

Chapter 9

Invasive Fruit, Cone and Seed Insects in the Mediterranean Basin

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Abstract Invasive fruit, cone and seed insects are considered the most important predators of tree seeds during the pre-dispersal phase of development. Although some species benefited from historical human movements across the Mediterranean Basin, the accelerating rate of international trade, travel and transport of wood products, including seeds, during the latter half of the twentieth century has increased the introduction of alien fruit, cone and seed insects in this area. The combination of almost inexistent phytosanitary regulations of tree seed trades and species biological characteristics favouring human-aided dispersal had a key role in successful invasions of Mediterranean forest ecosystems. Invasions may affect plant populations through increased direct trophic interactions such as seed parasitism and destruction, which can result in more complex indirect effects on natural regeneration processes. Many of the trees cone and seed insects feed upon have also been introduced by humans, but introduced insect species also may switch to native tree species congeneric to their original host and are then likely to interact with native seed feeders. In this chapter, we gathered current knowledge on seven insect species with invasive populations in the Mediterranean Basin. We put an emphasis on: (i) both anthropogenic and biological features involved in such invasion pathways, (ii) the ecological mechanisms involved in the establishment and the spread of invasive populations, (iii) the impacts of alien invasive species on Mediterranean ecosystems, and (iv) the issues related to the management of invasions in the fruit, cone and seed insect group.

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9.1 Introduction

The increase in worldwide exchange and trade of tree reproductive materials combined with phytosanitary regulations limited or non-existent in many countries, have resulted in the establishment of numerous species of fruit, cone and seed insects outside their native range (Langor and Sweeney 2009; Essl et al. 2011; Vaes-Petignat and Nentwig 2014). It is especially true for seed-borne insects and mites, because isolated seeds are preferred to whole cones and fruits for trade of conifers and of most broadleaved tree species (Roques et al. 2003, 2006). The guild of seed feeders/borers¹ is proportionally more represented in the alien fauna than in the European fauna (Kenis et al. 2007), but taxonomic difficulties related to this group could partly induce an underestimation of successful establishments in the Mediterranean Basin. Currently, a few alien species specialized on fruiting structures are recorded in Mediterranean forest ecosystems. Possible explanations are the low number of checklist of alien arthropods in many Mediterranean countries, the cryptic way of life of most of cone and seed insects, which does not usually allow detection easier than using X-ray radiography, and the lack of phytosanitary regulations in many countries (Auger-Rozenberg and Roques 2012).

The small number of invasive fruiting structure insects in Mediterranean ecosystems allows us to detail them on a case-by-case in this chapter. Their general biological traits and their guild characteristics are similar to those provided on native fruiting structure insects in Chap. 4. Once introduced in Sect. 9.2, we propose an overview of entering pathways of the species concerned (Sect. 9.3), of the factors that facilitate the invasion processes (Sect. 9.4) and then of the different kinds of impacts caused by the invasive pests to Mediterranean forest ecosystems (Sect. 9.5).

9.2 Diversity of Invasive Fruit, Cone and Seed Insects in the Mediterranean Basin

In this chapter, invasive fruiting structure species established in Mediterranean Basin will be referred to as *external invasives* when they originate from other continents. When different countries within the Mediterranean Basin constitute invasion sources, the species concerned will then be referred to as *internal invasives*. Each of the species mentioned in the literature as external or internal invasives in Mediterranean forest ecosystems will be presented in this section.

¹This term refers to both spermatophage and external seed predator feeding guilds defined in Chap. 4.

9.2.1 External Invasives (Introductions from Outside of the Mediterranean Basin)

Biogeographic Patterns Although Asia has supplied the major part of the alien arthropods occurring in Europe since the middle of the twentieth century, alien fruiting structure insects currently established in the Mediterranean Basin originate from North America, except those originating from Australasia that were mostly linked to the introduction of *Eucalyptus* and *Acacia* spp. in this area (Roques et al. 2010). A total of four external invasives have been recorded to date.

Taxonomy There are only three feeding guilds² of invasive fruiting structure insects introduced from outside of the Mediterranean Basin. The first invasive feeding guild corresponds to the *spermatophages* of the *Megastigmus* genus (Hymenoptera: Torymidae), which develop exclusively within seeds. Several native species belonging to this genus already exist in Mediterranean ecosystems, basically attacking Cupressaceae and Pinaceae species. These seed chalcids (also called seed wasps) associated with conifers are generally considered to be highly specialized, being either species-specific (even when several potential host species coexist in a same place) or restricted to a conifer genus (Auger-Rozenberg et al. 2006). *Megastigmus* invasive species are present throughout Europe on gymnosperms and angiosperms, but in Mediterranean forest ecosystems, only two North American *Megastigmus* species associated with firs are recorded and shifted from American to Mediterranean firs in south of France, *M. pinus* on *Abies alba*, and *M. rafni* on several Mediterranean firs (Fig. 9.1) (Roques and Skrzypczynska 2003). Likely benefiting from multiple introductions in France during the second half of twentieth century (Auger-Rozenberg et al. 2006), they are not yet recorded in other Mediterranean countries.

The second invasive feeding guild corresponds to the *inflorescence-feeders*, which are represented by a single species on *Eucalyptus* species, the chalcidoid wasp *Quadrastichodella nova* (Hymenoptera: Eulophidae; Fig. 9.1). Despite Eulophidae are often known as entomophagous,³ this wasp is a gall-inducer in the placenta of one of the locules in the seed capsule of a flower bud (Klein et al. 2015). This prevents seed set (Kim and La Salle 2008). Although Australian in origin, *Q. nova* is now recorded from different Mediterranean countries including Tunisia (M. Branco, pers. observ.), Israel, Spain, Italy, and Turkey (Doğanlar and Doğanlar 2008; Kim and La Salle 2008), following its host tree.

The third invasive feeding guild corresponds to an *external seed predator* that feeds directly upon the seeds from the cone surface, namely the polyphagous Western conifer seed bug, *Leptoglossus occidentalis* (Hemiptera: Coreidae; Fig. 9.1). The third alien species is of particular interest because it is the only

² See Chap. 4 for definitions of the terms used.

³ Primary or hyper parasitoids.

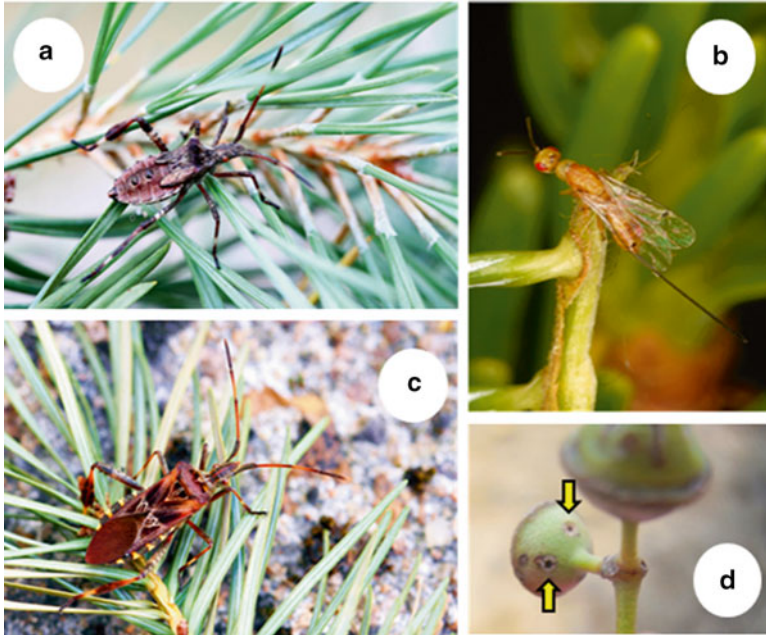


Fig. 9.1 The Western conifer seed bug, *Leptoglossus occidentalis* in south of France (**a**) immature nymph and (**b**) adults. The fir seed chalcid *Megastigmus rafni* in southeastern France (**c**). Eucalyptus seed capsule with two typical circular exit holes of the chalcidoid wasp *Quadrastichodella nova* in Tunisia (**d**) (Photos: D. Lees (**b**), V. Lesieur (**a**, **c**) and M. Branco (**d**))

polyphagous species of the list. *Leptoglossus occidentalis* is a pest widely distributed pest in western North America, which has been accidentally introduced in northern Italy in 1999. It expanded its range very quickly and spread over most Europe in about one decade (Lesieur et al. 2014). There is strong evidence that the fast invasion of this bug in Europe proceeds from multiple introductions (Lesieur 2014). Recorded for several years on the northern rim of Mediterranean Basin (EPPO 2014), it was recently found in North Africa (Ben Jamaa et al. 2013). This provides evidence that the bug is now becoming a highly successful worldwide invader that feeds on cones of a large number of conifer species. Both adults and immature nymphs consume individual seeds in developing and mature cones during the growing season, and whatever the already or soon invaded countries, Mediterranean forest ecosystems represents a suitable habitat of *L. occidentalis* (Zhu et al. 2014).

9.2.2 *Internal Invasives (Introductions Within the Mediterranean Basin)*

Biogeographic Patterns Invasions of fruiting structure insects can also occurred inside the Mediterranean Basin. Although little is currently known about the potential of Asia Minor and/or the Near East to provide such invaders, the three case studies presented in this section suggest an orientation of invasion movement in a northerly direction (according to the division of the main geographic sub-regions presented in Chap. 4, Sect. 4.3.2). This is consistent with greater interests of countries of the Northern Rim of the Mediterranean Sea (France, Greece, Italy, Spain and Portugal) for Mediterranean tree species importation and plantation than countries of the southwestern and southeastern Rim.

Taxonomy Internal invasive species belong to the sole feeding guild of spermatophages and genus *Megastigmus*. The first species is *Megastigmus wachtli*, a seed chalcid mainly associated with the Mediterranean cypress, *Cupressus sempervirens* (Fig. 9.2). This conifer is native to the eastern Mediterranean region and has been widely cultivated for millennia away throughout the whole Mediterranean region. Concurrently, *M. wachtli* populations have been accidentally introduced in most occidental Mediterranean countries probably by the ancient Greeks and the Romans inside the seeds (Roques et al. 1999).

Far more recently, two cedar seed chalcids have been introduced in cedar forests of southeastern France (Auger-Rozenberg et al. 2012). Most of such French cedar stands have been infested by *Megastigmus pinsapinis* (Fig. 9.3), which has probably been introduced from North Africa during the importation of seeds of *C. atlantica* for reforestation programs over more than a century ago. A second species, *M. schimitscheki* (Fig. 9.3), which native area covers *C. libani* and *C. brevifolia* forests in the Middle-East, has been accidentally introduced in southeastern France from seeds of *C. brevifolia* in the early 1990s. French populations of this chalcid were founded from a unique introduction event of an extremely restricted number of individuals that realized a host switch from *Cedrus brevifolia* to *C. atlantica* (Auger-Rozenberg et al. 2012). *M. schimitscheki* colonized most of southeastern French *C. atlantica* stands (Lander et al. 2014), which resulted in a niche overlap with *M. pinsapinis* (Boivin et al. 2008; Fabre et al. 2004) that led to strong competitive inter-specific interactions between them (Gidoïn et al. 2015).

9.3 Invasion Pathways

Many natural barriers between regions, countries and continents are bypassed due to the increase of international trades. Alien species favoured by such human activity are increasingly recognized as invasive species, posing great threats to biodiversity and economy (Walther et al. 2009). Whatever the insect group to be considered,

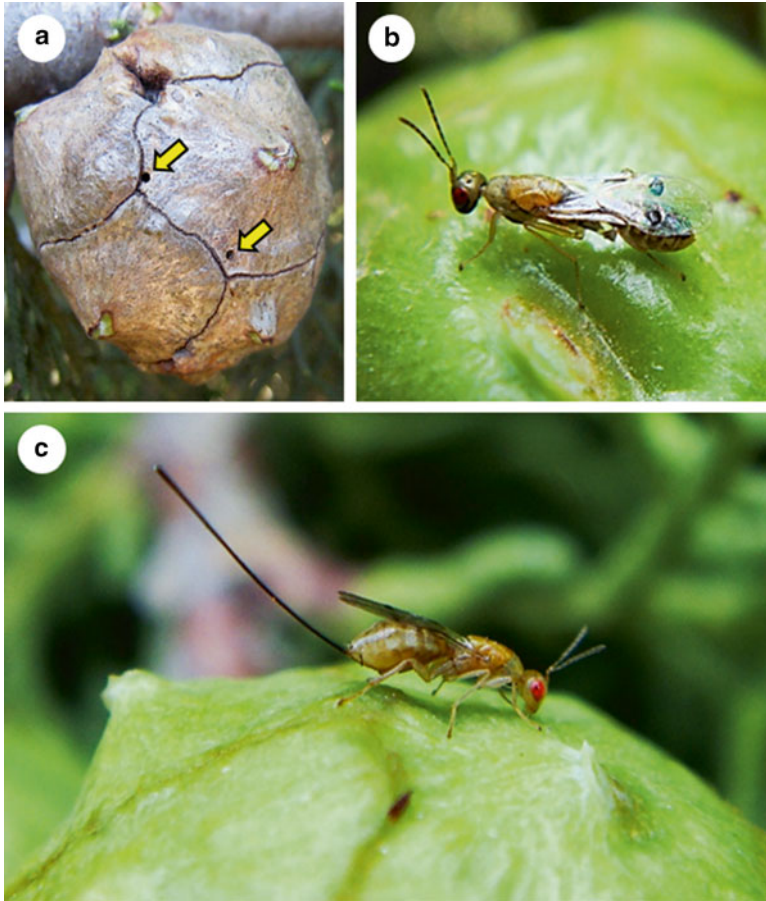


Fig. 9.2 The cypress seed chalcid *Megastigmus wachtli* in southeastern France. Two-year old cone of the evergreen cypress *Cupressus sempervirens* with two typical circular emergence holes of *M. wachtli* adults (**a**, arrows). Male and female of *M. wachtli* (respectively) on a 1-year old cone of *C. sempervirens* (**b**, **c**) (Photos: T. Boivin (**a**) and J. Safrana (**b**, **c**))

the invasion processes in invertebrates are commonly linked to the intensity of anthropogenic disturbance and hence to the pathways of introduction (Hulme et al. 2008; Pysek et al. 2010). Recent studies suggest that ca. 90 % of the alien invertebrates were introduced unintentionally through human activity (Roques 2010; Roques et al. 2009). Anthropogenic dispersal usually occurs from and to regions where important human activity coincides with a particular life stage that favours dispersal (e.g. Robinet et al. 2009; Kaňuch et al. 2013).

In the seminiphagous wasps *Quadrastichodella nova* and *Megastigmus* spp., the life stage that is most likely to be transported as a result of human activity is the

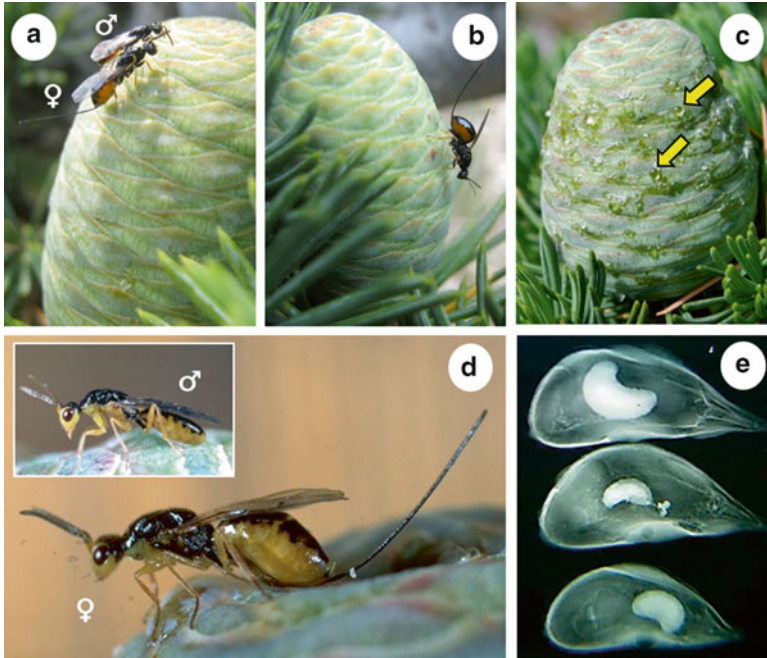


Fig. 9.3 The cedar seed chalcids *Megastigmus schimitscheki* (a, b) and *M. pinsapinis* (d) on 1-year cones of the Atlas cedar *Cedrus atlantica* in southeastern France. One-year old cone of *C. atlantica* with resin droplets (arrows) resulting from seed chalcid oviposition through the cone scales with their ovipositor. Note that the chalcids mainly target the central part of the cone during oviposition (c). X-ray radiography of seeds of *C. atlantica* parasitized by seed chalcids, whose larvae have consumed both seed embryo and reserve organs before entering diapause (e) (Photos: T. Boivin (a–c), J.-P. Fabre (d) and A. Chalon (e))

diapausing larval stage. Because all spermatophages have an endophytic life-cycle,⁴ diapausing larvae remain within seeds from their harvest to their use in tree nurseries and may be transported as a result of seed trade at international, national and regional scales (Kim and La Salle 2008; Auger-Rozenberg and Roques 2012). Seminiaphagous insect species require special attention because they can cause massive seed losses, and because the lack of regulatory measures on global trade in tree seeds facilitated their entry in Europe, including the Mediterranean Basin. They are actually considered as contaminants of traded goods, associated to commodities intentionally introduced by man (Hulme 2009), as in the case of seeds exchanges of exotic tree species⁵ (Roques and Auger-Rozenberg 2006). As detailed in Sect. 9.2, the *Megastigmus* genus is becoming the major supplier of invasive seed insects in the Mediterranean Basin. In particular, the case of *M. schimitscheki* recently

⁴Insects spending their entire pre-imaginal development (egg to pupa) within the fruiting structure.

⁵Mainly used in commercial seed market for plantations and ornamentals.

introduced from Near East to southeastern France highlights the implications of unregulated seed trade probably associated to seed imports for clandestine ornamental purposes (Auger-Rozenberg et al. 2012). Similarly, although introduction pathways of *Q. nova* in the Mediterranean Basin are not clearly known, it is likely that they were related to the *Eucalyptus* seed trade all over the world (Paine et al. 2011).

The introduction in Europe of the Western conifer seed bug *Leptoglossus occidentalis* resulted from another typical invasion pathway referred to as stowaway transport, in which species are directly associated with human transport but arrive independently of a specific commodity (e.g. Rabitsch 2010; Roy et al. 2011). Stowaway transport is the most likely vector of external seed predators, which feed and develop outside fruiting structures. The aggregative behaviour of *L. occidentalis* for the overwintering phase or the high mobility of isolated individuals probably favoured transportation of propagules by ship in containers, e.g. timber logs or wood panels related to timber shipments, from the USA to Europe (Dusoulier et al. 2007; Malumphy et al. 2008).

9.4 Factors of Invasion Success and Secondary Spread

Identifying the drivers of successful invasions is a key step in predicting and avoiding subsequent invasions of pest species belonging to the same guild. Invasion success refers to the ability of a species to increase from low population density (Shea and Chesson 2002). Characteristics of both the recipient community and the new environment are critical drivers of the demographic response of an introduced population, e.g. through the presence of natural enemies or by affecting resource availability.⁶ Introduced populations generally face a heterogeneous world in which abiotic conditions, resource distribution and abundance, and density in native species⁷ vary in both space and time. Such environmental heterogeneity is likely to affect population growth in both introduced and expanding populations. Displaying or evolving towards life-history traits that provide adaptive responses to such demographic and environmental constraints is a key to establishment, persistence and secondary spread in the new environment (Sakai et al. 2001). In this section, we will illustrate how these concepts can help understanding the successful invasion of Mediterranean forest ecosystems by the Western conifer seed bug and by *Megastigmus* seed chalcids (Fig. 9.4). Unlike *Quadristichodella nova*, these species have been well studied and have proved to be of particular interest for two reasons. First, they result from different introduction histories, i.e. multiple and single introductions. Second, they suggest that patterns of establishment success can drastically differ according to the species concerned.

⁶Resource availability may depend the presence of native competitors and on spatio-temporal variation in fruiting structure abundance.

⁷Native species may be associated with facilitation, competition or predation.

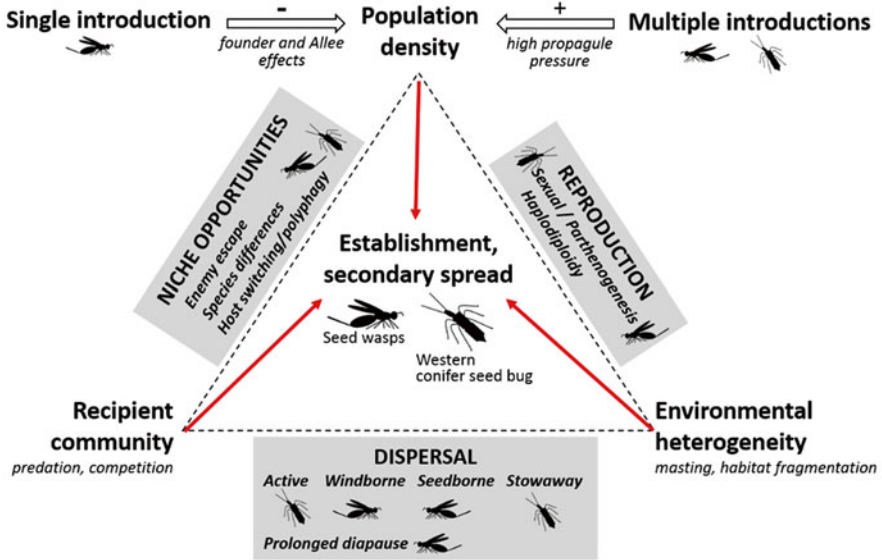


Fig. 9.4 Conceptual framework of the main drivers of invasion success in seed chalcids (*Megastigmus* spp.) and the Western conifer seed bug (*Leptoglossus occidentalis*) in the Mediterranean Basin. Establishment and secondary spread depend on the effects of the environment, the recipient community and population density on population growth of introduced populations. Such effects may vary in both space and time. Invasive populations may benefit from niche opportunities and both advantageous reproductive and dispersal strategies to grow and spread in their new environment

9.4.1 Reproduction

Reproductive strategies can play a key role in circumventing the demographic cost of severe founder effects in introduced populations or in those located at the front of expansion range (Sakai et al. 2001; Yamanaka and Liebhold 2009). Parthenogenesis is a typical reproductive strategy in seed chalcid wasps, in which females can produce asexually either males (i.e. arrhenotoky) or females (i.e. thelytoky) (Boivin et al. 2014). This trait is a likely factor of chalcids’ invasion success in Mediterranean forests by reducing to risk of extinction and favouring population growth at low initial density (Auger-Rozenberg et al. 2012, Fig. 9.4). Recent work on the invasive cedar seed chalcid *M. schimitscheki* also demonstrated an absence of Allee effect as fertility reaches its maximum at low population density (Gidoïn et al. 2015). Moreover, as all Hymenoptera, seed chalcids exhibit a haplodiploid sex-determination system, in which males develop from unfertilized eggs and are haploid, and females develop from fertilized eggs and are diploid. In haplodiploid organisms, a genetic load that is hidden in heterozygous female diploids should be expressed and thus purged by selection in the haploid males (Werren 1993). This might have limited adverse effects of inbreeding depression during the first steps of *Megastigmus* invasions (Auger-Rozenberg et al. 2012).

9.4.2 *Niche Opportunities*

Suitable Host Availability In any insect invasion the presence or absence of suitable resource and oviposition sites in the invaded range is a key factor of establishment success, even more in the context of climate change, which can facilitate a sustainable establishment of an invasive species in a new suitable ecosystem (Walther et al. 2009; Bacon et al. 2014). This may have a more critical meaning for specialists such as most of fruiting structure insects, for which the possibility of refugia on alternative habitats is generally almost null.⁸ In this context, invasive seed feeders of the *Megastigmus* genus are unique because many of the trees they feed upon have also been introduced by humans in recent times, particularly since the development of international trade in the twentieth century. Because they are highly specialized seed feeders (Auger-Rozenberg and Roques 2012), the introduction of their host trees facilitates their own accidental introduction. Seed chalcids may also exhibit phenotypic plasticity and successfully switch to native tree species when these belong to the same genera as their original host (Roques et al. 2006). Host shifting generally results in a niche overlap with native specialized seed feeders that can lead to interspecific competition for the seed resource, as shown in Mediterranean fir and cedar stands (Auger-Rozenberg and Roques 2012; Gidoïn et al. 2015). In the absence of suitable hosts in the native tree community, invasion of specialists succeeds at the sole condition that the original host has been also widely introduced. This was illustrated by the invasion of *Quadrastichodella nova* in *Eucalyptus* plantations across southern Europe and Middle-East (Kim and La Salle 2008; Paine et al. 2011). Conversely, invasion success in the Western conifer seed bug *Leptoglossus occidentalis* results from three typical features of host use in external seed predators: (1) generalist feeding habits, (2) external food intake,⁹ and (3) strong active flight capability in adults (Fig. 9.4). *L. occidentalis* displays polyphagous feeding habits in the invaded European regions where it feeds on both native pine species and introduced exotic conifers. Such a combination of traits allows *L. occidentalis* to move rapidly and at rather long-distance to find suitable host trees (Lesieur et al. 2014).

Niche Use Differences between native and invasive specialist species are also important factors of invasion success as they may promote niche partitioning. Niche partitioning is a mechanism favouring coexistence provided invasive and resident species differ in their resource use (Byers and Noonburg 2003). Niche-based hypotheses to explain invasion success also rely on species differences that allow invaders to either access unused resources (empty niche hypothesis) or be more competitive in exploiting shared and limited resources (niche replacement hypothesis) (Ricciardi et al. 2013). In southeastern France, the successful invasion of *M.*

⁸ See Chap. 4 about host plant specialization in fruiting structure insects.

⁹ Unlike most other fruiting structure insects that develop inside the cones or the seeds (see Chap. 4).

schimitscheki results from earlier phenology than its resident competitor *M. pinsapinis*. As cedar seeds are as yet unused by *M. pinsapinis* upon the adult emergence and oviposition of *M. schimitscheki*, this resource availability may be equivalent to an empty niche for *M. schimitscheki* and may have favoured its establishment. This scenario was supported by high probabilities of invasion failure in simulation approaches, in which *M. schimitscheki* has a similar phenology as *M. pinsapinis* (Gidoïn et al. 2015). A similar empty niche mechanism may explain the successful invasion of *M. pinus* on French firs as this species has an earlier spring emergence than both the native *M. suspectus* and the invasive *M. rafni* (Boivin and Auger-Rozenberg, pers. observ.). By contrast, phenology cannot explain the great invasiveness of *M. rafni*, which it is the latest species related to firs in Europe to oviposit in spring. Alternatively, *M. rafni* has a longer ovipositor than any other fir chalcid species, which may allow oviposition in seeds that are not accessible to *M. pinus* and *M. suspectus* anymore due to the continuous development in size of cones (Auger-Rozenberg and Roques 2012). This may have facilitated the early stages of the invasion of *M. rafni*.

Enemy Escape Opportunity Another niche opportunity that a new environment can provide to invasive species is a low or null impact of natural enemies on population growth, a mechanism referred to as enemy escape opportunity (Shea and Chesson 2002). This may arise either in the absence of specialist enemies in the recipient community,¹⁰ or when indigenous generalist and specialist enemies are inefficient in attacking invaders. Enemy escape opportunity may have contributed to successful invasions of both *Megastigmus* spp. and *L. occidentalis* in the Mediterranean Basin, as no specialist enemies known in the native areas of these species have been detected yet (Auger-Rozenberg and Boivin, pers. observ.; Lesieur 2014, Fig. 9.4).

9.4.3 Dispersal

Invasive species' range expansion occurs through many of the same mechanisms as range expansion of non-invasive species (Lawson Handley et al. 2011). Species may expand into adjacent habitats by regional diffusion as a function of population growth rate and a diffusion coefficient (Ciosi et al. 2010), or into distant patches and new environments by long-distance dispersal (Hastings et al. 2005). There may also be more complex dispersal patterns which combine short-distance diffusion with long-distance dispersal, referred to as stratified dispersal (Darling and Folino-Rorem 2009). Secondary spread of invasive fruiting structure insects can involve such diverse mechanisms, each depending on species' life-cycles or life stages (Fig. 9.4). In *L. occidentalis*, individuals live exclusively outside the cones and disperse primarily as adults, a highly mobile stage that can actively fly from a few

¹⁰Because they did not successfully established or they were not introduced.

hundred meters to 30 km. Moreover, its habits to aggregate inside man-made structures in the fall to seek shelter for overwintering clearly facilitated stowaway secondary translocations within Europe (Lesieur et al. 2014). In seed chalcids, for which active flight capacity is unlikely to exceed host stand size (Jarry et al. 1997), passive long-distance dispersal, either windborne, seedborne¹¹ or both, was the most likely driver of colonization of new suitable sites across highly fragmented Mediterranean forest landscapes (Lander et al. 2014, Fig. 9.4).

As a temporal dispersal mechanism, strong propensity to prolonged diapause in seed chalcids may also help to buffer population collapses in years of low seed production by its obligate host, contributing to population sustainability following introduction and during expansion.¹² This has been demonstrated in *M. schimitscheki* (Suez et al. 2013). Similarly, *M. rafni* displays the strongest propensity to prolonged diapause among seed chalcid species feeding on French Mediterranean firs, which may have contributed to its successful establishment and expansion in this area (Boivin T., unpublished results).

9.5 Ecological and Economic Impacts

Alien species are considered as invasive when they have negative ecological and economic impacts in their novel environment. Their introduction contributes to damage ecosystems and affect economy and human health, and they are recognized as one of the major threats to biodiversity. Among them, alien insects cause a multitude of negative environmental impacts and billions of dollars in economic losses annually (Kenis et al. 2009; Vila et al. 2009; Roy et al. 2011; Simberloff et al. 2013; Jeschke et al. 2014). From a general point of view in forest ecosystems, it is mainly xylophagous invasive pests (e.g. the Asiatic *Anoplophora* species) that are responsible of higher environmental and economic impacts (Vaes-Petignat and Nentwig 2014). Fruiting structure insects are for their part generally considered the most important predators of tree seeds during the pre-dispersal phase of development (Turgeon et al. 1994; Auger-Rozenberg and Roques 2012). In this section, we will detail the different impacts that can be caused by the invasive fruiting structure insects in Mediterranean forest ecosystems. Because there is no specific data on the impacts of the *Eucalyptus* galling wasp *Quadrastichodella nova*, we will focus on those estimated in invasive conifer pests, namely the spermatophagous chalcid species (*Megastigmus* spp.), and the Western conifer seed bug.

¹¹Seedborne dispersal is referred to as man-aided displacement of infested seeds through seed trade.

¹²See Chap. 4 about the adaptive significance of prolonged diapause in populations of fruiting structure insects.

9.5.1 Ecological Impacts

The ecological impact of an invasion refers to the effect(s) that an established invasive species may have on a community at different levels of biological organization (Shea and Chesson 2002). Communities invaded by alien invasive species experience new species assemblages leading to novel interspecific interactions with potentially strong effects on the dynamics of both communities and invaders. This makes ecological impacts of invasive fruiting structure difficult to predict. They may occur at the genetic level through hybridization, and/or at the individual, population and community levels through seed consumption and competition for this resource or through transmission of diseases or parasites to native species (Kenis et al. 2009; Vaes-Petignat and Nentwig 2014).

9.5.1.1 Genetic Effects

Genetic effects through hybridization between invasive and native species of insects and other terrestrial invertebrates remain largely unexplored, whereas it is known to be the main type of impact for birds for example (Kenis et al. 2009; Langor and Sweeney 2009; Kumschick et al. 2015). Some examples are known on pollinating insects including species of honeybees and bumblebees in Mediterranean ecosystems, but cases of fruiting structure insects are largely unknown. The opportunities of hybridization depend on the presence of native species close to invasive species, which is not the case of the hymenopteran species on Eucalyptus (Kim and La Salle 2008, <http://www.nhm.ac.uk/research-curation/research/projects/chalcidoids/data-base/>). This is also not the case of *Leptoglossus occidentalis*, which is the only one species of the genus present in Europe, whereas the other occur only in Nearctic and sub-tropical regions (Brailovsky 2014). Conversely, resident and invasive species of the *Megastigmus* genus live in sympatry in the Mediterranean Basin, e.g. *M. pinsapinis* and *M. schimitscheki* on cedar (respectively), but no trace of genetic hybridization was yet detected between them. Intermediate morphotypes linked with intermediate genetic distances were however observed between the fir chalcid *M. suspectus* and *M. pinsapinis* (Auger-Rozenberg et al. 2006). This could indicate a species complex structured by host genus, rather than hybrids, so as both *M. suspectus* and *M. pinsapinis* exhibit thelytokous parthenogenesis and probably a loss of sexual function in females or in both sexes (Boivin et al. 2014).

9.5.1.2 Population and Community Effects

Effects on Host Populations As external seed predators and spermatophages, invasive populations of *L. occidentalis* and *Megastigmus* spp. (respectively) directly affect seed viability, potentially leading to similar demographic and evolutionary impacts on Mediterranean host populations as those associated with native insect

communities.¹³ Briefly, insect damages to seeds may influence: (1) host spatial dynamics through interferences with natural regeneration processes (Tamburini et al. 2012), and (2) host evolution if insects differentially decrease seed production among trees that vary individually in some heritable traits (Kolb et al. 2007). Invasions of seed insects might result in greater seed damages in invaded areas in the two following ways: (1) when hosts are evolutionarily naïve regarding their invasive seed predators so they did not develop adequate defence mechanisms (Raffa et al. 2008), or more likely (2) when seed predation rates by invasive predators cumulate to those of native seed predators (Auger-Rozenberg and Roques 2012; Lesieur et al. 2014). In the latter case, the impact of an invasive species on host dynamics can be hardly disentangled from that of native ones. Moreover, the long term effects of an invasive seed predator on a host population remain difficult to establish without clarifying the dynamics of the interactions that may arise with the other seed predators of the recipient community. In a community of seed specialists, niche overlap is the source of strong interspecific competition that may affect the demography of both invasive and native species, potentially maintaining global seed damage at a lower level than the sum of the damages caused by each species in the absence of a competitor. This has been shown in southern French natural stands of *Cedrus atlantica*, where the demographic growth of the invasive seed chalcid *M. schimitscheki* has progressively driven the sympatric populations of the resident *M. pinsapinis* to nearly extinction in about 10 years (Fig. 9.5). This contrasted with the stationary state of its allopatric populations escaping competition. As a result, the global seed infestation percentage in sympatric areas progressively converges towards that of the dominant chalcid species. This demonstrates that interspecific interactions in fruiting insects can modulate, in the long term, the cumulative effect of an invasion on seed outputs in invaded host populations.

Finally, invasive fruiting structure insects may affect native host populations through the potential transmission of diseases or parasites. Nevertheless, little data is available on the transmission of fungal diseases in the Mediterranean Basin, but *Leptoglossus occidentalis* may be a likely vector of *Diplodia pinea*, a native fungal disease which causes a tip-blight of the crown of Mediterranean pines (Luchi et al. 2012).

Effects on the Indigenous Entomofauna The outcome when an invasive species faces an indigenous species that uses the same resource may be coexistence, competitive displacement of the indigenous species or extinction (Sakai et al. 2001; Reitz and Trumble 2002). Shared ecological specialization on a discrete resource is perceived as one of the reliable predictors of competition in insect communities (Denno et al. 1995). Ecological specialization is indeed a mechanism that limits the possibility of refugia, which is particularly prone to enhance species niche overlap and consequently to strengthen interspecific competition. This may have a particular meaning for native and invasive fruiting structure insects that display high degrees of specialization at both the resource and host plant levels. Moreover,

¹³ See Chap. 4.

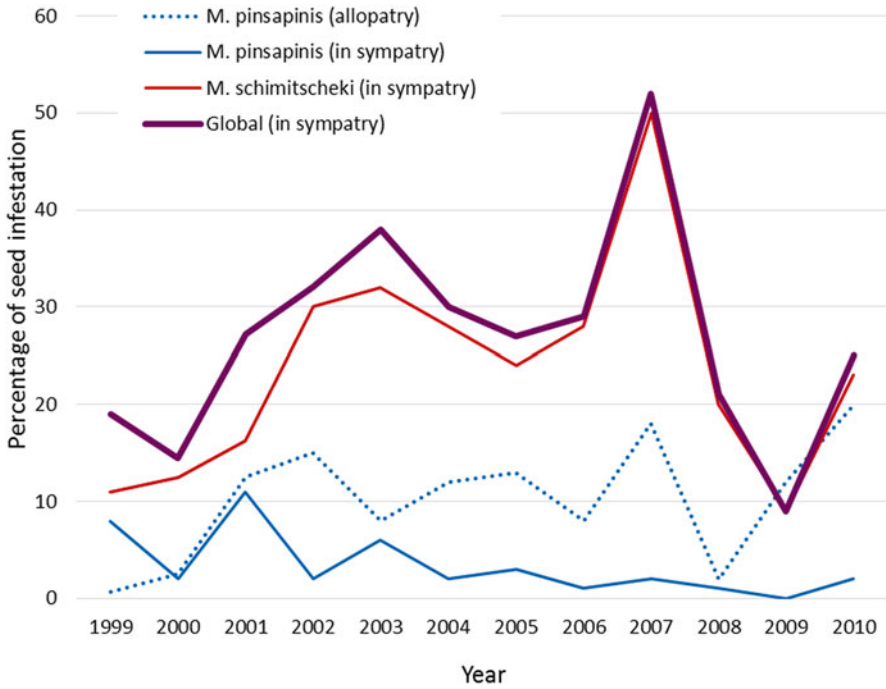


Fig. 9.5 Temporal pattern of the mean seed infestation percentages by the competing seed chalcids *Megastigmus schimitscheki* (invasive since 1994) and *M. pinsapinis* (resident) in southern French stands of *Cedrus atlantica*

biological invasions generally produce novel species assemblages of specialists that share the same host but that did not co-evolve, which may prevent diverse ecological factors (e.g. antagonists, mutualists and host plant effects) from modulating the strength of competition and then restrict coexistence opportunities (Ness and Bronstein 2004; Smith et al. 2008).

In southeastern France, cedar seed chalcids provided recent evidence that an absence of such ecological competitive trade-offs can lead to competitive displacement rather than stable coexistence in specialist invaded communities (Fig. 9.5). The invasive *Megastigmus schimitscheki* displays a long-term negative impact on the resident *M. pinsapinis*, through a resource pre-emption that results from both earlier phenology and larvae's cannibal behavior (Boivin et al. 2008; Gidoïn et al. 2015). Similar niche replacement has been presumed in most French Mediterranean fir stands, where the invasive *M. rafni* has become the dominant seed chalcid species by displacing the native *M. suspectus*, following an important secondary spread in the 1990s (Roques 1983; Auger-Rozenberg and Roques 2012). Conversely to *M. schimitscheki*, *M. rafni* has the latest spring emergence, which results in a delayed access to the seed resource compared to other fir chalcid species and thus precludes niche replacement through resource pre-emption. If several factors may explain the

invasion success of *M. rafni*,¹⁴ the mechanisms driving its negative impact on native fir entomofauna are still unclear. However, interspecific competition in seed chalcids is not necessarily the rule as *M. pinus* has been increasingly observed in natural southeastern French stands of *Abies alba*, coexisting with *M. rafni* or with both *M. rafni* and *M. suspectus* (Auger-Rozenberg and Roques 2012).

9.5.2 Economic Impacts

Many recent studies review the socio-economic impacts of alien arthropods in Europe (Langor and Sweeney 2009; Vila et al. 2009; Vaes-Petignat and Nentwig 2014), and the importance of ecosystem services provided by insects is important and it is now obvious that their disruption can produce enormous costs. Nevertheless, few impact assessment studies exist for fruiting structure insects in Mediterranean forest ecosystems. When they do exist, they are often related with seed trade and have taken place in intensively-managed seed orchards and plantations for example, not in natural stands (Auger-Rozenberg and Roques 2012). Economic impacts due to the other invasive *Megastigmus* species (i.e. associated with firs) are far less known.

The seed bug *Leptoglossus occidentalis* is regarded as a major economic pest in the seed orchards designed to produce genetically superior tree seeds in the native American range. In France, bug damages could be a threat for yields in high-value seed orchards but they reached higher levels in natural stands (up to 25 % and 70 %, respectively) (Lesieur et al. 2014). Moreover, this pest could have a negative impact on the production of pine-seeds for human consumption in Italian stone pine stands (Bracalini et al. 2013). The bug is besides often considered an urban pest, causing alarm and social nuisance when swarms of adults invade buildings for overwintering and damage common plumbing material (Tamburini et al. 2012). Accurate identification of seed bug damage is very difficult because damage is not visible externally on fed-upon seeds, and internal damage (revealed through seed dissection or radiography, provided availability of such monitoring techniques in Mediterranean countries) may have been caused by weather, poor pollination, or other environmental factors rather than seed bug feeding. Bugs impacts are then easier to evaluate in planted and/or managed forests than in natural and unmanaged woodlands.

¹⁴ See Sect. 9.4.

9.6 Conclusion

Forest ecosystems of the Mediterranean Basin host only four non-native species of insect of tree reproductive structures. These include both the spermatophages *Megastigmus rafni* and *M. pinus* and the external seed predator *Leptoglossus occidentalis* that were introduced from North America, and the inflorescence feeder *Quadristichodella nova* that was introduced from Australia. To these species can be added three other spermatophages, *M. schimitscheki*, *M. wachtlei* and *M. pinsapinis*, that are native to the Mediterranean Basin but that accidentally spread across this area from their native sub-regions. Thus, a total of seven species can be regarded as comprising invasive populations within forest ecosystems in the Mediterranean Basin. This contrasts with evidence of higher invasion pressure of fruiting structure insects in Northern Europe, where no less than 11 species have been introduced from all over the world as regards solely the *Megastigmus* genus (DAISIE European Invasive Alien Species Gateway: <http://www.europe-aliens.org>, accessed 29th May 2015). The multiple factors explaining such discrepancies are still difficult to assess, partly because many taxonomic uncertainties remain within such insect communities, and because many areas and host tree species remain to be sampled in the Mediterranean Basin. However, one could primarily speculate that both bioclimatic and vegetation specificities of the Mediterranean Basin provide a poor fit with those of the main provider areas of invasive forest insect species, e.g. China, Northern America or Africa. This may constitute a greater barrier to invasion success, especially since most fruiting structure insect species are specialists at both resource type and host scales. Little is known about the potential for other Mediterranean areas worldwide to be, or to become, substantial contributors to invasive entomofauna on tree reproductive structures in forest ecosystems of the Mediterranean Basin.

The case studies described in this chapter provide evidence that propagule pressure, chance events, ecological traits of invasive species and the properties of invaded ecosystems may be of primary importance to explain both invasion success and invasion impacts in Mediterranean forests. Once introduced and established, alien species may spread through both natural and human-aided dispersal (Hulme et al. 2008). A more and more common phenomenon is hereafter known as the bridgehead effect, namely a primary site of invasion with other territories subsequently invaded from this site. This process has been already revealed in diverse forest insects in the Mediterranean Basin, e.g. the maritime pine bast scale (Kerdelhue et al. 2014) and the red palm weevil (Rugman-Jones et al. 2013). We postulate here that the life cycle and the ecological features of fruiting structure insects make them ideal candidates for bridgehead effects, as recently demonstrated with the dispersal of the Western conifer seed bug *Leptoglossus occidentalis* in whole Europe (Lesieur 2014) and as suggested in the cedar chalcid *Megastigmus schimitscheki* (Auger-Rozenberg et al. 2012). It is likely that European populations of invasive fruiting structure insects could act as a bridgehead for latter invasions in

the Mediterranean Basin, and beyond, especially in the context of unregulated international seed trade.

The management of this type of invasives may involve similar crop-monitoring and prophylactic techniques as those described for native species in Chap. 4 (Sect. 4.7). However, it is clear that an effective control of introduced populations would primarily rely on a considerable improvement of regulation measures in seed trade to minimize the risk of new introductions. Since the mid-1990s, globalization and worldwide movements of goods have drastically accelerated accidental introductions of exotic insects developing within seeds of cultivated or ornamental plants. Reasons for this include: (i) cones and seeds of woody plants are excluded by European Union directives from any controls at import from non-European countries, and (ii) cryptic insect life cycles impede detection and phytosanitary interventions (Auger-Rozenberg and Roques 2012). One such example is the *Megastigmus* genus cited in this chapter. In this context, the development of effective monitoring and control strategies that are specific to invasive populations strongly depend on our ability to disentangle the processes of post-establishment spread in the Mediterranean Basin. Most of current field survey methods detect populations only once they are relatively large and already serving as sources of emigrants. We emphasize a crucial need for monitoring programs aiming at detecting populations at an early stage of establishment, involving new alternative survey techniques, e.g. a suction trap network in case of windborne invasive populations (Lander et al. 2014). Given fruiting structure insects are generally highly host plant specialized, integrating specific monitoring of ornamental host specimens could provide valuable insights into the contribution of spatially isolated host individuals as stepping stones in population spread.

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