

1.A. Detailed description of the research area and research plan

Context of the proposal

Biological invasions (bioinvasions) are defined as the successful establishment and spread of species outside their native range. They act as a major driver of global changes in species distribution. Diverse organisms and ecosystems may be involved, and although not all invasions have a negative impact, the ecological consequences often include the loss of native biological diversity and changes in community structure and ecosystem activity. There may also be additional negative effects on agriculture, forests, fisheries, and human health.

National governments, intergovernmental structures like the European Commission and international organizations such as EPPO, CABI and IUCN have therefore mobilized to (i) introduce international laws on invasive species, (ii) organize international networks of scientists and stakeholders to study bioinvasions, and (iii) formalize the cooperation between national environmental or agricultural protection agencies (e.g. the French Agence Nationale de Sécurité Sanitaire, ANSES). Several billion euros are spent annually to address the problems caused by bioinvasions and the scientific community has focused on predicting and controlling future invasions by understanding how they occur. A peer-reviewed journal entitled "Biological Invasions" has been published since 1999. Ecologists have long drawn attention to the negative ecological effects of invasive species, whereas the evolutionary aspects of bioinvasions have received comparatively little attention. This reflects the fact that: i) invasive populations were thought to experience significant bottlenecks during their introduction to new environments and thus possess a limited potential to evolve; and ii) evolution was considered too slow to play a significant role given the relatively short timescale of the invasion process. However, interest in the evolution of invasive populations emerged in the 1990s when advances in DNA sequencing allowed the reconstruction of geographic pathways and evolutionary histories. Concurrently, quantitative genetic studies uncovered patterns of phenotypic evolution associated with invasion events. The evolutionary processes and genetic attributes of invasive populations are now considered important for their success.

Although case studies of rapid evolutionary changes linked to bioinvasions are accumulating, few research programs have attempted to address specific genetic mechanisms underlying adaptive evolution during invasions, and only in simplified systems. The evolutionary forces that generate populations with a greater propensity to invade are largely unknown, but the development of new molecular tools for genome-wide analysis and their integration with targeted experimental studies now makes this goal achievable.

One of the principal objectives of this proposal is to decipher the adaptive changes that occurred during the invasion of the harlequin ladybird (*Harmonia axyridis*) through the close integration of evolutionary genomics with experimental studies.

Another main scientific theme for the Biodiversa call is about the demonstration and characterisation of the impacts of biological invaders. Recent studies provide evidence that introduced populations of *H. axyridis* compete with indigenous ladybird species and ultimately cause their decline. We recently discovered that *H. axyridis* carries a high load of obligate parasitic microsporidia in its hemolymph, which can be transferred to native ladybird species when they feed on microsporidia-contaminated *H. axyridis* eggs or larvae. The parasites carried by *H. axyridis* therefore appear to be used as biological weapons against native intraguild predators. In this project, we also propose to determine whether and to what degree the negative impact of biological invaders can be attributed to *H. axyridis* and its ability to conduct 'germ warfare'.

***Harmonia axyridis*: an emblematic invasive species and a model to study contemporary adaptations**

H. axyridis originates from eastern Asia and has been widely used as a biological control agent, particularly in North America and Europe. *H. axyridis* has been introduced intentionally many times since 1916 but established populations were not observed before 1988 in the

USA, 2001 in Belgium and 2004 in England^{1,2}. *H. axyridis* is now also found in South America and South Africa. The main negative impacts¹ include: biodiversity deterioration through non-target prey and intraguild predation; pullulation in houses (often causing allergies); and the deterioration of taste and quality in fruit products, including wine. Population genetic analysis carried out by the French applicants in this proposal have reconstituted the distribution modes and invasion routes of *H. axyridis* over the whole invaded area with a high level of precision and confidence, and have demonstrated the nature and intensity of the accompanying demographic events³. These studies have shown that the native range has been the origin of two independent principal foci in the East and West of North America. It is not clear whether these were accidental or related to the introduction of populations for biological control. Europe seems to have been invaded by a mixture of individuals originating from Northeast America and a biological control strain imported from Asia by INRA. Finally, the invasive foci in South America and South Africa probably originate from the invaded area in Northeast America. The long delay between the first (intentional and targeted) introductions and the worldwide invasion suggests that evolutionary shifts have been needed to achieve invasive success. The French applicants on this proposal have therefore initiated quantitative genetics studies of several life-history traits that may be decisive for invasion. Noticeably, the biocontrol individuals have a poor survival rate during quiescence at low temperatures and suffer significantly more from fungal infection than individuals collected from different native or invasive populations⁴. This suggests that mass rearing of biocontrol agents can induce genetic changes in life-history traits that are important for the success of field releases or for the evolutionary trajectory of wild populations, providing an appealing explanation for the inability of biocontrol populations to establish themselves for longer periods following the many releases that have been attempted to encourage acclimation. These studies have also revealed the existence of significant differences in several life-history traits between native and invasive populations of *H. axyridis*. Invasive individuals have shorter generation times and higher fecundity than native populations without paying a cost in terms of life expectancy⁵ (also B. Facon, unpublished results). Invasive populations also do not appear to experience the inbreeding depression suffered by native populations. Therefore, rather than posing a barrier to invasion as often assumed, bottlenecks may enable the evolution of invaders by purging deleterious alleles and maintaining fitness even when inbred⁵. Based on interspecific comparisons and biochemical analysis, the German and Belgian applicants in this proposal have characterized two further traits that may have played an important role in the invasive success of *H. axyridis*⁶: a strong immune response (reflected by the production of large numbers of antimicrobial peptides⁷ and the alkaloid harmonine⁸) and a spectacular aggregation behavior (linked to recently-identified pheromones). Thus far, these traits have been characterized in populations representing only a small area within the global invasive range of *H. axyridis* (i.e. Germany and Belgium). The Belgian applicant is studying the aggregation behavior of *H. axyridis* inside buildings and dwellings during unfavorable winter conditions, which allows the invasive beetle to survive cold winters in the invaded areas⁹. Overwintering aggregation behavior in *H. axyridis* involves five steps¹⁰. First, ladybirds leave feeding sites and orientate to the macrosite, defined as the visual feature on the horizon towards which ladybirds fly to aggregate. Second, the beetles alight on the surface of the macrosite. Third, they choose to stay or not

¹ Koch (2003) J Insect Sc 3:1-16; ² Majerus et al. (2006) Ecol Entomol 31: 207-215; ³ Lombaert et al. (2010) PLoS ONE 5: e9743; ⁴ Tayeh et al. (2012) Evol Appl 5: 481-488; ⁵ Facon et al. (2011) Curr Biol 21: 424-427; ⁶ Schmidtberg et al. (2013) Biol Letters, in press; ⁷ Vilcinskas et al. (2013) Proc Royal Soc B 280: 2012-2113; ⁸ Röhrich et al. (2012) Biol Letters 8:308-311; ⁹ Labrie et al. (2008) Ann Entomol Soc Am 101: 860-866; ¹⁰ Nalepa et al. (2005) Env Entomol 34: 425-431

according to the substrate features. Fourth, they search for a microsite shelter wherein ladybirds take refuge to overwinter. Finally, they settle at the microsite. The Belgian applicant has shown that pheromones and other area-marking semiochemicals are involved in the process of aggregation site selection in invasive strain of *H. axyridis*^{11, 12} although there are no data concerning the ability of native *H. axyridis* strains to produce, release and perceive semiochemicals in the aggregation process.

Overall objective and main challenge

This project aims to decipher the adaptive pathways underlying the global invasive success of *H. axyridis* and to assess the negative impacts on native ladybird species. We will carry out genome-wide comparisons of appropriate populations (native, invasive and biocontrol) taking demographic history into account to avoid erroneous inferences from genomic regions under selection. Such misinterpretations can occur if populations have recently endured extreme demographic events (bottlenecks and admixtures). We will avoid this potential pitfall by using an interdisciplinary approach combining genomics, population genetics modeling, statistics, and experimental evolutionary biology.

More specifically, we will improve on the traditional blind population comparison approach by 1) using improved statistical methods and simulation studies to help with the interpretation of results, 2) complementing the data using a candidate-trait approach focusing on the adaptive response of three traits already known to have evolved during invasion as well as two traits that, based on interspecific comparisons and biochemical analysis, may have play an important role in the invasive success of *H. axyridis*. Three traits are known to have evolved during invasion but there are no data concerning their genetic determinism, so we will use experimental selection to produce laboratory populations that have evolved new phenotypes for each of these traits. Genome-wide comparison of these laboratory-evolved populations will provide insight into the adaptive pathways in a simplified context, identifying the corresponding genomic regions. There are some data available for the other two candidate traits, i.e. harmonine biosynthesis and antimicrobial gene expression for the strong immune response and pheromone production for the aggregation behavior, but it is unclear whether these traits differ among native, invasive and biocontrol *H. axyridis* populations. We will therefore carry out quantitative genetics experiments to investigate potential adaptive shifts during invasion by testing for consistent phenotypic differences exist between native, invasive and biocontrol populations, and match these data against the genome-wide comparisons to determine the nature of evolutionary changes during invasion.

Specific objectives and associated challenges

The scientific program has been divided into six work packages, each led by the most competent expert scientists involved in the project.

WP.01: DEVELOPMENT OF GENOMIC AND TRANSCRIPTOMIC RESSOURCES/DATA AND ASSOCIATED STATISTICAL METHODS

Task coordinators: A. Estoup, H. Vogel

Task participants: M. Gautier, A. Loiseau, A. Vilcinskas, R. Lehmann, H. Ringys-Beckstein, S. Gebauer-Jung, a PhD student, and a 24-month post-doctoral scientist.

We will optimize available *H. axyridis* genomic and transcriptomic resources, produce new genomic and RNA-Seq data for the various populations studied in WPs 03-05 and improve available statistical methods or develop new ones to identify genomic regions with selection

¹¹ Verheggen et al. (2007) J Chem Ecol 33: 2148-2155; ¹² Durieux et al. (2012) J Ins Phys 58: 801-807

signatures from population SNP data. Over the last two years, the French applicants have produced a large amount of *H. axyridis* genomic data (de novo genome sequences from various shotgun sequencing projects, as well as preliminary population genomic data from RAD sequencing) and the German applicants have produced *H. axyridis* transcriptomic data. We will pool these large NGS datasets into a single genomic resource (i.e. first annotated draft assembly for the ~350 Mb *H. axyridis* genome) and expand the NGS dataset mainly through the production of RAD or shotgun sequence data using population pools to reduce costs in order to answer the evolutionary questions posed in the other WPs. Genome sequencing and annotation will be enhanced by generating a tissue- and treatment-specific expression map of *H. axyridis*, including a wide range of tissues from adults, different larval instars and pupae. This transcriptome will be assembled de novo to generate a backbone, which will be used to map individual tissue, developmental and treatment-specific RNA-Seq data (see WP.04) and to support gene identification in the genomic datasets. In turn, the genomic draft assembly will be used to map the transcriptome data from the different developmental stages and the RNA-Seq data obtained from the different *H. axyridis* populations. For comparison, we will also use RNA-Seq to generate tissue- and treatment-specific expression maps of two native European ladybird species (*Coccinella septempunctata* and *Adalia bipunctata*), which are endangered by *H. axyridis* (see WP.06 for details).

We will identify genomic regions involved in laboratory-based experimental evolution and during natural invasions using established statistical methods as well as new ones developed by Mathieu Gautier in collaboration with researchers from the INRA-sponsored IGGIPop “jeune équipe” group specializing in statistical methods applied to population genetics and genomics (also located at CBGP).

Risks: The production of genomic resources and data is in progress and there are no substantial risks at this stage. If it may not be possible to produce new and more relevant statistical methods, we will rely on already established ones.

WP.02: SIMULATION-BASED INVESTIGATIONS TO DETERMINE GENOMIC SIGNATURES OF ADAPTATION

Tasks coordinators: M. Gautier, A. Estoup

Task participants: B. Facon (in collaboration with the main author of the software QuantiNemo, i.e. Dr S. Neuenschwander, University of Lausanne, Switzerland)

We will use the individual-based, genetically explicit stochastic simulation program QuantiNemo¹³ to simulate appropriate datasets. QuantiNemo was developed to investigate the effects of selection, mutation, recombination and drift on quantitative traits with varying architectures in isolated or structured populations connected by migration and located in different habitats. The program is highly flexible at various levels, e.g. population models, selection features, trait architecture (especially the number of genes involved), neutral marker types (SNP or microsatellites), genetic maps for QTLs and/or markers, environmental features, demography and mating system. In order to fit the situations studied in WPs 03 and 05, the datasets simulated using QuantiNemo will verify appropriate designs regarding the above components. We will use the statistical methods described in WP.01 to identify key genomic regions that will be used to analyze the datasets simulated with QuantiNemo. These simulation-based studies will allow the proper interpretation of genome analysis data in this project.

Risks: AE and MG both have expertise in simulation-based testing of the robustness and power of population genetics methods. CBGP has sufficient computer resources. S. Neuenschwander has agreed to provide help with QuantiNemo if necessary. We therefore believe there are no major risks in this work package.

¹³ Neuenschwander et al. (2008) *Bioinformatics* 24: 1552-1553

WP.03: LABORATORY SELECTION EXPERIMENTS AND THE GENETIC BASIS OF THREE TRAITS THAT EVOLVE DURING INVASION

Task coordinator: B. Facon

Task participants: A. Estoup, B. Serrate, A. Loiseau, a two-year temporary appointment (CDD level AI), and an engineer (recruitment at the end of 2013).

In this work package we will carry out laboratory experiments to mimic adaptive shifts that may occur during the introduction of invasive species into a novel environment. The first objective will be to measure the adaptive response (amplitude, speed and associated trait shifts) of three traits known to be associated with invasiveness in *H. axyridis*. We will then analyze the genomic basis of the phenotypic changes in evolved populations. This will i) validate the genomic tools acquired in WP.01, ii) provide information on the genetic architecture of these traits (a small number of major genes vs. a large number of weak-effect genes) and the homogeneity or heterogeneity of evolutionary trajectories among replicates, and iii) provide candidate genes/genomic regions, which we will monitor during the analysis of field populations in WP.05. The three traits we will study are cold resistance¹⁴, generation time and inbreeding depression⁵, all of which have played a role during invasion in *H. axyridis* and show phenotypic differences among native, invasive and biocontrol populations. The experiments will involve a native *H. axyridis* population (probably from China) or an invasive population with significant phenotypic and genetic variation (e.g. Southeastern French population). Before selection experiments per se, we will determine the amount of genetic variability for these three traits in the F₁ generation. If the standing genetic variation is so low that it will compromise the experiment, we will create an artificial *H. axyridis* population by mixing several populations from the native area. As with any admixture, this will create undesirable linkage disequilibria, which we will reduce by allowing the populations to evolve for 4-5 generations.

From the initial population, we will establish five selected and five control lineages per trait. For generation time, we will select for both higher and lower trait values. For cold resistance, we will select only for greater resistance since the imposed selection pressure (cold shock) kills individuals with lower trait values. For inbreeding depression, we will create serially inbred (full-sib crosses) and control lines. Preliminary results suggest that deleterious mutations may be purged in as little as three generations.

The mean generation time is approximately one month. We will therefore let the experiment run for each trait for 8-10 generations before measuring the phenotypic responses of both the trait under selection and other major fitness traits (e.g. fecundity and larval survival) to the different selection regimes, in order to detect potential trade-offs. Inbreeding depression will be measured on egg hatching and larval survival. We will then carry out a comparative whole-genome analysis of the control and selected lines using the high-density SNP markers developed in WP.01. The genomic data will be analyzed in the light of recommendations obtained in WP.02. Ultimately, this will identify a number of genomic regions that have responded to artificial selection.

Risks: The main risk reflects the potential failure of experimental evolution. However, the applicants are experts in the rearing of *H. axyridis* in the laboratory and using this species for experimental evolution and selection studies, and it is already known that standing genetic variation exists in natural populations for the three chosen traits. Failure in this task also does not compromise the natural population aspects of the project.

WP.04: QUANTITATIVE GENETIC ANALYSIS OF PHENOTYPIC DIFFERENCES IN AGGREGATION BEHAVIOR, IMMUNITY AND STRESS RESPONSES BETWEEN THE THREE TYPES OF *H. AXYRIDIS* POPULATIONS

¹⁴ Lombaert et al. (2008) *Biocontrol* 53: 89-102

Task coordinators: F. Verheggen, A. Vilcinskas

Task participants: H. Vogel, H. Schmidtberg, R. Röhrich, R. Lehman, H. Ringys-Beckstein, S. Gebauer-Jung, E. Joie, A. Vandereycken and two PhD students

The aim of this WP is to determine whether aggregation behavior, immunity and stress responses have evolved during *H. axyridis* invasions. We will study phenotypic differences using quantitative genetics from first principles (e.g. for aggregation behavior caused by pheromones and hormones, and the unusually strong immune response).

The aggregation behavior observed in autumn and winter in most invaded areas is induced by volatile and non-volatile molecules produced by *H. axyridis* specifically at this time of year. These molecules guide the individuals toward aggregation sites over long and short distances. We will collect the semiochemicals that guide this aggregation behavior, separate them by gas chromatography and quantitatively identify them by mass spectrometry to determine differences in composition and quantity in the three *H. axyridis* populations. We will focus on two groups of semiochemicals: (1) beta-caryophyllene, previously shown to attract individuals at a distance and induce aggregation¹¹ and (2) non-volatile cuticular hydrocarbons (including saturated and unsaturated C23 to C31), which are deposited on the surface the beetles are exploring to guide individuals toward their aggregation site. The Belgian applicants have previously shown that aggregation behavior is present in autumn/winter but not in spring/summer (Durieux et al, unpublished). We propose a hypothesis that the three *H. axyridis* populations will show different behavioral responses toward the aggregation-promoting semiochemicals discussed above. Behavioral assays will be carried out using mixtures of overwintering individuals and individuals belonging to the three strains. Finally, electrophysiological assays will be carried out to study differences in the organization of the antennal olfactory system, which allow the beetles to perceive these semiochemicals.

The innate immunity and stress responses (e.g. heat shock response) will initially be studied by the comparative analysis of immune competence and stress-related traits in the three different populations of *H. axyridis*. Candidate genes will then be identified by comparing RNA-seq-based gene expression dynamics between non-challenged and immune-challenged beetles, and between non-challenged beetles and those subjected to abiotic stress conditions such as heat shock or water deprivation. These comparisons will be carried out using the three different *H. axyridis* populations and also the native European ladybird species *C. septempunctata* and *A. bipunctata*. The data will enable us to compare the native and invasive ladybird beetle populations at several levels: a) the complexity and number of immune effector and stress-related transcripts, b) the extent of immune and stress responses at the transcriptome level, and c) candidate genes with a specific selection pattern not only between *H. axyridis* populations but also between *H. axyridis* and the two native ladybird species (see also WPs 05 and 06). Finally we will functionally characterize selected immunity and stress related genes using RNAi.

Risks: The participants are experts in the analysis of semiochemicals and behavior (FV) and immunity and stress responses (AV and HV) in a number of species, and we can thus foresee no substantial risks at this stage. Although the effectiveness of RNAi can differ depending on the insect species, this method for the targeted knock-down of transcripts has worked exceptionally well in Coleoptera.

WP.05: IN NATURA GENOMIC STUDIES OF RAPID ADAPTIVE SHIFTS ASSOCIATED WITH INVASION

Task coordinator: B. Facon

Task participants: A. Estoup, A. Loiseau, M. Gautier, F. Verheggen, A. Vilcinskas, H. Vogel, S. Gebauer-Jung, R. Lehman, a PhD student and a 24-month post-doctoral scientist (see WP. 01)

This WP will involve a candidate-trait genomic study using natural populations, focusing on the candidate genomic regions and transcripts identified in WPs 03 and 04. To detect evolutionary

changes that may (at least in part) explain invasiveness, we will first compare several native populations with invasive populations whose introduction history is well known³. We will also compare biocontrol populations and natural populations (from both native and invaded areas) to help explain why biocontrol populations have not become invasive despite repeated introduction attempts. We propose that traits selected involuntarily during the breeding of biocontrol strains in the laboratory could be responsible for this lack of success (e.g., poor cold resistance).

Comparisons between populations from invaded areas will help to identify post-invasion evolutionary changes. We will first compare populations along transects from the core to the front of invasion. This will show whether spatial sorting, which is already known to be associated with heterogeneity in dispersal, also sorts individuals according to other traits (e.g. generation time). We will then test for local adaptation patterns, specifically targeting cold resistance, by comparing populations along latitudinal gradients in both invaded and native areas.

We will particularly seek to determine (i) whether the observed patterns of adaptation are congruent between experimentally-selected populations and natural invasive populations, (ii) whether the observed adaptations result from the action of a few genes with major effects or a large number of genes with weak effects; (iii) the type of selection process involved (positive, balancing, disruptive or background selection); (iv) whether the adaptations are due to the emergence of new variants (mutations) or variants already present (“standing variation”). Finally, the use of several replicate populations from each population type (biocontrol, invasive and native) in all comparisons will determine whether or not evolution consistently relies on the same genetic trajectories (parallel evolution).

In practice, the patterns of differentiation over the entire genome will be analyzed with high-density SNP markers in populations sampled in the field. Pools of 30-50 individuals from each population will be sequenced, as this represents the most cost-effective strategy for the large-scale deployment of this approach¹⁵. The pertinence of this approach will be tested in WP.02. Many samples from native, invasive and biocontrol populations of *H. axyridis* are already available (stored in ethanol). Additional samples will be obtained to complete latitudinal gradients and gradients from the core to the invasive front for each invaded zone.

By comparing “controlled” laboratory approaches and more observational approaches using naturally-evolved populations, this task will provide insight into the suitability of pangenomic SNP markers to i) reconstruct the genetic architecture of traits of interest, and ii) decipher the genetic basis of contemporary adaptation in natural situations.

Risks: The risk here is that the results are inconsistent with experimental selection. WP.02 has been designed to facilitate the interpretation of such results. Even unfavorable result would be of interest from both a methodological point of view (relevance of experimental selection) and a fundamental point of view (evolution proceeding through random genetic pathways)

WP.06: CHARACTERIZATION OF THE ROLE OF *H. AXYRIDIS*-ASSOCIATED MICROSPORIDIA IN INDIGENOUS LADYBIRD DECLINE

Task coordinator: A. Vilcinskis

Task participants: H. Vogel, B. Facon, A. Estoup, H. Schmidtberg, R. Röhrich, H. Ringys-Beckstein and a PhD student

We will experimentally test whether indigenous ladybird species become infected with microsporidia when they feed on *H. axyridis* eggs and larvae by screening for their presence in indigenous ladybird species collected in areas where *H. axyridis* is present or absent. To do so, we will use a variety of previously-described primer sets for the specific amplification of the microsporidial 16S rRNA gene in ladybird eggs and tissues¹⁶. Specimens will be collected from different sites throughout Europe.

¹⁵ Futschik & Schloetterer (2010) *Genetics* 186:207-218; ¹⁶ Vilcinskis et al. (2013) *Science*, in revision

We will also determine (under laboratory conditions) the transferability of *H. axyridis* microsporidia to indigenous ladybird species. Addressing this issue we will expose microsporidia-contaminated *H. axyridis* eggs and larvae to predation by indigenous ladybird species such as *Adalia bipunctata* and *Coccinella septempunctata* to assess the pathogenicity as well as the horizontal or vertical transmission of the introduced microsporidia. We will also analyze DNA samples from microsporidia isolated from *H. axyridis* populations originating from different countries all over the world (provided by the French applicants) to determine how many microsporidial species occur in *H. axyridis*.

Risks: We have tried to reproduce the Harmonia-associated microsporidia in sf9 and other insect-derived cell-lines in order to provide sufficient inocula for experiments, but this was not possible. Thus, the amount of microsporidia that can be purified from ladybird hemolymph limits the experiments that can be performed to test their pathogenicity and virulence against a variety of native ladybird species. However, the most important question whether *H. axyridis* is able to conduct 'germ warfare' can be addressed with the planned combination of field and laboratory studies.

Novelty and originality

The mechanisms underlying successful species invasions are not well understood either generally or at the molecular level, thus the genomic analysis of successful invasions is a highly novel research area. The EXOTIC project will combine genomic and phenotypic approaches in a highly relevant invasive species to identify adaptive genes related to invasive success. This will be achieved by combining genome level and gene expression analysis with the detection of signatures of selection and phenotypic responses to experimental and natural selection for different traits in native, invasive and biocontrol populations. Next-generation sequencing allows the rapid development of genomic tools in non-model organisms, providing an opportunity to gain mechanistic insights into major ecological and evolutionary questions within the timeframe of this project. Understanding both gene regulation signatures of selection in response to new environments in invasive populations will help us to predict the conditions under which successful invasions can be enhanced or suppressed. This in turn increases our functional understanding of the dynamic processes by which insects adapt to new or changing environments, which is necessary to develop efficient solutions to control invasive species.

European added value

The combined expertise of the applicants is highly complementary, providing the foundation for a European initiative that will deliver cutting-edge research on a topic of central importance to both pure and applied science. The partners in the EXOTIC project have been chosen based on their strong record in evolutionary biology, ecological and/or functional genomics, chemical ecology and population genetics. Only by integrating the expertise of all of these partners will there be sufficient competence and synergism to address all the objectives of this project. Understanding the regulation and selection signatures of adaptive genes in insects responding to novel or changing environments, as well as those responsible for stress responses, growth and other metabolic processes, will help us to predict the conditions under which invasiveness can be enhanced or suppressed. The sequence information and expression data generated in the EXOTIC project will be made available, providing information on thousands of genes that may not be directly involved in invasive success or the traits we have chosen for analysis, but may nevertheless improve our general understanding of insect ecophysiology and metabolism, and will therefore be of general interest and value to the research community, providing data for functional genomics research in many areas including systematics, comparative physiology, functional genomics and biodiversity research. The EXOTIC project will also lead to synergistic effects with other

projects related to invasive species or biological pest control, such as the Grand Federative project BIOFIS and FP7 programs “PURE” and “IPRABIO”.

Scientific justification of requested resources

Total budget from French team: 349 973,70 €

- Staff : Total = 167 113,20 €
 - One 24 months post-doc (advanced level) on the analyses of genomic resources and data. Cost: 101 079.12 €.
 - One 24 months technical assistant (INRA level “assistant ingénieur”) in order to help during the course of the experimental selection studies (WP.03). Cost = 66 034.08 €.
- Operating costs : Total = 169 400 €
 - Subcontracting : Total = 110 400 €
 - NGS data production and “basic” bioinformatics treatment involving: two public platforms (MGX, Montpellier, France and/or GenePool, Edimburgh, UK), one private platform (probably MGW, Germany) and sequencing actions to improve HA genome assembly (e.g. PacBio-like technology or mate pair library sequencing): 35 000 €.
 - NGS data production on population pools:
 - 30 laboratory controlled populations (10 populations per traits, 3 traits, 1300 € per pop = 39 000 €) and 28 populations collected in natura (invasion routes and others – e.g. transects, 1300 € per pop = 36 400 €).
 - Missions : Total = 19 000 €
 - Missions related to the project management (6000 €). For the final international workshop, additional funding will be requested noticeably to INRA. We will allocate 1 attendance at an international congress for the requested post-doc and the three researchers (B. Facon, M. Gautier and A. Estoup = 6 000 €). 3) Field trips are planned in native different invaded areas of HA. The presence of international collaborators in each location will allow us to reduce the number of trips and their duration (7 000 €).
 - Other expenses: Total = 40 000 €
 - Computer consumables (especially data storage disk/space): 2 000 €.
 - Food needed for the lab-rearing of HA (Epehestia eggs from a biofactory): 23 000 €.
 - Small equipment for field sampling and experimental studies: 2 000 €.
 - Two computers for the post-doc and one applicant: 3 000 €.
 - Books, publications of articles in scientific journals: 4 000 €.
 - Costs justified by internal invoices: DNA extraction, multiplex PCR, consumables, and entrance fees for the three platforms (Molecular Biology, Rearing and Phenotyping of insects and Computer Cluster): 6 000 €.
 - Overheads: 4% of the requested resources = $336\,513,20 \times 4\% = 13\,460,50$ €.

Total budget of German team: 306.475 €

- Staff : Total = 187.440 €
 - Two PhD students (at TV-L 13 50%) for the entire 36-month period for: analysis of the gene expression (RNA-Seq) data and help in identifying candidate genes between HA populations and the native ladybird species (WP.01 & 04); conducting field collecting of native ladybird populations, identification of microsporidia and performing exposure experiments (WP.04 & 06). Cost: 168.300 €.
 - Two student helper/assistant (Studentische Hilfskraft, SHK) for a period of 24 months in order to help in the lab rearing, field collections and general molecular work during the course of the experimental studies (WP.04 & 06). Cost: 19.140 €.
- The Ph.D. student in the group of AV will attend training courses at the “Giessen-Graduate-School for Life Sciences” (GGL), Section “Bioresources and Biotechnology” to which the supervisor contributes as a lecturer and laboratory trainer. The student assistant is required

for the extensive workload during insect rearing, field collections and to support the PhD student in the general lab work. The Ph.D. student in the group of HV will attend and be trained at the International Max Planck research School (IMPRS). The student assistant is required for the extensive workload and to support the PhD student in the general lab work.

- Consumables : Total = 85.000 €
 - NGS RNA-Seq data generation (transcriptome backbone as well as differential gene expression analyses in several populations and treatments) for HA and both native ladybird beetles (HA with up to 12 populations and 3 populations for each native ladybird species (= number of replicates) and four different treatments = 72 samples. We will utilize the Max Planck Genome Center in Cologne as a platform for the NGS data generation which can be used on a self-cost basis within the MPG: 45.500 €
 - Molecular biology kits and consumables: RNA extraction and analysis (e.g. Agilent Bioanalyzer Chips), DNA extraction, qRT-PCR primers and consumables, Cloning, plasmid minipreps & Sanger sequencing etc: 29.000 €
 - General lab consumables: 4.500 €
 - Consumables for lab-rearing of HA, *C. septempunctata* and *A. bipunctata*: 6.000 €.
- Travel expenses : Total = 19.000 €
 - Project meetings and workshops within EXOTIC project: 5.000 €
 - Attendance of international conferences, congresses and symposia: e.g. Molecular Parasitology Meeting 2015 (2 Ph.D. students, 2 PIs), ISDCI meeting 2014, Evolutionary Biology ESEB meeting 2014 and/or 2015 etc: 10.000 €
 - Field trips for collecting populations of two native ladybird species throughout Europe (A. Vilcinskas and PhD student): 4.000 €
- Other expenses : Total = 3.250 €
 - Publication fees: For publication expenses 750 €/year is approximated and requested. The publications will be open access publications whenever possible. Total for 3 years: 2.250 €
 - Additional computer data storage/disk space: 1.000 €.
- Overheads : 4% of the requested resources = $294.690 \times 4\% = 11.787,60\text{€}$.

Total budget from Belgian team: 110.000 €

The Belgian partner has two running research projects on invasive insect species. One of them is focused on *Harmonia axyridis*, the insect model species of the present proposal. Because the same equipment will be used in this Biodiversa proposal, these two research projects will cover all operating costs (equipment, insect rearing, travels, publications,...). The entire solicited budget (110.000 €) is therefore allocated to a three year-PhD student, who will be in charge of the experimentations to be conducted in WP.04 and 05.

1.B. Communication plan

The information generated in this project will be disseminated primarily in the following ways:

- Via a dedicated EXOTIC project website hosted by the CBGP, with open-access and restricted areas. Computer programs and scripts associated with the statistical proposed statistical analysis will also be made available on the CBGP website (<http://www1.montpellier.inra.fr/CBGP/>).
- After critical data analysis and publication, the EST and genomic sequence data will be contributed to GenBank for general use by the scientific community. Prior to this, at the discretion of the partners, some data may be shared or exchanged with other researchers on a limited basis in order to facilitate comparative studies on EST and genomic data (i.e. groups working on phylogenetic analysis).
- Through workshop reports to be produced by the EXOTIC consortium. These would not constitute peer-reviewed publications, but would allow both project partners and external project reviewers to monitor progress.
- Through publications in prestigious peer-reviewed journals, with priority to open access publications. We recognize peer-reviewed primary publications as the major way to demonstrate the novelty and relevance of our work. Taking into account our interdisciplinary approach, many of these papers should be cosigned by several partners.
- Through the publication of graduate student theses from this project.
- Through participation at events such as international congresses (e.g. Ecological Society of America, ESEB) and workshops, in order to communicate our most recent results to the scientific community and exchange ideas with other groups with similar interests. We also envisage joint meetings with other Biodiversa-related scientific groups or funded projects.
- EXOTIC will also benefit from the participation of the French applicants in the Grand Federative project BIOFIS (Bioagressors and invasive species: from individual to population to species) of Montpellier Agropolis Foundation (2010-2014). One objective of BIOFIS is to formalize recommendations in management practices against bioagressors and invasive species. We will thus capitalize on this growing network (mainly national services such as ANSES, technical institutes, producers) to boost the dissemination of the EXOTIC research results to other scientists (such as European projects FP7 "PURE" and "IPRABIO") and to non-scientific stakeholders and the general public. An annual newsletter will be published with project updates and findings, and to ensure efficient management planning.
- EXOTIC will endeavor to disseminate key project results to the media, using the communication departments from each partner, to increase public awareness of the nature and risks of biological invasions in terms of both public health and negative impacts on native biodiversity.

At the end of the project, we will organize an international workshop to focus on the role of contemporary evolution in biological invasions, to release new tools and methods that facilitate investigations focusing on the genetic basis of quantitative traits using jointly targeted experimental studies and genomics. This symposium will be open to 1) scientists interested in similar approaches applied to different biological models, 2) experts involved in research into the management/control of invasive species (e.g. ANSES, France; CABI, Switzerland), and 3) stakeholders involved in the management of invasive species or biodiversity conservation. We expect that the information and technology produced in the EXOTIC project will be useful well beyond the project lifespan. The coordinating institution will maintain the project website for at least one year beyond the project cycle.

1.C. Justifications of changes since pre-registration

WP.03. The French applicants have decided to discard one of the four chosen traits because, after careful consideration, it appears more feasible to conduct experimental selection studies in three traits only during the three-year period of the project. We decided to discard body size because it shows the least differences between native, biocontrol and invasive populations of *H. axyridis*.

Very recently, the German applicants discovered that *H. axyridis* carries a high load of obligate parasitic microsporidia in its hemolymph, which can infect native ladybird species such as *Coccinella septempunctata* when transferred. This suggests that native ladybird species can become infected and ultimately killed if they feed on microsporidia-contaminated eggs or larvae of the invasive ladybird because intraguild predation is a major selective force among competing ladybird species, and has been addressed in many recent publications. Establishing our collaboration with the French applicants, we studied populations from different countries all over the world. In each sample, we found the beetles were loaded with microsporidia that clearly caused no harm to the carrier. This unprecedented load of tolerated parasites is plausibly used as a biological weapon against native intraguild predators (Vilcinskis et al., 2013, Science, in revision). The introduction of exogenic pathogens or parasites by invasive species is major threat to indigenous biodiversity, and our recent findings require further detailed analysis to test whether this negative impact of biological invaders can be attributed to *H. axyridis*. We therefore decided to add a new WP (WP. 06) dedicated to this topic. In addition to themes T2 (Understanding mechanisms of biological invasions and levers for mitigating and/or reversing the impacts of biological invaders) and T5 (Biological invasions and adaptation) already addressed by the former proposal, this new WP allows us also to address theme T1 (Demonstrating and characterizing the impacts of biological invaders).

Accordingly with the Belgian contact point (Aline van der Werf), the Belgian applicant decided to increase the requested resources (up to 110000 euros). This budget will be entirely allocated to a three year-PhD student.

2. Time schedule and working programme

	Year 1				Year 2				Year 3			
Months	3	6	9	12	3	6	9	12	3	6	9	12
WP.01	Genome assembly and annotation											
	Transcriptome backbone assembly											
					Methods to identify genomic regions bearing signatures of selection							
WP.02	Simulation-based investigation of genomic signature of adaptation associated with laboratory experimental populations											
					Simulation-based investigation of signature of adaptation associated with natural populations							
WP.03	Sampling and preliminary tests											
			Experiments of selection in the lab									
							Phenotypic measurements and analyses					
							Genome genotyping and statistical analysis of laboratory populations					
WP.04	Semochemical collection, quantification and identification			Electrophysiology								
	Chemical defense profile analyses in HA populations				Immune and stress-related trait assays							
			Gene expression analysis of HA population and species-specific responses to stress									
			Behavioral assays									
			Functional characterization of selected genes using RNAi									
WP.05	Sampling of natural populations											
			Genome genotyping of natural populations									
							Genomic statistical analysis of natural populations					
WP.06	Collection of native ladybird species populations											
			Screen for microsporidia in indigenous ladybird species									
			Assess pathogenicity & transmission of introduced microsporidia in native ladybirds									
			Determine complexity of microsporidian species in HA populations									

3. Description of project management

The EXOTIC project includes three countries: Belgium (three persons), France (six persons) and Germany (two persons) as well as 7 non-permanent staff to be recruited thanks to this proposal. B. Facon (CBGP, FRANCE) will assume the management of the project. The CBGP has a large support infrastructure for international projects and considerable experience in the administration of both EU projects and other non-EU grants.

A symposium (kick-off meeting) will be organized at the beginning of the EXOTIC project at Montpellier, with all project personnel as well as invited experts. This symposium will summarize and potentially refine the scientific objectives and sampling strategies proposed to meet the different goals in the project. All scientific, financial and administrative aspects of the project will be fixed at this point so that the work can begin quickly and efficiently. Short-term objectives will be discussed and the scientists involved will meet to organize an operational schedule for the first 6 months, to ensure that the first deliverables will be achieved on time. This kick-off meeting is especially important because the project partners will rely on the exchange of samples (*H. axyridis* populations) and data throughout the duration of the project.

EXOTIC is a relatively small research consortium (partners from three countries) and does not require a large and complex organizational structure. The underlying philosophy of the EXOTIC project is to focus energy and resources on the scientific elements (by which the success of the EXOTIC project will be evaluated) and to minimize administrative costs and effort to that which is essential for the proper coordination of the project. Each participating institute has a different expertise and the individuals involved in the program are in the best position to judge how the work can be accomplished more efficiently. Thus the organization of the entire consortium will be directed primarily towards the integrative aspects of the research and not the micromanagement of internal functions.

In contrast to many research consortia, EXOTIC does not have a multitude of themes to be addressed in various ways. Instead the program is divided into six different work packages that either share a common methodological approach or common resources (i.e. *H. axyridis* populations). Some of the WPs involve partners from different countries, showing that the project will foster new international collaborations. Each WP will be led by one or two persons in a way that is most appropriate for that WP. This means that it is most appropriate for the team leaders from each institute to be responsible for the individual EXOTIC work packages and these can be handled on an institutional basis.

A committee will be established under the direction of the project coordinator (B. Facon), with representation (at least one member) from each participating institute. To minimize the costs of committee meetings and to ensure scientific efficiency, in most cases the institutional partner represented on the committee will be the same individual as the team leader or work package leader and will therefore be actively involved with the research activities and thoroughly knowledgeable about the research undertaken in the respective group. The function of the committee is to set research priorities, prepare detailed research plans, provide internal guidance to researchers in each work package, prepare meetings and workshops, and evaluate research progress. The committee will be chaired by the project coordinator (B. Facon) and its main task can be summarized as follows:

- Facilitate all individual interactions, as well as group interactions, of the participants. This can be achieved primarily through the co-ordination and hosting of meetings and workshops.
- Provide a focal point for, and conduit through which information and activities can be monitored and coordinated.
- Act as the project “watchdog” to ensure schedules and deadlines are met.
- Provide the interface between the project participants and special interest groups, companies, universities and other relevant organizations.

- Co-ordinate technology transfer, exploitation and information dissemination activities.
- Organize a special meeting to prepare the international workshop described in part 1B. This meeting will aim to explore solutions for additional funding and help for this workshop, and to distribute tasks among participants.

In order to help the participants stay aware of progress and enable the informal exchange of ideas and questions, a wiki-like website will be set up with a discussion forum open to all participants, as well as an updated list of publications related to the project and written by the partners, the planned meetings with their schedules, slide presentations and all documents considered useful for the group.

Once per semester, a general meeting organized by the project coordinator will take place in one of the partner institutes. The duration of each general meeting will be at least one day and the program will have two parts, one devoted to one specified WP and the other to discuss specific points arising in other WPs. For the specified WP, presentations will be more formal and external collaborators will be invited if their skills could help the group on relevant topics. These meetings will have three main goals: (1) to evaluate the results from each WP and check if all deliverables and milestones have been achieved; (2) to schedule activities and strategies for the subsequent 6 months, taking into account previous experience (both failures and successes); and (3) to make decisions about communication strategies. The WP coordinators will also organize specific ad hoc meetings for participants in key tasks if such meetings are required. In addition to these two levels of meetings, and depending on progress, participants (specifically students) will be encouraged to visit the other partner institutions as well as external collaborators when required.

The EXOTIC project will be subject to a Mid-term Assessment at approximately the half-way point. In addition to critical self-examination by the project participants, two external reviewers will be invited to consider the EXOTIC project achievements against stated objectives and milestones. This will include a review of overall progress, as well as that of individual participants, providing an opportunity to analyze the first half of the project and to redefine any goals, milestones or deliverables. The EXOTIC committee will also be able to outline its plans for the remainder of the project. Organization of the Interim Assessment will be undertaken prior to the midpoint, with the intention of organizing the meeting between the project participants and the committee in or shortly after month 18. This will yield an 18-month plan for the second half of the project, which will be formally reported and adopted.

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RESEARCH CAREER

2008 - present: Permanent research position at INRA (Institut National de la Recherche Agronomique) (CR2) at the Centre de Biologie pour la Gestion des Populations (CBGP) in Montpellier, France.

2007 - 2008: Post-Doc at the Centre de Biologie pour la Gestion des Populations (CBGP) in Montpellier, France (Head : Dr Arnaud Estoup).

2006 - 2007: Post-Doc at the Institut of Evolution Sciences, University of Montpellier 2, (France; Head: Prof. Isabelle Olivieri).

2004 - 2006: Post-Doc at the Department of Ecology and Evolution, University of Lausanne (Switzerland; Head: Prof. Jérôme Goudet).

2003 - 2004: Post-Doc at the Laboratory of Animal Biology on the University of Perpignan (France; Head: Dr André Théron).

2000 - 2003 : PhD at the University of Montpellier 2, in the CNRS laboratory CEFE (Centre d'Ecologie Fonctionnelle et Evolutive). Supervisors : Patrice David and Philippe Jarne.

Competencies and interests: Evolutionary biology, biological invasions, quantitative genetics, life history traits, mating systems.

Publications (rank A)

- Tayeh A., ... & B. **Facon** (in Press) Investigating the genetic load of an emblematic invasive species : the case of the invasive harlequin ladybird *Harmonia axyridis*. *Ecology & Evolution*.
- Foucaud J., ..., **Facon** B. et al. (in Press) Thermotolerance adaptation to human-modified habitats occurs in the native range of the invasive ant *Wasmannia auropunctata* before long-distance dispersal. *Evolutionary Applications*.
- Rey O., ... & B. **Facon**. (2012) Where do adaptive shifts occur during invasion? A multidisciplinary approach to unravelling cold adaptation in a tropical ant species invading the Mediterranean area. *Ecology Letters* 15 : 1266-1275.
- Tayeh A., ... & B. **Facon** (2012) Evolution in biocontrol strains: insight from the harlequin ladybird *Harmonia axyridis*. *Evolutionary Applications* 5 : 481-488.
- Macke E., ..., **Facon** B. & I. Olivieri (2012) Mating modifies female life history in a haplodiploid spider mite. *The American Naturalist* 179: E147-E162.
- Hufbauer R.A., **Facon** B. et al. (2012) Anthropogenically-induced adaptation to invade (AIAI): contemporary adaptation to human-altered habitats within the native range can promote invasions. *Evolutionary Applications* 5: 89-101.
- Lawson Handley L-J., ..., **Facon** B., et al. (2011) Ecological genetics of invasive alien species. *Biocontrol* 56: 409-428.
- Rey, O., Loiseau, A., **Facon**, B.... et al. (2011) Meiotic recombination dramatically decreased in thelytokous queens of the little fire ant and their sexually produced workers. *Molecular Biology and Evolution* 28: 2591-2601.
- Turgeon J., ..., **Facon** B. et al. (2011) Experimental evidence for the phenotypic impact of admixture between wild and biocontrol Asian ladybird (*Harmonia axyridis*) involved in the European invasion. *Journal of Evolutionary Biology*.

- Facon** B. et al. (2011) Inbreeding depression is purged in the invasive insect *Harmonia axyridis*. *Current Biology* 21: 424-427.
- Macke E., ..., **Facon** B. & I. Olivieri (2011) Sex allocation in haplodiploids is mediated by egg size: evidence in the spider mite *Tetranychus urticae* Koch. *Proceedings of the Royal Society B-Biological Sciences* 278: 1054-1063.
- Facon** B., Crespin L., Loiseau A., Lombaert E., Magro A. & A. Estoup (2011) Can things get worse when an invasive species hybridizes? The harlequin ladybird *Harmonia axyridis* in France as a case study. *Evolutionary Applications* 4: 71-88.
- Lombaert E., ..., **Facon** B. & A. Estoup (2010) Bridgehead Effect in the Worldwide Invasion of the Biocontrol Harlequin Ladybird. *Plos One* 5: e9743.
- Escobar* J.S., **Facon*** B., Jarne P., Goudet J. & P. David (2009) Correlated evolution of mating strategy and inbreeding depression within and among populations of the hermaphroditic snail *Physa acuta*. *Evolution* 63 : 2790-2804. (* Ces 2 auteurs ont contribué également à l'article)
- Orivel J., ..., **Facon** B. et al. (2009) Ecologically heterogeneous populations of the invasive ant *Wasmannia auropunctata* within its native and introduced ranges. *Ecological Entomology* 34 : 504-512.
- Facon** B., Pointier J.P., Jarne P., Sarda V. & P. David (2008) Multiple introductions and the evolutionary potential of invasive populations. *Current Biology* 18: 363-367.
- Facon** B., Ravigné V. & J. Goudet (2008) Gender-role alternation in the simultaneously hermaphroditic freshwater snail *Physa acuta*: not with the same partner. *Behavioral Ecology and Sociobiology* 62: 713-720.
- Facon** B., Ravigné V., Sauteur L. & J. Goudet (2007) Effect of mating history on gender preference in the hermaphroditic snail *Physa acuta*, *Animal Behaviour* 74: 1455-1461.
- Chapuis E., Trouvé S., **Facon** B., Degen L. & J. Goudet (2007) High quantitative and no molecular differentiation of a freshwater snail (*Galba truncatula*) between temporary and permanent water habitats. *Molecular Ecology* 16: 3484-3496.
- Facon** B. & P. David (2006) Metapopulation dynamics and biological invasions: a spatially explicit model applied to a freshwater snail. *The American Naturalist* 128: 769-783.
- Facon** B., Ravigné V. & J. Goudet (2006) Experimental evidence of inbreeding avoidance in the hermaphroditic snail *Physa acuta*. *Evolutionary Ecology* 20: 295-406.
- Facon** B., Genton B., Shykoff J., Jarne P., Estoup A. & P. David (2006) A general eco-evolutionary framework for understanding bioinvasions. *Trends in Ecology and Evolution* 21: 130-135.
- Facon** B., Jarne P., Pointier J.P. & P. David (2005) Hybridization and invasiveness in the freshwater snail *Melanoides tuberculata*: hybrid vigour is more important than the increase in genetic variance. *Journal of Evolutionary Biology* 18: 524-535.
- Facon** B., Machline E., Pointier J.P. & P. David (2004) Variability in desiccation tolerance in freshwater snails and its consequences on invasion ability. *Biological Invasions* 6: 283-293.
- Facon** B., Pointier J.P., Glaubrecht M., Poux C., Jarne P. & P. David (2003) Molecular phylogeography reveals invasions are not always rare events: the case of a freshwater snails family, the Thiariids. *Molecular Ecology* 12:3027-3039.

A few communications

2007 Introductions multiples et potentiel évolutif des espèces invasives: le cas de *Melanoides tuberculata* à la Martinique. Colloque « Invasions biologiques et traits d'histoire de vie » - 11èmes rencontres francophones (Rennes, France).

2008 Pour une biologie évolutive des invasions. Conférence invitée. VIIèmes rencontres de phytopathologie/mycologie de la Société Française de Phytopathologie (Aussois, France).

2009 Consequences of hybridization between invasive and biocontrol individuals of the harlequin ladybird *Harmonia axyridis* in France. Meeting du IOBC/WPRS working group "Benefits and risks of exotic biological control agents", Engelberg, Switzerland (IOBC wprs/OILB srop).

2012 Evolution au cours du processus d'invasion: le cas d'*Harmonia axyridis*. Séminaire invité au sein de l'UMR PVBMT à Saint-Pierre (Réunion).

Contributions to research management

2011-2012 Co-leader of the task EMERGE in the INRA meta-program SMaCH (Sustainable Management of Crops Health)

2010- Co-leader of the group « Biology of Adaptation : Genetics, Genomics & Life-history traits » in the CBGP

2010- Elected member of the Scientific Council of the CBGP

2008-2011 Manager of the phenotyping Platform in the CBGP

2010 Co-organizer of the session « Invasions biologiques: au croisement de l'écologie et de l'évolution » at the first national congress of Ecology « Ecologie 2010 » in Montpellier

2005 Co-organizer of the symposium "Evolutionary ecology of invasive species and species invasions", 10th congress of European Society for Evolutionary Biology, Cracow in Poland

2008- Jury for 5 PhD defenses

2012- Member of the hiring committee for 3 permanent positions

Some funded projects

2007-2011 ANR-Biodiversité Project « Etude des invasions biologiques à partir d'introductions intentionnelles et non intentionnelles d'insectes » (headed by T. Guillemaud). Participant.

2009-2010 INRA-SPE Project « Evolution de la résistance d'un insecte ravageur invasif à des agents de lutte biologique : le cas de l'aleurode du tabac *Bemisia tabaci* ». Leader

2010-2014 Grand Federative Project of Montpellier Agropolis Fondation « Bioagressors and invasive species: from individual to population to species » (BIOFIS, headed by A. Estoup & JY. Rasplus). Leader of the task « Key evolutionary questions associated to the emergence of invasive populations: experimental axis ».

Referee

Reviewer for the following journals : Ecology Letters ; Molecular Ecology ; Proceedings of the Royal Society B : Biological Sciences ; Evolutionary Applications ; Diversity & Distribution ; PLoS One ; Biological Invasions ; Biological Control ; Perspectives in Plant Ecology, Evolution & Systematics.

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RESEARCH CAREER

2009 - present: Head of the Department Bioresources at the Fraunhofer Institute of Molecular Biology and Applied Ecology in Giessen, Germany

2006 – present: Managing Director of the Institute of Phytopathology and Applied Zoology at Interdisciplinary Research Center of the Justus-Liebig-University of Giessen, Germany

2004 – present: Full Professor (W3) for Applied Entomology in the Institute of Phytopathology and Applied Zoology at Interdisciplinary Research Center of the Justus-Liebig-University of Giessen, Germany

1999 - 2004: Associated Professor for Evolutionary Biology and Zoology at the Institute of Biochemistry and Biology, University of Potsdam, Germany

1994 - 1998: Post-Doc and Group Leader at the Institute of Zoology, Free University of Berlin, Germany

1992 - 1994: PhD at the at the Institute of Zoology, Free University of Berlin, Germany (Head: Prof. Götz).

1990 - 1991: Research Associate at the Fisheries Board of Berlin, Germany

Competencies and interests: Evolutionary Ecology, Host-parasite-Coevolution, Genome Biology, Insect Biotechnology, Invasion Biology,

Publications (rank A, last 5 years only)

- Schmidtberg, H., C.R. Röhrich, H. Vogel & **A. Vilcinskis** 2013: A switch from constitutive chemical defense to inducible innate immune responses in the invasive ladybird *Harmonia axyridis*. *Biology Letters* in press.
- Mukherjee, K., T. Hain, R. Fischer, T. Chakraborty & **A. Vilcinskis** 2013: Brain infection and activation of neuronal repair mechanisms caused by the human pathogen *Listeria monocytogenes* in the lepidopteran model host *Galleria mellonella*. *Virulence* 4(4): in press.
- Vilcinskis A.** 2013: Evolutionary plasticity of insect immunity. *J. of Insect Physiology*, in press
- Grünwald S., J. Stellzig, I.V. Adam, K. Weber, S. Binger, M. Boll, E. Knorr, R.M. Twyman, **A. Vilcinskis** & U. Wenzel 2013: Longevity in the red flour beetle *Tribolium castaneum* is enhanced by broccoli and depends on nrf-2, jnk-1 and foxo-1 homologous genes. *Genes and Nutrition*, in press.
- Gökçen, A., **A. Vilcinskis** & J. Wiesner 2013: Methods to identify enzyme that degrade the main extracellular polysaccharide component of *Staphylococcus epidermidis* biofilms. *Virulence* 4(1):
- Vilcinskis, A.**, K. Mukherjee & H. Vogel 2013: Expansion of the antimicrobial peptide repertoire in the invasive ladybird *Harmonia axyridis*. *Proceedings of the Royal Society B* 280 (1750), 20122113. doi: 10.1098/rspb.2012.2113.
- Altincicek, B., A. Elashry, N. Guz, F. Grundler, **A. Vilcinskis** & H.-W. Dehne 2013: Next generation sequencing based transcriptome analysis of septic-injury responsive genes in the beetle *Tribolium castaneum*. *PLoS One* 8(1): e52004. doi:10.1371/journal.pone.0052004.

- Mukherjee, K., R. Fischer & **A. Vilcinskis** 2012: Histone acetylation mediates epigenetic regulation of transcriptional reprogramming in insects during metamorphosis, wounding and infection. *Frontiers in Zoology* 9:25
- Freitag, D., E. Knorr, H. Vogel & **A. Vilcinskis** 2012: Gender and stressor specific miRNA expression in *Tribolium castaneum*. *Biology Letters* 8, 860-863.
- Behnam, F., **A. Vilcinskis**, M. Wagner & K. Stoecker 2012: A Straightforward DOPE (Double Labeling of Oligonucleotide Probes)-FISH (Fluorescence In Situ Hybridization) method for simultaneous multicolor detection of six microbial populations. *Applied and Environmental Microbiology* 78(15), 5138-5142.
- Röhrich, R., C. J. Ngwa, J. Wiesner, H. Schmidtberg, T. Degenkolb, R. Fischer, G. Pradel & **A. Vilcinskis** 2012: Harmonine, a defense compound from the harlequin ladybird, inhibits mycobacterial growth and demonstrates multi-stage anti-malarial activity. *Biology Letters* 8, 308-311.
- Koch, A., W. Khalifa, G. Langen, **A. Vilcinskis**, K.-H. Kogel & J. Imani 2012: The antimicrobial peptide thanatin reduces *Fusarium graminearum* infection in Arabidopsis. *Journal of Phytopathology* 160, 606–610.
- Rahnamaeian, M. & **A. Vilcinskis** 2012: Defense gene expression is potentiated in transgenic barley expressing antifungal peptide metchnikowin throughout powdery mildew challenge. *Journal of Plant Science* 125(1), 115-124.
- Dobson, A.J., P.R. Johnston, **A. Vilcinskis** & J. Rolff 2012: Identification of immunological expressed sequence tags in the mealworm beetle *Tenebrio molitor*, *Journal of Insect Physiology*, 58(12), 1556-1561.
- Knorr, E. & **A. Vilcinskis** 2011: Post-embryonic functions of HSP90 in *Tribolium castaneum* include regulation of compound eye development. *Dev. Genes & Evolution* 211, 357-362.
- Vilcinskis, A.** 2011: Insects emerge as valuable model hosts to explore virulence. *Virulence* 2:5, 376-378.
- Arolas, J., T. Bothello, **A. Vilcinskis** & X. Gomis-Rüth. 2011. Structural evidence for standard-mechanisms inhibition in metallopeptidases from a complex poised to resynthesize a peptide bond. *Angewandte Chemie – International Edition*, 50(44), 10357-10360.
- Vogel, H., C. Badapanda & **A. Vilcinskis** 2011: Identification of immunity-related genes in the burying beetle *Nicrophorus vespilloides* by suppression subtractive hybridization. *Insect Molecular Biology* 20(6), 787-800.
- Degenkolb, T., R.-A. Düring & **A. Vilcinskis** 2011: Secondary metabolites released by the burying beetle *Nicrophorus vespilloides*: chemical analyses and possible ecological functions. *Journal of Chemical Ecology* 37(7), 724-735.
- Vogel, H., B. Altincicek, G. Glöckner & **A. Vilcinskis** 2011: A comprehensive transcriptome and immune-gene repertoire of the lepidopteran model mini-host *Galleria mellonella*. *BMC Genomics* 12:308.
- Vilcinskis A.** 2011: Anti-Infective therapeutics from the lepidopteran model host *Galleria mellonella*. *Current Pharmaceutical Design* 17 (13), 1240-1245.
- Mukherjee, K., M. Abu Mraheil, S. Silva, D. Müller, F. Cemic, J. Hemberger, T. Hain, **A. Vilcinskis** & T. Chakraborty 2011. Anti-Listeria activities of *Galleria* hemolymph proteins. *Applied and Environmental Microbiology* 77(12), 4237-4240.
- Kirsch, R., H. Vogel, A. Muck, J. Pasteels, **A. Vilcinskis** & W. Boland 2011: To be or not to be convergent in salicin-based defense in chrysomeline leaf beetle larvae: Evidence from *Phratora vitellinae*. *Proceedings of the Royal Society B* 278, 3225-3232.
- Lehtovirta-Morley, L., K. Stoecker, **A. Vilcinskis**, J. Prosser & G. Nicol 2011: Cultivation of an obligate acidophilic ammonia oxidizer from a nitrifying acid soil. *Proceedings National Academy of Sciences USA*, 108 (38), 15892-15897.
- Mayer, C., **A. Vilcinskis** & J. Gross 2011: Chemically mediated multitrophic interactions in a plant–insect vector-phytoplasma system compared with a partially nonvector species. *Agricultural and Forest Entomology* 13, 25-35.

- Jiang, H., **A. Vilcinskis** & M. Kanost 2010: Immunity in lepidopteran insects. *Advances in Experimental Medicine and Biology* 708, 181-204.
- Wiesner, J. & **A. Vilcinskis** 2010: Antimicrobial peptides: the ancient arm of the human immune system. *Virulence*, 1:5, 440-464.
- Altincicek, B., M. Fischer, M. Fischer, K. Lüersen, M. Boll, U. Wenzel & **A. Vilcinskis** 2010: Role of matrix metalloproteinase ZMP-2 in pathogen resistance and development in *Caenorhabditis elegans*. *Developmental and Comparative Immunology* 34, 1160-1169.
- International Aphid Genomics Consortium 2010: Genome Sequence of the Pea Aphid *Acyrtosiphon pisum*. *PLoS Biology*, 8(2):e1000313. Accompanying publication:
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- Vilcinskis A.** 2010: Coevolution between pathogen-derived proteinases and proteinase inhibitors of host insects. *Virulence* 1:3, 206-214.
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- Tribolium Genome Sequencing Consortium 2008: The genome of the developmental model beetle and pest *Tribolium castaneum*. *Nature* 425, 949-955. Accompanying publication:
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A few recent communications

- 2012: 3 invited talks at the XXIV International Congress of Entomology, Daegu, Korea, 19.8.-25.8.2012 Symposium 306: Evolutionary plasticity of insect immunity
Symposium 507: Gender- and stressor specific microRNA expression in *Tribolium castaneum*
Symposium 511: Symbiont-mediated invasive success of the Harlequin ladybird *Harmonia a.*
- 2012: Invited talk: Epigenetic regulation of innate immunity in insect model hosts. 2nd International Conference on Model Hosts, Rhodos, Greece 1.9.-6.9.2012
- 2012: Invited talk : Does harmonine-based chemical defense mediate invasive success of the harlequin ladybird *Harmonia axyridis*? 28th Meeting of the International Society of Chemical Ecology, Vilnius, Lithuania, 22.7.-26.7.2012
- 2012: Exploring the role of epigenetics in host-parasite-coevolution. DFG-Winterschool in the Priority Programm Host-Parasite Coevolution, Vienna, Austria 27.2.-1.3.2012
- 2012: Invited talk: Insect Biotechnology, George Washington University, Washington DC, USA, 29.10.2012
- 2012: Invited talk: Insect models in preclinical and epigenetic research, Harvard Medical School, Boston, USA. 28.10.2011
- 2011: Invited talk: Evolutionary plasticity of Insect Immunity. Sixth International Symposium on Molecular Insect Science, Amsterdam, 2.10.-5.10.2011

2011: Invited talk : Exploring mechanisms behind the invasive success of the ladybird *Harmonia axyridis* Meeting of the German Entomological Society, Berlin, Germany, 21.3.-24.3.2011

2011: Invited talk : Insect Biotechnology: How to translate biodiversity into products and services. European Parliament Seminar, Brüssel, Belgium, 15.3.2011

Contributions to research management

2013-2011 Coordinator and spokesperson of the LOEWE Research Focus « Insect Biotechnology »

Funded by the Hessian Ministry for Science and Art (Budget : €4.5 million)

2010-2012 Second coordinator and spokesperson of the LOEWE Research Focus « AmbiProbe »

Funded by the Hessian Ministry for Science and Art (Budget : €4.5 million)

2009-2010 Coordinator and spokesperson of the starting grant for the the Fraunhofer Project Group

Bioresources in Giessen (Budget : €4.0 million)

2006-2012 Member of the faculty panel « Faculty of agriculture and environmental management »

Some funded projects

2009-2015 Member of the DFG Priority Program 1399 “Host-Parasite-Coevolution – rapid reciprocal adaptation and its genetic basis“ Project 1 (VI 219/3-1): Reciprocal

genetic diversification and adaption of host proteinase inhibitors and parasite-associated proteinases during coevolution of insects and entomopathogenic fungi

Budget: €160,000 (including a PhD student for 3 years), funding period 2009-2012

Project 2 (VI 219/3-2): Role of epigenetics in host-parasite-coevolution

Budget: €180,000 (including a PhD student for 3 years), funding period 2012-2015

Referee

Reviewer for Scientific Journals:

Acta Parasitologica, Archives of Insect Biochemistry & Physiology , BMC Biology, BMC Genomics, BMC Biochemistry, Cellular & Molecular Life Sciences, Comparative Biochemistry & Physiology, Current Genetics, Developmental & Comparative Immunology, European Journal of Biochemistry, Frontiers in Zoology, Insect Biochemistry and Molecular Biology, Insect Molecular Biology, Journal of Applied Entomology, Journal of Immunology, Journal of Insect Physiology, Insectes Sociaux, Journal of Insect Science, Journal of Pest Science, Microbes and Infection, Peptides, PLOS One, PNAS, Proceedings of the Royal Society B, Virulence.

Reviewer for Grant Agencies

BBSRC - Biotechnology and Biological Sciences Research Council UK, German Research Foundation (DFG), European Research Council (ERC), Alexander von Humboldt-Stiftung , DAAD, Swiss National Fond

Editorial Board Member

Archives of Insect Biochemistry and Physiology, Journal of Invertebrate Immunity, Virulence

CURRICULUM VITAE



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Education

Master (2003) : **Diplôme d'ingénieur chimiste et des bio-industries** - FuSaGx

PhD (2008) : **Docteur en Sciences agronomiques et Ingénierie biologique** - FuSaGx

Publications et communications

PhD and Master thesis

- Verheggen, F. (2008). Production of alarm pheromone in aphids and perception by ants and natural enemies. Unpublished doctoral thesis, Université de Liège, Belgium.
- Verheggen, F. (2005). Contribution à l'étude des relations tritrophiques entre la tomate (*Lycopersicon esculentum* Miller), le puceron vert du pêcher (*Myzus persicae* Sulzer) et le syrpe ceinturé (*Episyrphus balteatus* DeGeer). Unpublished DEA/DES thesis, Université de Liège, Belgium.
- Verheggen, F. (2003). Electrophysiological and behavioural study of some secondary metabolites from *Tribolium confusum* (Du Val) (Coleoptera: Tenebrionidae). Unpublished master thesis, Université de Liège, Belgium.

Patent

- Leroy, P, Capella, Q, Verheggen, F, Francis, F, & Haubruge, E. (2009). Treatment method using biological control. Belgium: Office de la Propriété intellectuelle.

Publications in peer review Journals

As first or last author

- Sablon, L, (...) & Verheggen, F. (in press). Consumption of Immature Stages of Colorado Potato Beetle by *Chrysoperla Carnea* (Neuroptera: Chrysopidae) Larvae in the Laboratory. *American J Potato Research*.
- Sablon, L, (...) & Verheggen, F. (2013). Chemical Ecology of the Colorado Potato Beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), and Potential for Alternative Control Methods. *Insects*, 4(1), 31-54.

- Vandereycken, A, (...) & Verheggen, F. (2012). Habitat diversity of the Multicolored Asian ladybeetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in agricultural and arboreal ecosystems: a review. *BASE*, 16(4), 553-563.
- Caparros Megido, R, (...) & Verheggen, F. (2012). First evidence of deuterotokous parthenogenesis in the tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *J Pest Science*.
- Durieux, D, (...) & Verheggen, F. (2012). Role of long-chain hydrocarbons in the aggregation behaviour of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). *J Insect Physiology*.
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- Razafimanantsoa, T, (...) & Verheggen, F. (2012). Silk moths in Madagascar: Biology, uses and challenges related to *Borocera cajani* (Boisduval, 1833) (Lepidoptera – Lasiocampidae). *BASE*, 16(2), 269-276.
- Vandermoten, S, (...) & Verheggen, F. (2012). Aphid alarm pheromone: An overview of current knowledge on biosynthesis and functions. *Insect Biochemistry & Molecular Biology*, 42, 155-163.
- Verheggen F, et al. (2012). Aphid Alarm Pheromone as a Cue for Ants to Locate Aphid Partners. *PLoS ONE*.
- Abdoul Habou, Z, (...) & Verheggen, F. (2011). Insecticidal effect of *Jatropha curcas* oil on the aphid *Aphis fabae* (Hemiptera: Aphididae) and on the main insect pests associated with cowpeas (*Vigna unguiculata*) in Niger. *Tropicicultura*, 29(4), 225-229.
- Verheggen, F, & Haubruge, E. (2011). Les phéromones d'alarme dans le règne animal. *Faunistic Entomology*, 63(4), 259-274.
- Verheggen, F, & Haubruge, E. (2010). Les phéromones d'alarme dans le règne animal. *Faunistic Entomology*, 63(4).
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- Verheggen, F, et al. (2009). Tomato-aphid-hoverfly: A tritrophic interaction incompatible for pest management. *Arthropod-Plant Interactions*, 3, 141-149.
- Verheggen, F, et al. (2009). Mutualisme pucerons-fourmis : étude des bénéfiques retirés par les colonies d'*Aphis fabae* en milieu extérieur. *BASE*, 13, 232-242.
- Verheggen, F, et al. (2009). Social environment influences aphid production of alarm pheromone. *Behavioral Ecology*, 20(2), 283-288.
- Verheggen F, et al. (2008). Aphid and plant volatiles induce oviposition in an aphidophagous hoverfly. *J Chem Ecology*, 34, 301-307
- Verheggen, F, et al. (2008). What makes *Episyrphus balteatus* (Diptera: Syrphidae) oviposit on aphid infested tomato plants? *Comm. Agricult. Appl. Biol. Sc.*, 73(3), 371-81.
- Verheggen, F, et al. (2008). Emission of alarm pheromone in aphids: A non-contagious phenomenon. *J Chem Ecol*, 34(9), 1146-1148.
- Verheggen, F, et al. (2008). Mothflies (Diptera : Psychodidae) in hospitals: A guide to their identification and methods for their control. *Acta Clinica Belgica*, 63(4), 251-255.
- Verheggen, F, et al. (2007). Electrophysiological and behavioral responses of the multicolored asian lady beetle, *Harmonia axyridis pallas*, to sesquiterpene semiochemicals. *J Chem Ecol*, 33(11), 2148-2155.
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As a coauthor

- Dekeirsschieter, J, Frederickx, C, Verheggen, F, Drugmand, D, & Haubruge, E. (2013, July). Diversity of forensic rove beetles (Coleoptera, Staphylinidae) associated with decaying pig carcass in a forest biotope. *J Forensic Sciences*.

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- Leroy, P, Heuskin, S, Sabri, A, Verheggen, F, Farmakidis, J, Lognay, G, Thonart, P, Wathelet, J.-P, Brostaux, Y, & Haubruge, E. (2012). Honeydew volatile emission acts as a kairomonal message for the Asian lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *Insect Science*, 19(4), 498-506.
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- Heuskin, S, Lorge, S, Godin, B, Leroy, P, Frère, I, Verheggen, F, Haubruge, E, Wathelet, J.-P, Mestdagh, M, Hance, T, & Lognay, G. (2011, July). Optimisation of a semiochemical slow-release alginate formulation attractive towards *Aphidius ervi* Haliday parasitoids. *Pest Management Science*.
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- Leroy, P, Sabri, A, Heuskin, S, Thonart, P, Lognay, G, Verheggen, F, Francis, F, Brostaux, Y, Felton, G, & Haubruge, E. (2011). Microorganisms from Aphid Honeydew Attract and Enhance the Efficacy of Natural Enemies. *Nature Communications*, 2.
- Leroy P, Sabri A, Verheggen F, Francis F, Thonart P & Haubruge E (2011) The semiochemically mediated interactions between bacteria and insects. *Chemoecology*, 21
- Leroy, P, Wathelet, B, Sabri, A, Francis, F, Verheggen, F, Capella, Q, Thonart, P, & Haubruge, E. (2011). Aphid-host plant interactions: Does aphid honeydew exactly reflect the host plant amino acid composition? *Arthropod-Plant Interactions*, 5, 1-7.
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- Leroy, P, Verheggen, F, Capella, Q, Francis, F, & Haubruge, E. (2010). An introduction device for the aphidophagous hoverfly *Episyrphus balteatus* (De Geer) (Diptera: Syrphidae). *Biological Control*, 54(3), 181-188.
- Almohamad, R, Verheggen, F, Francis, F, & Haubruge, E. (2010). Intraguild interactions between the predatory hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) and the Asian

- ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae): Effect of larval tracks. *European J Entomology*, 107, 41-45.
- Almohamad, R, Verheggen, F, Francis, F, Lognay, G, & Haubruge, E. (2010). Assessment of oviposition site quality by aphidophagous hoverflies: reaction to conspecific larvae. *Animal Behaviour*, 79, 589-594.
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 - Durieux, D, Verheggen, F, Vandereycken, A, Joie, E, & Haubruge, E. (2010). Synthèse bibliographique : l'écologie chimique des coccinelles. *BASE*, 14(2), 351-367.
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 - Dekeirsschieter, J, Verheggen, F, Gohy, M, Hubrecht, F, Bourguignon, L, Lognay, G, & Haubruge, E. (2009). Cadaveric volatile organic compounds released by decaying pig carcasses in different biotopes. *Forensic Science International*, 189, 46-53.
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 - Almohamad, R, Verheggen, F, Francis, F, & Haubruge, E. (2008). Impact of aphid colony size and associated induced plant volatiles on searching and oviposition behaviour of a predatory hoverfly. *Belgian J of Entomology*, 10, 17-26.
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 - Almohamad, R, Verheggen, F, Francis, F, & Haubruge, E. (2007). Predatory hoverflies select their oviposition site according to aphid host plant and aphid species. *Entomol Exp et Appl*, 125(1), 13-21.
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Book Chapters

- Sloggett, J, Magro, A, Verheggen, F, Hemptinne, J.-L, Hutchison, W, & Riddick, E. (2011). The chemical ecology of *Harmonia axyridis*. In H., Roy, R., Ware, L., Handley-Lawson, P., De Clercq, & E., Wajnberg (Eds.), *Invasive arthropod predators and parasitoids: an ecological approach*. Springer.
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