crawley, 2002) if they deter herbivores in the invaded range, or if the loss of conditionally mutualistic

endophytes functions as an enemy release allowing greater spread of the host-plant in the exotic range. Fungal endophytes of plants are diverse (Saikkonen et al., 2006), and can span the continuum from having positive to negative direct effects on their hosts depending on the interaction and the ecological context (Johnson et al., 1997). In its exotic range where it is invasive, the grass *Brachypodium sylvaticum* has lost the fungal endophyte that is ubiquitous in its native area (Vandegrift et al., 2015). Endophyte-free genotypes in the introduced range display enhanced growth and competitive ability relative to symbiotic clones, but also suffer increased herbivory pressure. These observations suggest that the net effect of this endophyte can be that of a specialist enemy, and its loss can thus facilitate invasion (Vandegrift et al., 2015).

2.1.3 Other invasion hypotheses linked with enemy release

The ERH is strongly connected with other invasion hypotheses (Jeschke, 2014). Based on an optimal defense theory, the Evolution of Increased Competitive Ability (EICA) Hypothesis states that escape from parasites should favor introduced species by means of a change in resource allocation along an implicit allocation trade-off. If introduced host populations are free from enemies, then selection should favour the reallocation of some resources (usually invested in defenses and immunity) towards life-history traits more directly related to invasion success, such as faster maturity, higher reproductive effort or dispersal ability (Blossey and Nötzold 1995). Indeed, the release of avian malaria pathogens has been invoked to explain the dampening of inflammatory responses in the invasive house sparrow (Martin et al., 2014). In animals, testing this hypothesis has however proven to be more challenging than initially thought (Cornet et al., 2016). Soil feedback experiments on the invasive plant *Solidago gigantea* have shown that introduced genotypes are still resistant to the negative effects of their original soil biota, thus suggesting the occurrence of generalist pathogens in their invasive range (Maron et al., 2015).

The Resource Availability Hypothesis states that plant invasion is facilitated by high resource availability (Davis et al., 2000). Reviewing studies on 243 European plant species naturalized in North America, Blumenthal et al. (2009) showed that species adapted to high resource availability experience stronger release of pathogenic fungi compared to species requiring less resources, suggesting that enemy release and increases in resource availability would thus act synergistically to favor exotic species (Blumenthal et al., 2009).

2.2 Changes in mutualist assemblages

Invasive species do not only lose their pathogens and parasites, but loss of mutualistic symbionts can also occur. Similar mechanisms operate for pathogens, parasites and mutualistic symbionts: invasive populations are founded by few individuals and only a subset of their microorganisms, including mutualistic symbionts, is introduced in the invasive range. The consequences of this process are, however, radically different depending on the nature of the relation between symbionts and their hosts: while enemy loss will benefit the invasive species, mutualist loss will have negative consequences on host fitness. Worthy of note is that the risk of mutualistic symbiont loss is high for secondary (e.g. facultative) mutualistic symbionts but not for primary (obligatory) mutualistic symbionts: invasive populations of pea aphids or whiteflies always carry their primary symbionts since these microorganisms are strictly required for host survival (Gueguen et al., 2010; Henry et al., 2013). By contrast, facultative mutualistic symbionts can be present at low frequency in the native range and can thus be lost during invasion process.

No clear example of loss of mutualistic symbionts is documented to our knowledge in invasive insect species. Obviously, any organism losing its beneficial symbionts would have lower chance to become invasive, and this may explain why this process is rare and thus under-documented. Interestingly, possible cases may be found with *Wolbachia*, which is commonly lost in invasive populations of various ant species as stated above (Schoemaker et al., 2000; Tsutsui et al., 2003; Reuter et al., 2005; Rey et al., 2013; Yang et al., 2010). This symbiont is commonly viewed as a reproductive parasite of terrestrial arthropods, such as ants, e.g. manipulating the reproduction of their host species towards the production or survival of infected female hosts. However, it is now clear that *Wolbachia* is not simply a reproductive parasite since it has recently emerged as a conditional mutualist conferring advantages under certain environmental conditions in many insect species. For instance, *Wolbachia* increases fecundity of fruit flies reared on iron-restricted or -overloaded diets, and can thus confer a direct fitness benefit during periods of nutritional stress (Brownlie et al., 2009; Fellous and Salvaudon, 2009). *Wolbachia* can also protect their hosts against attack by natural enemies. *Wolbachia* infection interferes with the replication and transmission of a wide range of pathogens and parasites (including RNA viruses, bacteria, protozoa and nematodes), and protects its host from parasite-induced mortality (Hedges et al., 2008; Moreira et al., 2009; Zélé et al., 2012). These properties suggest that multiple potencies (e.g. reproductive manipulations and conditional mutualism) may be a global feature of *Wolbachia*. In this context, loss of *Wolbachia* in invasive ant populations can be beneficial on the one hand because of the loss of reproductive manipulation (see paragraph 2.1), but negative on the other hand because of the loss of beneficial *Wolbachia* effects as defensive

effects. In addition, if the loss of *Wolbachia* is incomplete, this can create infection polymorphism that may hamper invasion: mating between infected males and uninfected females can be infertile due to cytoplasmic incompatibility and then limit population growth (Engelstadter and Hurst, 2009). Overall, this underlines how the effect of *Wolbachia* infection on an insect host is more complex than previously considered with multiple (and contrasted) impacts on host fitness.

3. EFFECTS OF MICROORGANISMS HOSTED BY THE ALIEN SPECIES

A typical feature of invasive species is their rapid growth and spread of their populations after establishing a bridgehead in new habitats. There, they encounter local species competing for the same resources and which are well-adapted to the local environment. Parasitic micro-organisms have been postulated to play a key role in determining the outcome of biological invasions (Hatcher et al., 2006). Thus, in this context, pathogens (especially generalist) can be viewed as biological weapons hosted by invasive species that can potentially infect and kill native competitors. There are many examples of invasive species benefiting from their ability to carry pathogens or parasites, therefore conferring a selective advantage during the invasion process (Figs. 1 and 2). Indeed, disease can then 'spill-over' from the non-indigenous host species to infect susceptible native competitors, increasing the probability of a successful invasion.

The plant literature also demonstrates that soil microbiota can have dramatic positive effects on invasive species as they expand their range. For example, in the invaded range, invasive plants often experience more positive plant-soil microbe feedbacks than do native plants (where a feedback quantifies the extent to which soil conditioned by the growth of the previous generation affects the fitness of the current one).

3.1 Spill-over

De Castro and Bolker (2005) have collected a number of examples showing that co-introduced parasites can result in extinction of native species (Figs. 1 and 2). Increasing evidence is available that co-introduced parasites can become invasive too, and their spread often indirectly drives the decline of native host species. There are widely known spill-over examples described in literature. As a first illustration, we can cite the parapox virus which has

been co-introduced with the grey squirrel (*Sciurus carolinensis*) into the United Kingdom, and which has helped this invasive species to outcompete the native red squirrels (*S. vulgaris*). Both squirrels compete for the same resources and the virus helps the invading grey squirrels by causing high mortality in the native species while the invasive one acts as a pathogen reservoir (Darby et al., 2014). Another intriguing example is the decline of the noble crayfish (*Astacus astacus*) in Europe, which was caused by the fungal parasite *Aphanomyces astaci* that has been co-introduced with the signal crayfish *Pacifastacus leniusculus* from North America (Capinha et al., 2013; Söderhäll and Cerenius, 1999). In this context, we can also highlight the role of microsporidia closely related to *Nosemia thompsoni* which have recently been discovered in the invasive ladybird *Harmonia axyridis* (Vilcinskas et al., 2013a). These parasites do not harm the invasive carrier but do harm native ladybird species, which can become infected by microsporidia upon feeding on *H. axyridis* eggs or larvae. This predatory behavior facilitates microsporidia to cross the species barrier among ladybirds (Vilcinskas et al., 2015). Co-introduced parasites must not necessarily kill native competitors to benefit the invader. It is sufficient if they harm the fitness of the native competitors to tip the balance in favor of the invasive carrier in the long run. The spill-over of co-introduced parasites from invasive to native species represents an intriguing explanation for the success of many invaders, but is often not the only factor and has to be evaluated in the context of other mechanisms (Vilcinskas, 2015). The role of native parasites which are harmful for native competitors but are more or less tolerated by the invasive species has been neglected in the past because of their limited effects on their original host (Strauss et al., 2012).

3.2 Vertically inherited symbionts

Aside from pathogens, alien species can also carry mutualistic symbiotic organisms which can influence the invasive properties of their hosts. In insects, such symbiotic organisms are common and often maternally inherited, through egg cytoplasm (Moran et al., 2008; Wernegreen, 2012). They typically use specific adaptive strategies to spread and persist within insect populations (Ferrari and Vavre, 2011; Moran et al., 2008; Oliver et al., 2010). Invasive insects feeding on plants commonly benefit from associations with facultative symbionts: for instance, aphids are subject to a range of ecological stressors, including specific natural enemies such as entomopathogenic fungi and parasitoid wasps, heat, and changes in plant hosts. Facultative symbionts can compensate for limited adaptive capacities of their hosts to counteract these stressors (Moran et al., 2008; Oliver et al., 2010; Oliver et al., 2014). Infection frequencies by facultative symbionts are typically dynamic, varying across temporal and spatial

gradients and ecological associations. Hence, the pea aphid *Acyrtosiphon pisum* harbors a facultative symbiont, *Serratia symbiotica*, that confers heat tolerance: aphid clones infected by this bacterium substantiality improved survival during heat stress (Chen et al., 2000; Montllor et al., 2002). As a result, *S. symbiotica* population structure is most influenced by climate: infection frequency significantly increases during warmer seasons in natural populations (Russel and Moran, 2006), and reaches also higher values in arid region as Californian Central Valley than in temperate regions (Chen and Purcell, 1997; Henry et al., 2013). Therefore, the facultative association with a symbiont can facilitate the persistence of aphid populations in previously unsuitable habitats and enhance their invasive properties.

Interestingly, facultative symbionts can also mediate colonization of new plant species by invasive insect species (Moran et al., 2008; Oliver et al., 2010; Oliver et al., 2014). For example, pea aphids comprise several genetically distinct races that are specialized for feeding on a particular plant species and that host a distinct community of facultative symbionts which can directly assist them in exploiting a particular food plant (Henry et al., 2013; Tsuchida et al., 2004). The distribution of some of these facultative symbionts, such as *Regiella insecticola,* is structured by the host plant of the aphids they infect, a pattern suggesting a fitness benefit to the aphid on a particular host-plant (Henry et al., 2013). For instance, the successful transfer of *R. insecticola* from pea aphid to another aphid species that does not normally carry this symbiont enabled it to survive and reproduce on otherwise unsuitable clover (Tsuchida et al., 2004). This is a strong support for a direct effect of symbionts on host-plant utilization, and thus a role for symbionts in determining their aphid's ecological niche.

In recent years, a great deal of attention has been devoted to defensive symbionts that protect insects against attack by natural enemies (Jaenike et al., 2010; Oliver et al., 2008; Oliver et al., 2010; Oliver et al., 2014). The presence of these symbionts is particularly relevant for alien insect species because their range expansions may result in novel antagonistic interactions with enemies absent in their native ranges. Indeed, infection of the pea aphid by the facultative symbiont *Hamiltonella defensa* provides resistance to parasitoid wasps by killing the developing wasp larvae or embryos in the aphid hemocoel (Oliver et al., 2003; Oliver et al., 2005). Through reducing the mortality risk after wasp oviposition, the pea aphid thus relies heavily on *H. defensa* for its protection. Studies of caged populations have shown that *H. defensa* can rapidly invade in the presence of the parasitoid, but is not favored and decline in populations without this stress, a pattern suggesting that there are costs and benefits associated with this symbiont (Oliver et al., 2008; Polin et al., 2014). As a hypothesis, defensive symbionts can significantly enhance the capacity of alien insect species to colonize new habitats filled by native enemies. Although this

pattern has not been demonstrated, it is worthy to note that many invasive insect species carry defensive symbionts as *H. defensa* (Moran et al., 2005; Russell et al., 2003; Zchori-Fein and Brown, 2002), suggesting an adaptive role for these symbionts in invasion processes.

Perhaps the most remarkable recent observation is the speed at which symbiont-associated adaptation can occur as shown in populations of an invasive whitefly, *Bemisia tabaci*, in the southwestern United States. Fast evolution of these populations was observed after the spread of a new facultative symbiont, *Rickettsia* sp. nr. *bellii*, that spread from less than 1% of individuals infected to 97% in only 6 years and dramatically increased whitefly performance (Himler et al., 2011). *Rickettsia*-infected whiteflies produce offspring at nearly twice the rate of individuals lacking the infection, and a higher proportion of the offspring survived to adulthood. The *Rickettsia* infection also causes a strong female bias, favouring its diffusion through an increased production of the transmitting sex, that this will also enhance the intrinsic rate of increase of its host species (Himler et al., 2011). More recently, *Rickettsia* was further shown to decrease rate of death of its whitefly hosts due to *Pseudomonas syringae*, a common environmental bacterium of which some strains of which are pathogenic to insects (Hendry et al., 2014). The simultaneous expression of these distinct effects (e.g. enhancing fecundity and survival, reproductive manipulations and defensive symbiosis) by *Rickettsia* demonstrates the profound and potentially rapid effects of heritable symbionts. They should be increasingly recognized as major players in the ecology of animals, and will certainly be a key feature of agricultural entomology in years to come. An interesting ecological context to make these considerations in relation with biological invasions is when herbivorous insects introduced to control weed populations may fail to establish owing to attack from natural enemies (Julien and Griffiths, 1998), and could benefit from the presence of defensive symbionts. Facultative symbionts that influence host-plant range or thermal tolerance can also influence the pest status of an herbivorous insect, either aid or hamper biological control efforts.

Microbes hosted by alien plants can affect their invasiveness by acting as biological weapons, either allowing their host to escape enemies, or increasing the competitive abilities of their host (Johnson et al., 2013; Mitchell et al., 2006; Pringle et al., 2009; Reinhart and Callaway, 2006; Traveset and Richardson, 2014). In vertically inherited mutualisms in plant species, symbionts are transmitted through the seed from mother to progeny, with infrequent losses or gains of symbiosis over evolutionary time, and thus these symbionts typically co-invade with their invasive host plants by "hitch-hiking". In plants, vertically transmitted symbionts are also common and play important roles in plant evolution and ecology (Friesen et al., 2011). Vertically transmitted endophytes occur in a quarter of all grass species as well as a diversity of other

plant forms, in which they are systemic and can confer diverse benefits (Lymbery et al.; 2014; Mitchell et al., 2006; Rudgers et al., 2004; Strauss et al., 2012) such as enhancing resistance to herbivory due to mycotoxin and alkaloid production which can enhance host resistance to herbivory (Rudgers et al., 2004; Saikkonen et al., 2006). For example, the agriculturally important, but also invasive grasses, tall fescue (*Lolium arundicaceum*), and perennial ryegrass (*Lolium perenne*), experience reduced herbivory when infected with *Neotyphodium* endophytes, as compared to clones from which the endophyte has been excluded (Saikkonen et al., 2006). Fungal endophytes are diverse and can span the continuum from having positive to negative direct effects on their hosts depending of the context (Johnson et al., 1997). In the exotic range of the invasive grass, *Brachypodium sylvaticum*, the grass has lost its fungal endophyte that is ubiquitous in the native range (Vandegrift et al., 2015). Endophyte-free genotypes in the exotic range display increased growth and competitive ability relative to symbiotic clones, despite also showing increased herbivory pressure, suggesting that the net effect of this endophyte can be that of a specialist enemy and that the loss of this symbiotic enemy may facilitate invasion (Vandegrift et al., 2015). Fungal endophyte impacts are not exclusively mediated through herbivory. For example, environmentally acquired *Alternaria* endophytes can directly increase the competitive ability of *Centaurea stoebe*, a forb that is a problematic invader in grasslands, and this increased competitive ability is not mediated indirectly via reduced herbivore impacts on the host (Aschehoug et al., 2012).

3.3 Horizontally inherited symbionts

Environmentally acquired symbionts are taken up from the environment rather than passed from mother to offspring. These symbionts can either co-invade alongside their hosts, or hosts can switch to associate with different symbionts in the invaded range. As plants and mutualistic microorganisms co-invade across heterogeneous landscapes, the costs and benefits of mutualism can shift and co-invading partners can evolve specialized ecotypes that maximized mutualism benefits in a particular habitat type (Porter et al., 2011). Therefore, the co-invasive spread of critical microbial mutualists can drive invasion dynamics of invasive plants with specialized symbiotic requirements. Understanding how the interaction between invaders and their symbiotic microbes evolves during biological invasions is an exciting frontier—during invasion, environmental context can shift rapidly and symbionts could experience major changes in selection that intensify or reduce cooperation or antagonism (Nunez et al., 2009; Porter and Simms 2014; Porter et al., 2011; Pringle et al., 2009; Schwartz et al., 2006) and rapid

evolutionary responses in symbionts could play an important role in the invasion dynamics of their hosts.

Symbiotic microorganisms on alien species can function as novel biological weapons that facilitate invasion if they provide a selective advantage for invasive species over native ones (Lymbery et al., 2014; Strauss et al., 2012); this process being characterised as "spill-back" (see paragraph 4.1). When pathogens that are boosted by invasive plants have stronger negative effects on native than on invasive plants, pathogens shared by invaders and natives can promote invasion (Vilcinskas, 2015). For example, the destructive tropical weed *Chromolaena odorata* accumulates *Fusarium* fungal pathogens that suppresses native plant competitors (Mangla and Callaway, 2008), *Vincetoxicum rossicum* hosts soil fungal pathogens that can suppress the growth of native plants (Day et al., 2016), and cheatgrass (*Bromus tectorum)* accumulates the fungal seed pathogen *Pyrenophora semeniperda,* that then infects the seeds of native plants (Beckstead et al., 2010). More subtly, the spillover of even mutualistic symbionts from invasive plants to native ones can also lead to native plant decline if the symbionts are less beneficial to native plants. For example, there are exotic nitrogen-fixing *Bradyrhizobium* bacterial symbionts that are co-invading with the invasive plant *Acacia longifolia*. These exotic symbionts have become dominant within symbiont populations on co-occurring native species (Rodriguez-Echeverria, 2010), likely due to their amplification in exotic invasive hosts. However, these exotic rhizobia confer less benefit to native plants than do native rhizobia, and thus this symbiont community shift could contribute to native species decline (Rodriguez-Echeverria et al., 2012). Environmentally acquired *Alternaria* fungal endophytes can directly increase the competitive ability of the forb *Centaurea stoebe* that is a problematic invader in grasslands (Aschehoug et al., 2012).

A lack of appropriate microbial mutualists can be a major constraint to establishment if alien plant species with specialized microbial mutualist requirements are introduced to a novel area devoid of these symbionts (Parker, 2001; Pringle et al., 2009; Schwartz et al., 2006). For example, repeated introductions of exotic pine trees to novel continents can be unsuccessful until compatible exotic mycorrhizae were co-introduced (Nunez et al., 2009; Pringle et al., 2009; Schwartz et al., 2006). Similarly, the successful introduction of exotic leguminous forbs to novel areas for pasture development have depended upon co-introduction of compatible exotic rhizobium bacteria (Sullivan et al., 1995), and suboptimal densities of microbial mutualists in the invaded range can slow invasive spread until sufficient densities have been accumulated in the soil (Nunez et al., 2009; Parker et al., 2006). It is important to notice that the dynamics concerned with environmentally acquired symbionts on which we focus here is slightly different

to the one for vertically inherited symbionts. For these firsts, we emphasize that the constraint to establishment is that the new area is "devoid of symbionts", whereas in the case of loss of vertically transmitted symbionts, this would be due to failure to transmit the symbiont to the new portion of the range.

3.4 The role of immunity

Immune systems of native and invasive hosts determine their susceptibility for co-introduced microorganisms. Lee and Klasing (2004) postulated that invasive species should have a superior immune system in comparison with non-invasive — even closely — related species, because in the area of introduction invaders encounter parasites with which they have not co-evolved. On the other hand, investing into a more efficient immune system can trade off against other invasiveness-related traits such as fecundity or the ability to cope with enemies or competitors. The eco-immunology of invasive species has therefore emerged as a novel field in invasion biology (White and Perkins, 2012). The successful defense against spill-over of parasites from native species is solely mediated by a powerful immune system. This hypothesis has been supported by findings from the invasive ladybird *H. axyridis*, which is protected by a bi-layered defense system encompassing chemical defenses based on an anti-microbial alkaloid (called harmonine) and inducible anti-microbial peptides (Schmidtberg et al., 2013). Harmonine has shown to display antibacterial and anti-parasitic activities, and has been postulated as a constitutive defense compound providing protection in newly colonized habitats (Röhrich et al., 2012). Strikingly, a next generation sequencing-based analysis of the immunity-related transcriptome of *H. axyridis* resulted in the discovery of more than 50 putative genes encoding antimicrobial peptides. No other animal is known thus far to possess such a high number of antimicrobial peptides (Vilcinskas et al., 2013b), and the antimicrobial peptide repertoire of native ladybird species is significantly lower. Contrarily to the Enemy Release Hypothesis, these findings support the idea that invasive species have a superior immune system when compared with closely-related non-invasive species, at least until shortly after their arrival in their area of introduction. Interestingly, injection of bacteria into *H. axyridis* solely reflects a trade-off between fitness-related costs associated with the simultaneous decline of harmonine along with the induction of antimicrobial peptides synthesis (Schmidtberg et al., 2013): the fitness penalty for the constitutive synthesis of harmonine is inferior than that of the induced synthesis of a broad spectrum of antimicrobial peptides.

The postulated role of immunity in invasion biology can be expanded beyond the protection against pathogens encountered in newly colonized habitats, to include a role in keeping co-

introduced microbes under control which function like bioweapons. In the case of *H. axyridis* it has been postulated that harmonine is involved in keeping the growth of its associated microsporidia under control (Vilcinskas et al., 2015).

4. EFFECTS OF MICROORGANISMS HOSTED BY NATIVE SPECIES

4.1 Spill-back

In the context of introduced species, alien host species phylogenetically close to native ones increase the diversity of potential hosts that local parasites can infect in the community. Exotic and native species sharing the same cortege of parasites in the area of introduction can act as reciprocal reservoirs, cross-exchanging their parasites and directly infecting each other (Hudson and Greenman, 1998) (Fig. 1). Among hypotheses based on parasite transmission between native and introduced species, the Spill-Back Hypothesis states that if exotic hosts are appropriate and competent for native parasites, they may consequently act as new hosts for these native pathogens, and thus be considered as reservoirs from which native hosts can also be infected (Daszak et al., 2000; Dunn and Hatcher, 2015; Kelly et al., 2009; Prenter et al., 2004). This can profoundly alter the epidemiology of native parasites, and directly involve them in processes of apparent competition between local and introduced host species with respectively differential vulnerabilities, by affecting their dynamics, densities and life-history traits (Dunn et al., 2012). As a feedback, the introduction of a competent host can increase the abundance of the infectious stages of a local parasite in the invaded habitat (Figs. 1 and 2), including intensification of parasitism in local native populations (Kelly et al., 2009).

Parasites from the area of introduction represent a major part of the parasite cortege of invasive species (Kelly et al., 2009; Mastitsky et al., 2010). The 'Naive Host Syndrome theory' states that local parasites will have higher pathogenic effects on exotic hosts with which they did not co-evolve (Mastitsky et al., 2010). Moreover, under the Enemy Release Hypothesis, the immune capacity of invasive species should evolve towards attenuated responses (at least for costly pathways), and should in turn increase chances for parasite acquisition to occur. In the same vein, it seems also likely that a newly introduced host species can allow or facilitate the

proliferation of parasites previously co-introduced with another invasive species (Kelehear et al., 2013); such a process may illustrate the Invasional Meltdown Hypothesis (Ricciardi et al., 2013; Simberloff and Von Holle, 1999).

Until recently, parasite spill-back has rarely been considered in the literature (Kelly et al., 2009; Roy et al., 2012), and one reason to explain this lack of empirical data is a bias in considering a realistic context of hosts and parasites communities. For example, most studies related to spill-back in rodents (Lopez-Darias et al., 2008; Smith and Carpenter, 2006; Torchin et al., 2003) or birds (MacLeod et al., 2010) involve two host species (one native and one invasive), and one parasite group or even one parasite species. Host communities and associated parasites are rarely — if ever — considered in a more complex perspective, including both native and invasive species (Johnson et al., 2008). However, some convincing examples of spill-back processes involving microorganisms have been highlighted in the last years. For examples, in plants, Californian serotypes of barley and cereal yellow dwarf viruses appear to have been essential to the widespread invasion of Mediterranean grass species (Malmstrom et al., 2005). Flory and Clay (2013) reviewed some other potential examples of spill-back involving soil or seed pathogenic fungi in native host plants. In animals, community studies at biogeographical and local scales have convincingly shown that the invasion of brine shrimps (*Artemia franciscana*) in France was facilitated by native *Microsporidia* (Rode et al., 2013). Also, the spill-back of the native parasite *Myxosporea* is strongly suspected to explain a main part of the invasion success of the cane toad *Rhinella marina* (formerly known as *Bufo marinus*) to the detriment of native frogs in Australia (Hartigan et al., 2011). In birds, house sparrows (*Passer domesticus*) have been shown to increase the prevalence of Buggy Creek virus in native cliff swallows (*Petrochelidon pyrrhonota*), by increasing numbers and densities of hosts and vectors in mixed colonies as a result of their sedentary behavior (O'Brien et al., 2011).

However, acquisition of native parasites by alien species may have outcomes different than a spill-back process, and may contrarily result in a final benefit to native species. For example, invading hosts can be insufficiently competent to ensure the transmission of newly acquired native parasites, therefore representing a dead-end for them. Consequently, their transmission and abundance can thus decrease by a 'dilution effect' in the area of introduction, finally benefiting native hosts (Johnson et al., 2013). Another scenario is to consider that alien host species are too sensitive to these newly acquired native parasites, resulting in a considerable competitive advantage for native host species. As an illustration, the coexistence of native and invasive amphipods in benthic communities of St Lawrence River is facilitated by a parasitic

oomycete (the invasive character of which is still unknown), which is highly more virulent in the invasive host (Kestrup et al., 2012).

4.2 Invasive species interactions with beneficial native symbionts

In plants, invaders routinely associate with soil mutualists that are naturally hosted by native species, and they can play diverse roles in invasion dynamics (Johnson et al., 2013; Mitchell et al., 2006; Pringle et al., 2009; Reinhart and Callaway, 2006; Richardson et al., 2007; Traveset and Richardson, 2014). The microbial mutualists of native plants can be inhibited by invasive plants, according to the 'Degraded Mutualism Hypothesis' (Fedriani et al., 2012; Shah et al., 2009). This theory states that the disruption of the mutualistic relationship between microbes and native plants is caused by an invasive species, and can promote invasive spread (Brouwer et al., 2015; Johnson et al., 2013; Richardson et al., 2007; Traveset and Richardson, 2014). This can occur if native plants are more dependent on microbial mutualists than invasive ones (Shah et al., 2009). For example, invasion by species with low mycorrhizal dependence can reduce overall mycorrhizal density in the soil, resulting in decreased performance of native plants and facilitating further invasion (Meinhardt and Gehring, 2012; Vogelsang and Bever, 2009). This dynamics could be accentuated over the course of an invasion because, during range expansion, invasive plants species can be under selection to further reduce their dependence on microbial mutualists (Seifert et al., 2009). Native mutualisms can also be degraded if invasive species directly inhibit the microbial mutualists of natives (Cipollini et al., 2012). For example, allelopathic exudates from invasive garlic mustard, *Allaria petiolata*, disrupt the mutualism between native plants and both native mycorrhizae (Wolfe et al., 2008) and native rhizobium bacteria (Portales-Reyes et al., 2015), which can inhibit the growth of native plants (Callaway et al., 2008; Hale et al., 2016).

Alternatively, native plants can host mutualistic symbionts that benefit generalist invader species, according to the 'Enhanced Novel Mutualism Hypothesis' (Reinhart and Callaway, 2006; Richardson et al., 2007). This theory states that microbial mutualists present in native plants are also beneficial to invasive plants species. For example, some invaders like the spotted knapweed, *Centaurea maculosa*, are symbiotic generalists that can associate with arbuscular mycorrhizal fungi hosted by native plants and thus gain access to nutrient pools that contribute to invasive spread (Callaway and Ridenour, 2004; Harner et al., 2010). Similarly, invasive legumes that are symbiotic generalists, such as *Cytisus scoparius*, can benefit from the nitrogen fixation provided by novel *Rhizobium* symbiont partners that normally associate with native legumes (Horn et al., 2014). An interesting area for future research is the extent to which horizontal transfer of genes

or genomic regions from native microbes facilitates the invasion of exotic microbial symbionts and their associated host species. Such genomic chimerism (e.g. the transfer of exotic chromosomal symbiotic genes from exotic rhizobia to native soil microbes) was critical to the naturalization of *Lotus corniculatus* in New Zealand (Sullivan et al., 2002; Sullivan et al., 1995), and appears to play a role in the invasion of other legumes such as *Cytisus scoparius* (Horn et al., 2014), *Robinia pseudoacacia* (Wei et al., 2009), and *Biserrula pelecinus* (Nandasena et al., 2006).

Furthermore, the intergenerational feedbacks occurring when a plant species cultivates a microbial community that positively or negatively affects the growth of that species (Klironomos, 2002; Bever et al., 2012) can play an important role in invasion dynamics. Native plants often experience negative plant-soil microbe feedbacks, in that they accumulate soil microbial symbiont communities that have net negative impacts on the growth of the next generation of this species (Klironomos, 2002). However, plants successful at colonizing novel areas, such as *Centaurea maculosa* (Reinhart and Callaway, 2006)*,* can instead experience positive plant-soil microbe feedbacks in the invaded range, which can contribute to invasion (Callaway et al., 2004; Zhang et al., 2010). Over time, positive plant-soil microbe feedbacks for invaders can accelerate the decline of the native community and lead to invasional meltdown (Rodriguez-Echeverria, 2010; Simberloff and Von Holle, 1999), although meta-analysis suggests the role of feedbacks in plant invasions is complex and context-dependent (Suding et al., 2013).

The impact of native symbionts on invasion can be quite different in insects, in which research has revealed a role for horizontal transmission of beneficial symbionts that are usually maternally inherited. Here, maternally inherited symbionts originally hosted by native insect species can be acquired through horizontal transfer by alien insect species, and then favour their invasion. Whilst maternal inheritance ensures the maintenance of these symbionts within host species, occasional horizontal transmission between insect species also occurs: phylogenetic evidence indicates how the wide distribution of some facultative symbionts is largely due to their ability to shift insect species (Baldo et al., 2008; Cordaux et al., 2001; Jousselin et al., 2013; Vavre et al., 1999). For invasive species, their expanding ranges create new opportunities for horizontal acquisition of new symbionts from native species. In this context, HT can serve as an immediate and powerful mechanism of rapid adaptation resulting in the instantaneous acquisition by an invasive species of ecologically important traits, such as heat tolerance or parasite defense. This process can greatly facilitate the adaption of an alien species to a new habitat (Henry et al., 2013; Moran et al., 2008; Oliver et al., 2010), as in whitefly with *Rickettsia* (Himler et al., 2011).

5.   ANTHROPIC USE OF MICROORGANISMS

5.1 As tools to retrace invasion histories

A prerequisite for the understanding of biological invasions lies in a clear picture of the geographic pathways followed by propagules from their source to the introduced area. Indeed, a precise knowledge of the invasion routes is fundamental for (i) planning relevant strategies to prevent or control an invasion and (ii) testing meaningful hypotheses concerning the ecological and evolutionary factors driving invasive success (Estoup and Guillemaud, 2010). Initially, the reconstruction of invasion pathways hinged on historical introduction records of species invasions. However, this kind of survey data can be incomplete or even misleading (Fischer et al., 2015). More recently, population genetics studies using mitochondrial and microsatellite markers have allowed obtaining a much more in-depth understanding of the history of the invasion process including the origin and genetic composition of the invading populations, but also inferences about some demographic and genetic parameters (Estoup and Guillemaud, 2010). This genetic approach has pointed out some invasion stories with complex and counterintuitive introduction events (see for instance Gaudeul et al., 2011; Lombaert et al., 2014; Leduc et al., 2015). However, the reconstruction of invasion pathways may be unresolved for invasive organisms displaying pauperized genetic diversity and low population structure, mainly due to severe bottlenecks during introduction events or peculiar modes of reproduction such as parthenogenesis (Amsellem et al., 2000; Zhang et al., 2014). In this context, it has been suggested that microorganisms may serve as an alternative tool to better reconstruct invasion histories of genetically uniform hosts (Nieberding and Olivieri, 2007; Wirth et al., 2005). Indeed, when both actors (hosts and their associated microorganisms) are closely associated, microorganisms may offer a higher resolution picture of the invasion history of their host.

A first option is to focus on the comparison of microorganism communities in host populations from native and non-native areas. If these communities are composed of strict host-specific lineages, the presumption is that their composition may reflect the origin area of the invasive host. This approach is illustrated by the studies of associated bacterial communities to unravel the geographical sources of invasive marine green alga (Aires et al., 2013; Meusnier et al., 2001). For instance, using cloned bacterial 16S rDNA gene sequences from the associated

microflora of *Caulerpa taxifolia* collected from different areas, Meusnier et al. (2001) detected an analogous composition of the bacterial flora shared between the Australian and Mediterranean sites. They were thus able to conclude that the Australian sample was the original biogeographical source population of the accidental introduction into the Mediterranean Sea. By characterizing the bacterial communities associated to native and non-native populations of *C. racemosa* through pyrosequencing, Aires et al. (2013) also showed that bacterial community may be an effective tracer of the origin of invasion. An alternative method is to focus on a single microorganism species and use fast-evolving regions of DNA in the microorganisms as a magnifying lens to decipher introduction pathways of the invasive host (Wilfert and Jiggins, 2014). Indeed, studying the genetic structure of microorganisms may allow to detect recent demographic processes in host populations, when microorganisms have lower effective population size (N_e) and stronger population structure than their hosts (Criscione and Blouin, 2005; Holmes, 2004; Nieberding and Olivieri, 2007). Endosymbiotic bacteria in insects constitute an excellent illustration of this approach. For instance, the routes of invasion of the Russian wheat aphid *Diuraphis noxia*, one of the world's most invasive cereal (wheat and barley) crop pests, have been unresolved due to the limited polymorphism of the available markers (Liu et al., 2010; Zhang et al., 2014). By targeting genomic and plasmid DNA of its obligate endosymbiont *Buchnera aphidicola*, Zhang et al. (2014) succeeded in retracing the recent worldwide invasion of this damaging pest species. *Wolbachia* infections were also shown to confirm the common invasion history of several invasive populations of the little fire ant *Wassmania auropunctata* (Rey et al., 2013). For invasive plants, rhizobial symbionts may be as helpful. For instance, the phylogenetic analysis of several DNA regions of the *Bradyrhizobium japonicum* symbionts has allowed confirming the relationship between native populations from Australia and invasive populations from South Africa of its invasive host plant *Acacia pycnantha* (Ndlovu et al., 2013). Parasitic microorganisms may also mirror the invasion routes of their hosts. In the case of *Drosophila melanogaster*, its vertically transmitted sigma virus DMelSV has been recently used as a tool to infer the global invasion pattern of the fruit fly (Wilfert and Jiggins, 2014). The phylogenetic study of several genes from this parasitic virus has highlighted that its host invaded Europe from Africa and that the North American fruit fly population stemmed from of a single immigration from Europe in the late 19th century. To our knowledge, such an approach has never been conducted on fungal pathogens, while numerous phylogeographic studies indicate host tracking and thus congruent expansion histories between these microorganisms and their host plants (Gladieux et al., 2008; Stukenbrock et al., 2007; Vercken et al., 2010).

Despite the image of success provided by these different examples, the use of microorganisms as a tracer of the invasion pathways of their hosts requires some precautions. First, it is important to keep in mind that numerous microorganisms are lost by their host through drift or selection during the invasion process (see section 2 for more details). Microorganism populations or communities in invaded areas may thus be a pale reflection of those found in the native area, restricting their use as a reliable tracer of host invasion history. For both approaches (microorganisms community and genome of a single microorganism species), microorganisms need to share a common evolutionary history with their host (Nieberding and Olivieri, 2007). Several characteristics can influence this intimacy (Whiteman and Parker, 2005) such as the transmission mode (vertical *vs.* horizontal) or the type of biotic relationship (mutualistic endosymbiosis, commensalism, parasitism, …). For instance, it is widely assumed that microorganisms with vertical transmission should more realistically reflect the invasion history of their hosts (Johnson and Clayton, 2004). In the same vein, concerning parasitic microorganisms, it is much better to use a very specific parasite with a direct life cycle (Nieberding and Olivieri, 2007; Wirth et al., 2005). Several studies have illustrated that microorganisms are not always adequate tracers of the invasion history of their host. For instance, a characterization of the bacterial microbiota of *Aedes albopictus* by 16S rDNA metabarcoding showed no correlation between microbiota and the genetic structure (estimated on neutral genetic markers) of the host populations in invaded and native areas (Minard et al., 2015). This study provides support to the suggestion that the gut microbiota of animals would be rather a reflection of local environmental conditions than of host genotype (Boissière et al., 2012; Linnenbrink et al., 2013). Genetic differentiation has been shown to be higher in hosts than in parasites having complex cycles, free-living stages and hermaphroditic reproduction (Mazé-Guilmo et al., 2016). As another example, a population genetic study of the horizontally transmitted fungal pathogen *Microbotryum lychnidis-dioicae* of the invasive plant *Silene latifolia* confirmed contrasted invasion histories between the host and its specific parasite (Fontaine et al., 2013).

Concerning the monospecific approach (e.g. genome of a microorganism as a magnifying lens), additional recommendations has to be followed. An invasion occurs over a relatively short timescale and thus, to be informative, microorganisms have to accumulate more mutations in this short time period than their hosts. Selection may also result in artificial groupings of populations with different genealogies (Wirth et al., 2005) and thus alter the efficiency of microorganism to retrace the invasion routes. Therefore, asexual microorganisms should be avoided due to non-independence of loci and potential selective sweeps (Rosenberg and

Nordborg, 2002). Finally, genes used to reconstruct the invasion history have to be chosen in such a way as to prevent problems linked to horizontal gene transfer that could disturb the historical pattern (Lerat et al., 2005).

In conclusion, only few microorganisms have been used, up to now, as tracers for the invasion histories of their hosts. But the already existing case studies seem promising and, bearing in mind some caveats, such approaches could be helpful to precisely retrace the invasion history of an increasing number of species.

5.2 As tools to manage invasive species

Invasive species can induce detrimental consequences in both natural and human-altered habitats, including erosion of biodiversity, decrease of farm and forest productivity and impact on public health (Lodge, 1993; Murphy and Romanuk, 2014; Pimentel et al., 2001). In many situations, classic control methods (such as culling, trapping or chemical agents) have, in different ways and for different reasons, either failed to provide an adequate control or are too costly/detrimental for the environment and/or the health to be sustainable (Cleaveland et al., 1999; Di Giallonardo and Holmes, 2015). Biological control (e.g. the use of any organism, its genes, or its products that can cause negative impact on pest populations) has thus been considered as an alternative for managing invasive species (Thomas and Reid, 2007; Zavaleta et al., 2001). The idea behind this strategy is that release from enemies ('Enemy Release Hypothesis'; see paragraph 2.1) is commonly recognized as a major determinant of the successful invasion of an exotic species (Keane and Crawley, 2002). Thus, adding a specific enemy may reverse the trend and allows to reduce — if not suppress — invasive populations. Beside predator and parasitoid macroorganisms, a wide diversity of microorganisms can also serve as biocontrol agents against a range of invasive species in a wide diversity of circumstances (Lacey et al., 2001; Miller et al., 1983). Here, we first outline the different approaches that use microorganisms as control agents based on several emblematic examples. We then discuss the benefits and limitations of microorganism as biocontrol agents. Finally, we highlight future developments to improve the role of microorganisms as biocontrol agents in invasive species management.

As early as the 19th century, some biocontrol programs involving microbial control agents (mainly fungi) were carried out against invasive insects having devastating impacts on managed environments. However, the use of pathogenic microorganisms has really started with the discovery of the bacterium *Bacillus thuringiensis* (Bt) at the beginning of the 20th century (Lacey

et al., 2001). The mode of action of this bacterium against insects relies on several insecticidal proteins known as Cry, Cyt, Vip and Sip proteins (Palma et al., 2014). Since its first uses by farmers as a pesticide in 1920, Bt has become the main microorganism used in biological control and thousands of strains are now available (Hajek and Tobin, 2010; Miller et al., 1983; Mnif and Ghribi, 2015). Beside traditional formulations (such as suspensions), additional means of application have been developed to produce and deliver the toxins to the target insects such as other plant-colonizing bacteria and the insertion of Bt toxin genes into transgenic crops (Romeis et al., 2006; Sanahuja et al., 2011; Stock et al., 1990). Following the development of this leading microbial agent, the use of microorganisms as biocontrol agents has been diversified so that nowadays any type of pathogenic microorganisms (e.g. viruses, bacteria, fungi and protists) can be successfully used for eradicating or controlling a range of invasive species (e.g. arthropods, plants, nematodes, fungi and vertebrates) in diverse ecosystems worldwide (Hajek et al., 2007; Lacey et al., 2001; Meyer and Foudrigniez, 2011; Nakaew et al., 2015). It is noteworthy that genetic engineering techniques are now used to increase the efficiency of microorganisms used as biocontrol agents (Georgievska et al., 2010; Giddings 1998; Godfray 1995; Zwart et al., 2009).

In recent years, endosymbiont bacteria (especially those belonging to the genus *Wolbachia*) have also been recognized as powerful tools for biocontrol programs (Vavre and Charlat, 2012; Zindel et al., 2011). First, *Wolbachia* is well known for manipulating its hosts' reproduction through different mechanisms such as feminization of genetic males and parthenogenesis induction or cytoplasmic incompatibility (Vavre and Charlat, 2012). This attribute can be directly used to suppress invasive populations through the mass release of cytoplasmic incompatibility — *Wolbachia* infects males in a similar way to the 'Sterile Insect Technique' (Atyame et al., 2011; Zabalou et al., 2004). Reproductive manipulations by *Wolbachia* may also affect the rearing and establishment of macroorganisms used as biocontrol agents (Zindel et al., 2011). In the majority of parasitoid biocontrol agents for instance, only females are effective by laying their eggs in their hosts. Thus, parthenogenetic reproduction induced by *Wolbachia* may facilitate mass production and provide a large number of beneficial insects at the appropriate time (Zindel et al., 2011). In addition to the reproductive manipulation of their hosts, endosymbionts bacteria can affect a variety of traits such as resistance to host enemies, lifespan of their hosts or their vectorial capacity (Graham et al., 2012; Hoffmann et al., 2011; Vavre and Charlat, 2012). As it has been shown with *Wolbachia*, endosymbiont bacteria can be used to decrease the transmission of pathogens (such as dengue) by invasive insects either directly by reducing pathogen load in insect vectors or indirectly by reducing host lifespan (Hedges et al., 2008; Hughes et al., 2011; Hoffman and Turelli, 2013; McMeniman et al., 2009; Moreira et al.,

2009). Recent findings show also that *Wolbachia* can also be used to directly regulate invasive populations of insects through the increase of susceptibility of their hosts to viral infection (Graham et al., 2012).

There are also other reports proposing microsporidia as bioweapons of invasive insect species. The continent-wide decline of some North American bumblebee populations has been attributed to *Nosema bombi*, co-introduced with imported and commercially bred European bumblebees (Colla et al., 2006). A spillover of the microsporidial parasite *Nosema ceranae* from the Asian honey bee *Apis ceranae* to European honey bees (*Apis mellifera*) has been suggested as one of the causes contributing to the colony collapse syndrome of this major pollinator (Chen & Huang, 2010).

In the case of vertebrates, biocontrol strategies using pathogenic microorganisms (virus, bacteria, fungi and protozoans) have given mixed results (Saunders et al., 2010). Although some biocontrol programs are currently under investigation (Oliveira and Hilker, 2010; McColl et al., 2014), only three successful viral biocontrol have been identified to date: (i) the release of a parvovirus to eliminate cats on Marion island, and the well documented cases of (ii) *Myxoma* and (iii) Rabbit Haemorrhagic Disease (RHD) viruses, which have been released to control invasive rabbits around the world (Saunders et al., 2010). Following the *Myxoma* virus release, rabbit populations were suppressed over a decade, followed by a recovery of rabbit populations reflecting a combination of evolving virus attenuation and rabbit resistance (Saunders et al., 2010). Privately released as biocontrol in France, the virus spread rapidly through European rabbit populations, with a number of negative ecological and economic consequences (Di Giallonardo and Holmes, 2015). Viral-vectored immune-contraception was another use of microorganisms (e.g. species-specific viruses) envisaged to control mammals (Courchamp and Cornell, 2000). It gave promising results on the house mouse but required significant research efforts to implement (Campbell et al., 2015).

Obviously as any biocontrol agents, microorganism may allow to reduce or eliminate chemical use and their adverse consequences such as e.g. pollution (Bourguet and Guillemaud, 2016) and development of resistance (Rex Consortium, 2013; but see Asser-Kaiser et al., 2007). As compared to chemical pesticides, microorganisms used as biocontrol agents are mostly host-specific (Hajek and Tobin, 2010; Lacey et al., 2001). The absence of evidence that voluntary release of insect pathogens has resulted in long-term negative effects on non-target species or pathogen establishment supports this assertion (Cory and Myers, 2000). Their pretty narrow host range may allow using microorganisms in combination with other biocontrol agents, such

as predators or parasitoids (Miller et al., 1983). Besides, the production and storage of microorganisms as biocontrol agents are very often easier and cheaper than those of macroorganisms (Lacey et al., 2001).

There are also limits to the use of microorganisms as biocontrol agents. Historically, it was thought that resistance to microorganisms should be more difficult to evolve than resistance to chemical pesticides (Miller et al., 1983), but this precept is nowadays challenged. For instance, there are an increasing number of field-evolved resistance reports to *Bt* crops in several major pest species (Cory and Franklin, 2012; Tabashnik et al., 2013). Also in the case of Australian rabbits, resistance to Myxoma evolved in only a decade, suggesting the need to work precisely on the relationships between resistance, transmission and virulence (Kerr et al., 2015). Disadvantages of biocontrol strategies also include low environmental persistence, relatively slow action and ethical and environmental issues associated with the release of lethal pathogens (Bravo et al., 2011; Messing and Wright, 2006). In vertebrates, there is a high fear of inadvertent infection of other species (including humans), because barriers preventing successful host jumps are still largely unknown (Di Giallonardo and Holmes, 2015). Also, total eradication of the host is rarely achieved by a pathogen, and more intensive techniques are necessary to remove pest individual below the density corresponding to the threshold allowing pathogen establishment (McColl et al., 2014).

The use of microorganisms as cheap and safe tools to manage invasive species through microorganism is a clearly aimed objective. Achieving this goal still requires fundamental and applied studies combining genetic, molecular, theoretical and ecological approaches (Douglas, 2007; Thomas and Reid, 2007; Vinale et al., 2008). More specifically, the following advances are pivotal: first, we need to strengthen our understanding of the interactions not only between microorganisms and their hosts but also with the whole environment from which these partners belong and finally interactions among microorganisms within the host. This could consecutively improve the speed of action and the environmental persistence, but also allows a better management of potential pest resistance and enhance efficiency of production and application. Second, genetic engineering, noticeably with the new development of the CRISPR-Cas9 technology (which allows to make precise and targeted changes to the genome of living cells, Makarova et al., 2002), can offer great improvements in all these topics (Champer et al., 2016; Sander and Joung, 2014). However, we are only at the beginning of the use of this innovative technology, and obtaining a better understanding of its potential unintended consequences is of paramount importance (Webber et al., 2015).

6. CONCLUSIONS

Among the many potential biotic and abiotic factors that can interact to determine the invasiveness of a species in a newly invaded community, empirical studies have historically focused on macro-scaled processes, such as population dynamics (mainly of the introduced species, but also of those belonging to the native community; Huntley et al., 2010, Ibanez et al., 2014; Pearson and Dawson, 2003), or changes of the invasive species between its native range and area of introduction from a genetic (Amsellem et al., 2000; Cristescu, 2015; Fitzpatrick et al., 2012) or phenotypic points of view (Amsellem et al., 2002; Amsellem et al., 2001). It is now assumed that these macroscopic patterns often represent the visible consequences of underlying mechanisms occurring at (much) smaller scales. Hence, proximal inductors caused by biological activities and ecological roles of both native and co-introduced microorganisms are now totally doubtless about their beneficial or detrimental consequences on the determinism of biological invasion. Processes involving microorganisms are now widely considered because they are recognised as potential major determinants during biological invasions processes (Brown et al., 2014; Rizzo et al., 2016; van Elsas et al., 2012), and allow to have the largest overview and the most inclusive understanding of the biological and ecological concerned processes during the different invasion stages.

Most of the various case studies about microorganisms influencing the invasion process of their introduced host species depicted all along this presentation are focused on a short-time scale, whereas long-term balance of positive and negative interactions has received less attention (Agrawal et al., 2005; Gilbert and Parker, 2010). However, both host-microorganism interactions and biological invasions are prone to induce rapid and drastic changes over time, and long-term outcomes are rather hard to predict (Altizer et al., 2003; Kelehear et al., 2012; Lambrinos, 2004; Thompson 1998; Weeks et al., 2007). Pathogen accumulation constitutes an outstanding example to illustrate how the dynamic relationships between microorganism and their invasive hosts may induce potentially different and unexpected eco-evolutionary trajectories. While introduced species may initially benefit from the release of their pathogens (see section 2), several case studies mainly focused on plants species suggest that pathogen accumulation over time since their introduction could be widespread (Diez et al., 2010; Mitchell

et al., 2010; Phillips et al., 2010; Stricker et al., 2016; Strong and Levin 1975). Such pathogen accumulation can be driven by several ecological and evolutionary mechanisms, such as an increase in density of their invasive host species, co-introductions of coevolved microorganisms with the invasive candidate species, adaptation of native pathogens to invasive species and the evolution of reduced defences from the invasive species (EICA hypothesis — Flory and Clay, 2013). For now, potential consequences of pathogen accumulation in the area of introduction are poorly known, and may only be hypothesized according to several outcomes. First, pathogen accumulation can decrease the density and extent of invasive species and, as a consequence, facilitates recovery of native species over the long term (Stricker et al., 2016). Second, invasive species could respond to pathogen accumulation through phenotypic plasticity or tolerance, and thus not be truly affected through their population dynamics (Flory and Clay, 2013). Finally, pathogen accumulation may also strengthen the superiority of invasive species over native ones (spill-over and spill-back — Kelly et al., 2009) *via* increasing impacts of diseases on co-occurring native hosts (see paragraphs 3.1 and 4.1). These three alternate outcomes emphasize the urgent need for a deeper understanding of the long-term dynamics of the invasive species and their microorganism (Dietz and Edwards, 2006; Hawkes, 2007). Such an approach requires a multidisciplinary point of view, including experimental manipulations, long-term surveys of invasions of known ages, genomic studies of host-microorganism interactions as well as theoretical modelling of these interactions within an explicit invasion context (Flory and Clay, 2013; Hawkes, 2007). These complementary approaches would allow assessing the emergence of general patterns, and would thus enhance our knowledge about the outcomes of biological invasions (Flory and Clay, 2013; White and Perkins, 2012).

Beyond the putative significant role played by microorganisms during biological invasions, they can also have significant involvements in many related biological and ecological phenomena linked to biological invasions. For example, microorganisms may be considered in the context of conservation biology (i) to stop invasion processes (*via* their use through biological control), or (ii) to consider risks of new emerging diseases for native species (including humans) during or shortly after biological invasions processes (Bellard et al., 2016; Blackburn and Ewen, 2016; Santini et al., 2013). Moreover, we draw attention to conservation biology actions with potentially antagonistic effects differing from expectations, and putatively leading to important and irreversible damages. These dramatic outcomes may be caused during reintroduction of individuals on purposes or (i) to reintroduce some species in areas where they are not found anymore, either (ii) to genetically strengthen populations involved in a vortex of extinction. In both cases, the fact of not considering possible roles of co-introduced

microorganisms would be a mistake that could lead to consequences opposite to the expected ones (Seddon et al., 2014; Walker et al., 2008).

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FIGURE LEGENDS

(*__Note__*: Figure 1 has to occupy full width of the page)

Figure 1 Schematic representation of some hypotheses linking invasion success or failure and the presence of microbial (parasites or symbionts) passengers. Concordant processes apply to symbionts and parasites, but with possible contrasting outcomes (symbols represent introduced [solid] and native [dashed] hosts, with their respective original passengers):

(a) enemy (parasite) release will have positive impacts on exotic host fitness while symbiont loss may have negative impacts on exotic host fitness;
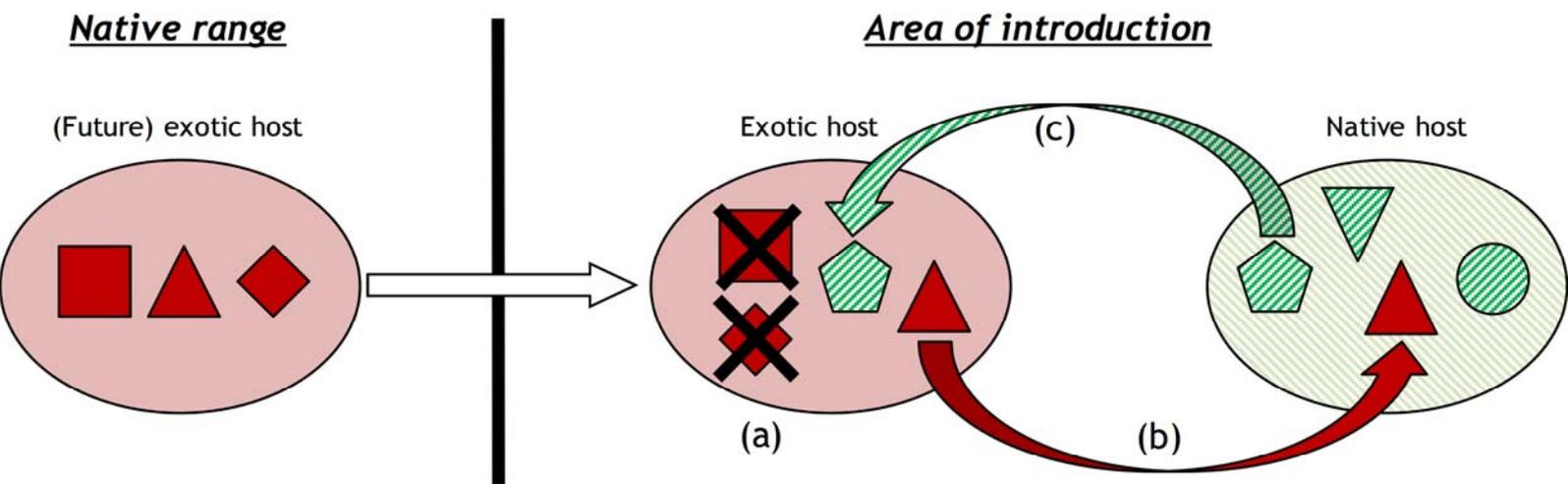
(b) co-invading pathogens can have negative impacts on host invasion, though exotic pathogen spill-over to native hosts can have positive impacts on host invasion. Exotic symbiont co-invasion could have positive impacts on host invasion, and symbiont spill-over to native hosts can accentuate these positive impacts on host invasion if exotic symbionts are less beneficial than native ones to native hosts;
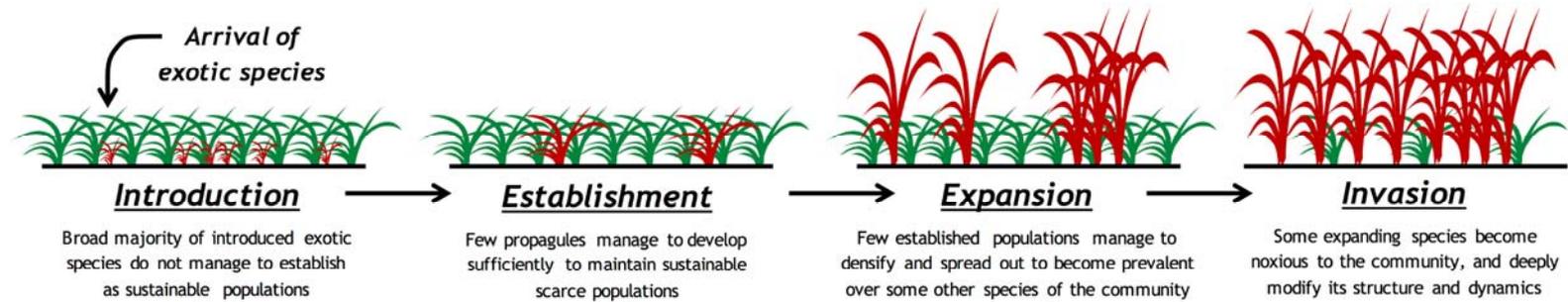
(c) acquisition of novel pathogens can have negative impacts on invasion, though the net effect of these pathogens can be positive on exotic hosts due to spill-back. Acquisition of novel symbionts can have positive impacts on invasion if increasing exotic host fitness.

(**Note**: For are more convenient readability, Figure 2 has to be in landscape mode and occupy a whole page)

Figure 2 Where microorganisms may play a beneficial or detrimental role during the different phases of a biological invasion process. (—) and (+) symbols represent respectively favorisation or prevention of alien species for reaching the next phase of in the invasion process.

Native range

(Future) exotic host

Area of introduction

Exotic host

(c)

Native host

(a)

(b)

Arrival of exotic species

Introduction → **Establishment** → **Expansion** → **Invasion**

Broad majority of introduced exotic species do not manage to establish as sustainable populations

Few propagules manage to develop sufficiently to maintain sustainable scarce populations

Few established populations manage to densify and spread out to become prevalent over some other species of the community

Some expanding species become noxious to the community, and deeply modify its structure and dynamics

From the native community :

(−) *Biotic resistance* : soil microbiota does not correspond to the needs, preventing or slowing down establishment.

(−) *Native pathogens* : the native pathogen cortege causes a huge parasitic load, preventing or slowing down establishment.

(+) *Favorisation* : soil microbiota is convenient, enhancing or accelerating establishment.

From introduced species :

(+) *Spill-over* : favorisation of the introduced parasites towards the native community, enhancing or accelerating establishment.

From the native community :

(−) *Native pathogens* : the native pathogen cortege prevents or slow down the expansion.

(+) *Favorisation* : soil microbiota enhances or favours the expansion.

From introduced species :

(+) *Spill-over* : favorisation of the established parasites towards the native community, enhancing or accelerating expansion.

(+) *Spill-back* : established species serve as a reservoir of native pathogens causing surinfection to the native community, enhancing or accelerating expansion.

From introduced species :

(+) *Spill-over* : favorisation of the established parasites towards the native community, enhancing or accelerating expansion.

(+) *Spill-back* : expanding species serve as a reservoir of native pathogens to definitely establish their prevalence in the native community, and thus becoming invasive.