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Evolutionary and ecological studies of insects

Carlos Lopez-Vaamonde

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UNIVERSITÉ D'ORLÉANS

Année Universitaire: 2011-2012

HABILITATION A DIRIGER DES RECHERCHES

Discipline: Science de la Vie

présentée et soutenue publiquement par :

Dr Carlos Lopez Vaamonde

Le 11 Avril 2012

JURY :

(Par ordre alphabétique)

- | | |
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| M. Thibaud DECAENS, Professeur des Universités
Université de Rouen | Rapporteur |
| M. Xavier FAUVERGUE, Charge de Recherche
INRA de Sophia-Antipolis | Rapporteur |
| Mme. Elisabeth HUGUET, Professeur des Universités
Université de Tours | |
| M. Francois LIEUTIER, Professeur des Universités
Université d'Orleans | |

Remerciements

First I would like to thank Jenny Cory; Jean-François Cosson, Thibaud Decaens, Xavier Fauvergue, Elisabeth Huguet and François Lieutier for accepting to participate to this HDR jury.

I wish to extend my gratitude to Marc Kenis for giving me the opportunity to work at Delémont and learn about biocontrol, Forest Entomology and Georges Brassens.

Special thanks must go to James Cook for his supervision during my M.Sc. and Ph.D. I owe Charles Godfray, Donald Quicke and Rob Belshaw a special word of thanks for their advice and support during my years at Silwood.

To Jean Yves Rasplus my most sincere thanks for sharing his passion about fig wasps and hospitality during my visits to Montpellier. To Andrew Bourke for his mentorship and sharing his knowledge about social insects.

Thanks to both Alain Roques and Sylvie Augustin for their help getting me started as a researcher in France.

I am also grateful to the people with whom I have had the pleasure of sharing the molecular labs at Silwood, Institute of Zoology and now at URZF.

Finally, my heartfelt thanks to Elisabeth for her constant support and encouragement.

Gracias a mi familia por su apoyo.

Scientists know far more about (and spend vastly more money studying) the systematics of stars than the systematics of earthly organisms. Consequently, they have as good a knowledge of the number of atoms in the universe – an unimaginable abstraction – as they do of the number of species of plants and animals.

-Robert May, 1992

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Fiche Signalétique

Nom : Carlos LOPEZ VAAMONDE

Date de naissance : 1 Novembre 1969

Emploi - Chargé de Recherche INRA

Institut National de la Recherche Agronomique (INRA)

Département: Ecologie des Forêts, Prairies et milieux Aquatiques

Grade: Chargé de Recherche - 1ère classe (CR1)

Recrutement: 01/07/2005

Directeur de recherche INRA: Alain ROQUES

Laboratoire:

N° Unité: URZF 0633

Laboratoire: Unité de Zoologie Forestière

Directeur: Dr Alain Roques – alain.roques@orleans.inra.fr

Adresse complète: 2163 Avenue de la Pomme de Pin CS 40001 Ardon, 45075 ORLEANS
Cedex 2, France

Parcours professionnel :

- Depuis 2005 Chargé de Recherche INRA (CR1)
Orléans, France
- 2001-2004 NERC Postdoctoral Research Associate (Postdoctorat CDD)
Zoological Society of London, Institute of Zoology, UK
- 1999-2002 NERC-British Council PhD Student (Doctorat)
Imperial College London, Silwood Park, UK
- 1997-1998 NERC Research Assistant (Ingénieur d'étude CDD)
Imperial College London, UK
- 1995-1996 Research Assistant (Ingénieur d'étude CDD)
CABI Bioscience, Silwood Park, UK
- 1993-1994 Research Assistant (Ingénieur d'étude CDD)
CABI Bioscience, Delémont, Suisse

Thématiques de Recherche :

- Depuis 2005 "Evolutionary Ecology and Molecular Systematics of forest insects"
- 2001-2004 "Kin-selected conflict in the bumble bee *Bombus terrestris* (Hymenoptera: Apidae)"
- 1999-2002 "Macroevolutionary studies of two Insect-Host plant systems "
- 1997-1998 "Molecular phylogenies of the subfamilies Braconinae (Hymenoptera: Braconidae)"
- 1995-1996 "Biological control of the coffee berry borer *Hypothenemus hampei*: rearing techniques and biology of its parasitoid wasp *Phymastichus coffea* "
- 1993-1994 "Classical Biological Control for Forestry Insect Pests "

Curriculum Vitae

Dr Carlos Lopez Vaamonde

Date of birth: 1 November 1969

Research Experience

- July 2005- Present.* **Research Scientist** at INRA-Orleans, Laboratoire de Zoologie Forestière, Ardon, France. "Evolutionary Ecology and Molecular Systematics of forest insects".
- October 2001-December 2004* **Postdoctoral Research Assistant** at Institute of Zoology, Zoological Society of London. "Kin-selected conflict in the bumble bee *Bombus terrestris* (Hymenoptera: Apidae)".
- October 1997-March 1998.* **Research Assistant** at the Department of Biology, Imperial College at Silwood Park, UK. "Molecular phylogenies of the subfamilies Braconinae (Hymenoptera: Braconidae)".
- January 1995-May 1996.* **Research Assistant** at CABI Bioscience, Silwood Park, UK. "Biological control of the coffee berry borer *Hypothenemus hampei*: rearing techniques and biology of its parasitoid wasp *Phymastichus coffea*".
- June-August 1993, June-September 1994 and June-September 1996.* **Research Assistant** at CABI Bioscience, European Station, Delémont, Switzerland. "Classical Biological Control for Forestry Insect Pests".

Academic Qualifications

- 1998-2002* **Ph.D in Evolutionary Biology**, Department of Biological Sciences, Imperial College London, UK. Dissertation: "Macroevolutionary studies of two Insect-Host plant systems". Supervisors: James Cook & Charles Godfray
- 1996-1997* **M.Sc. in Advanced Methods in Taxonomy and Biodiversity.**
The Natural History Museum, London and Imperial College, University of London, UK. Dissertation: "A combined Morphological and Molecular Phylogeny for *Pleistodontes* Pollinator Fig Wasp (Hymenoptera; Agaonidae)". Supervisor: James Cook
- 1987-92* **BSc. in Biological Sciences**, Speciality, Zoology, University of Santiago de Compostela, Galicia, Spain.

Grants & Awards

Submitted projects:

- 2012: Project: "Madagascar Lepidoptera barcoding for socioeconomic benefits". Funded by International Development Research Centre (Canada) grant call: "Applications of DNA barcoding". PIs: David Lees, Carlos Lopez Vaamonde & Rodolphe Rougerie (total: 20.268 CAD= 15.430 euros)
- 2012: Project: "Taxonomy and Phylogeny of leaf-mining moths and the evolution of green island formation: An integrated approach to systematic training" Preliminary proposal National Science Foundation (USA). PI: Akito Kawahara; Co-PIs: Carlos Lopez-Vaamonde, J. Gordon Burleigh, Donald R. Davis, David L. Wagner.

Awarded:

- 2012 : Project: " Quantifying cryptic diversity associated to host shifts in Lepidoptera". Department EFPA, INRA. Project Leader: Carlos Lopez-Vaamonde & Rodolphe Rougerie (Co-PI) (9.000 euros).
- 2010-2012: Evolution et Signification Adaptative du mode de vie Endophyte chez les Insectes (ENDOFEED), funded by Région Centre. Coordinator: David Giron (total : 248.000 euros ; INRA : 30000 euros)
- 2011: Consiglio Nazionale delle Ricerche. Short term mobility award to visit Umberto Bernardo's lab at Istituto CNR per la Protezione delle Piante, Sezione Di Portici, Naples, Italy.
- 2009-2010: Exploring tropical diversity and host plant interactions of leaf-mining moths: tapping into a megadiverse insect group. Research Grant Program (funded by CNRS). Coordinator: Carlos Lopez-Vaamonde (14000 euros)
- 2009-2011: European Seventh Framework programme. Project: "Development of a new diagnostic tool using DNA barcoding to identify quarantine organisms in support of plant health (QBOL)" Coordinator: Peter Bonants (3.000.000 euros).
- 2009-2010: "Studium" grant funded by "Region Centre, France" to host Dr David Lees in our lab for two years.
- 2008-2011: ANR Programme Biodiversité. Project: "Anticipation des effets du changement globale sur l'environnement et la santé des insectes forestiers et urticants ". Coordinator: Alain Roques (783.751 euros).
- 2008: Programme Egide/ Picasso. Project: "Assessment of the conservation status of a protected forest insect, *Graellsia isabelae* (Lepidoptera, Saturniidae)" Project Leaders: Carlos Lopez-Vaamonde (11.260 euros) and Marta Vila (11.950 euros).
- 2008-2011: Belgian Science Policy Research Programmes for the Federal Scientific Institutions. Project: "Biodiversity and molecular evolutionary studies of leaf mining moths in the Afrotropical region (Lepidoptera, Gracillariidae)" Project Leader: Marc De Meyer (Royal Museum for Central Africa Tervuren, Belgium) (260.000 euros) (MO/37/022).
- 2007-2008: Pilot Joint Call for Research and Thematic Network Projects with the Western

- Balkan Region (SEE-ERA.NET). Project: "Genetic survey of an invasive forest insect and its parasitoids in the Balkan region" (Project number: 10627RP). Project Leaders: Carlos Lopez-Vaamonde and Sylvie Augustin (20.000 euros).
- 2008-2010: Spanish Ministry of Science and Education. Project: "Conservation genetics of a protected moth, *Graellsia isabelae* (Lepidoptera, Saturniidae)" Project Leader: Marta Vila Taboada (University of La Coruna, Spain); Carlos Lopez-Vaamonde (Co PI) (121,500 euros+ PhD student + technician).
- 2007: Department EFPA, INRA. Project: "Development of a DNA non-lethal sampling method from adult moths for conservation genetics" Project Leaders: Marie-Anne Auger-Rozenberg & Carlos Lopez-Vaamonde (10.000 euros).
- 2006: Department EFPA, INRA. Project: "Genetics of invasion of the horse chest nut leaf miner *Cameraria ohridella* (Lepidoptera, Gracillariidae)". Project Leaders: Carlos Lopez-Vaamonde and Sylvie Augustin (10.000 euros).
- 2005: Royal Society travel grant to participate to the 3rd European Congress on Social Insects. University of St. Petersburg, Russia.
- 2004: NERC "Funding for transferable skills training" to participate in the Workshop on Molecular Evolution organised by the Marine Biological Laboratory in Woods Hole, Massachusetts.
- 2004: Royal Society travel grant to participate to the XXII International Congress of Entomology in Brisbane, Australia.
- 2002: Best student talk. Annual Winter Meeting of the British Section of the International Union for the Study of Social Insects. London, UK.
- 2001: Student grant to participate to conference on Systematics Funded by The Systematics Association, UK.
- 2000: Student grant to participate to symposium on Evolutionary Biology. Universitat de València, Spain.
- 2000: Student grant to participate in workshop. Biotechnology and Biological Sciences Research Council, UK.
- 1999: Student grant to participate in conference. The Systematics Association, UK.
- 1999: Grant to carry out field work in Australia and New Guinea. Funded by the European Science Foundation. Program on Tropical Canopy Research.
- 1998- 1999: Studentship to do my Ph.D. The British Council/Fundacion Pedro Barrié de la Maza scholarship.

Lectures and Conferences

Invited Lectures (19)

- 2012 Complexe Educatif Alphonse Mackanga Missandzou de la Wildlife Conservation Society at la Lopé National Park, Gabon:
"Ecology and conservation of obligate mutualisms in tropical rainforests"
- 2011 Nature Society Singapore.
"Ecology and conservation genetics of the protected Spanish moon moth, *Graellsia isabellae*"
- 2011 Annual Meeting of the EuroPhD Network in "Insect Sciences". Tours, France.
"Tracking origins of invasive leaf-mining moths using herbaria and archival DNA"
- 2011 Instituto CNR per la Protezione delle Piante, Portici, Italy.
"Tracking the origins of invasive leaf miners and new approaches to document host-parasitoid relationships"
- 2010 Laboratoire Evolution, Genomes et Speciation, CNRS, Gif sur Yvette, France
"Tracking the origins of invasive leaf miners and new approaches to document host parasitoid relationships"
- 2010 University of Tirana, Albania
"Tracking the origins of invasive leaf miners and testing for cryptic adaptation of their parasitoids"
- 2006 Royal Museum for Central Africa, Tervuren, Belgium.
"Molecular Phylogenetic studies of Gracillariidae leaf-mining moths"
- 2005 «International Symposium on Insect Pests of Coconuts in the island of Koh Samui», Samui, Thailand.
"Overview of insect pests of palm trees in Koh Samui"
- 2005 Department of Biology University of Granada, Spain.
"Intraspecific social parasitism in bumblebees"
- 2005 Museum of the North, University of Alaska, Fairbanks, USA.
"Conflicts between workers and queens in bumblebees: who has power?"
- 2005 The Central Association of Bee keepers, King's College, London, UK.
"Conflicts between workers and queens in bumblebees: who has power?"
- 2004 University of Tours, France.
"Intraspecific social parasitism in bumblebee workers"
- 2004 Imperial College London, Silwood Park, Ascot, UK.
"Relatedness and information in reproductive conflicts in bumblebees"
- 2004 University of Ulm, Department of Experimental Ecology, Germany
"Intraspecific social parasitism in bumblebee workers"
- 2004 University of Sussex, Department of Biology and Environmental Science, Brighton, UK
"Kin conflict over male parentage in bumblebees"
- 2004 USDA Beltsville Agricultural Research Center, Maryland, USA
"Molecular Phylogenetic studies of Gracillariidae leaf-mining moths"
- 2004 University of Vigo, Department of Genetics, Spain
"Conflicts over reproduction in bumblebees: who has power?"

- 2004 NERC Center for Ecology and Hydrology, Dorset, UK.
 “Conflicts over reproduction in bumblebees: who has power?”
- 2004 1st International Cameraria Symposium: Cameraria ohridella and other invasive leaf-miners in Europe. Institute of Organic Chemistry and Biochemistry, Prague, Czech Republic. (Opening lecture).
 “Evolution of host plant use in *Phyllonorycter* leaf-mining moths”
- 2003 International Symposium on Animal Evolution and Systematics, Zoological Museum, University of Zurich, Switzerland.
 “Evolution of host plant use and rates of diversification in leaf-mining moths”

Contributed Talks (30)

- 2012 Lees, D.C., Lack, H. W., Rougerie, R. Hernandez, A., Raus, T., Avtzis, N.D., Augustin, S. and Lopez-Vaamonde, C. Tracking origins of the highly invasive horse-chestnut leafminer using herbaria and minibarcodes. 7th European Conference on Biological Invasions. «NEOBIOTA Halting Biological Invasions in Europe: from Data to Decisions». Pontevedra, Spain.
- 2012 Lopez-Vaamonde C., Bengt Åke Bengtsson, Alain Cama, Helmut Deutsch, Gerfried Deschka, Endrit Kullaj, Ales Lastuvka, Zdenek Lastuvka, David Lees, Jurate De Prins, Stanislav Gomboc, Peter Huemer, John Langmaid, Marko Mutanen, Ian Sims, Paolo Triberti, Christian Wieser, Rodolphe Rougerie. Talk: DNA barcoding of European Gracillariidae leaf-mining moths, 3rd Slovenian Entomological Symposium with International attendance, Maribor, Slovenia.
- 2012 Mari Mena, N., Lopez-Vaamonde, C, Auger-Rozemberg, MA, Vila, M. Talk: Phylogeography of *Graellsia isabellae*. I Congreso Ibérico de Sistemática Animal. Madrid, Spain.
- 2011 Lees, D.C., Lack, H. W., Rougerie, R. Hernandez, A., Raus, T., Avtzis, N.D., Augustin, S. and Lopez-Vaamonde, C. Talk: “ Tracking origins of invasive leaf-mining moths using herbaria and minibarcodes” 4th International Barcode of Life Conference, Adelaide Australia.
- 2011 Lopez-Vaamonde C., Bengt Åke Bengtsson, Alain Cama, Helmut Deutsch, Gerfried Deschka, Endrit Kullaj, Ales Lastuvka, Zdenek Lastuvka, David Lees, Jurate De Prins, Stanislav Gomboc, Peter Huemer, John Langmaid, Marko Mutanen, Ian Sims, Paolo Triberti, Christian Wieser, Rodolphe Rougerie. Talk: DNA barcoding of European Gracillariidae leaf-mining moths, 4th International Barcode of Life Conference, Adelaide Australia.
- 2011 Lees D., Issei Ohshima, Atsushi Kawakita, Akito Y. Kawahara, Rodolphe Rougerie, Klaus Sattler, David Adamski and Carlos Lopez-Vaamonde. Talk: “Rapid inventory via DNA barcoding: cross-lepidopteran diversity survey of Nouragues inselberg, French Guiana”. 4th International Barcode of Life Conference, Adelaide Australia.
- 2011 Lees, D.C., Lack, H. W., Rougerie, R. Hernandez, A., Raus, T., Avtzis, N.D., Augustin, S. and Lopez-Vaamonde, C. Talk: “ Tracking origins of invasive leaf-mining moths using herbaria and archival DNA” Journée de l’IRBI, Tours, France.
- 2011 Lopez-Vaamonde C., Bengt Åke Bengtsson, Alain Cama, Helmut Deutsch, Gerfried Deschka, Endrit Kullaj, Ales Lastuvka, Zdenek Lastuvka, David Lees, Jurate De Prins,

- Stanislav Gomboc, Peter Huemer, John Langmaid, Marko Mutanen, Ian Sims, Paolo Triberti, Christian Wieser, Rodolphe Rougerie. Talk: DNA barcoding of European Gracillariidae leaf-mining moths, The XVIIth European Congress of Lepidopterology. Luxembourg.
- 2011 Lees D., Issei Ohshima, Atsushi Kawakita, Akito Y. Kawahara, Rodolphe Rougerie, Klaus Sattler, David Adamski and Carlos Lopez-Vaamonde. Talk: Rapid inventory via DNA barcoding: cross-lepidopteran diversity survey of Nouragues inselberg, French Guiana. The XVIIth European Congress of Lepidopterology. Luxembourg.
- 2009 Lees, D.C. and Lopez-Vaamonde, C. Lepidopteran Diversity and Biogeography across the Western Indian Ocean. Evolution and Extinction of the Terrestrial Biota of the western Indian Ocean archipelagoes, Linnean Society of London, UK.
- 2009 Hernandez, A. R. Rougerie, R. Tomov, M. Kenis, G. Grabenweger, S. Augustin, A. Roques, C. Lopez Vaamonde. Host tracking or cryptic adaptation? A DNA barcode study of a parasitoid of the horse chestnut leafminer. Third International Barcode of Life Conference, Mexico.
- 2009 Lopez-Vaamonde C., Goussard, F. Mari-Mena N, Auger-Rozenberg MA, Vila M. Génétique de la conservation *et identification de la pheromone sexuelle de Graellsia isabelae* Annual meeting of Groupe des Entomologistes Forestiers Francophones, Semur en Auxois, France.
- 2008 Lopez-Vaamonde C., Vila M. Auger-Rozenberg MA, Mari-Mena N, Goussard, F. Génétique de la conservation de *Graellsia isabelae*. Annual meeting of Groupe des Entomologistes Forestiers Francophones, Bedoin, France
- 2008 Lopez-Vaamonde, C., Valade, R. Lakatos, F., Augustin, S., Kenis, M. DNA barcoding reveals the area of origin of the highly invasive horse chestnut leaf-miner *Cameraria ohridella*. 23rd International Congress of Entomology, Durban, South Africa.
- 2007 Lopez-Vaamonde, C., Valade, R. Lakatos, F., Augustin, S., Kenis, M. "Invasion genetics of *Cameraria ohridella*". International Conference on Alien Arthropods in South East Europe, crossroad of three continents" Sofia, Bulgaria.
- 2005 Lopez-Vaamonde, C., Koning, W, Brown, R., Jordan, B., Bourke, A. "Intraspecific social parasitism in bumblebees". 22-27 August 2005: 3rd European Congress on Social Insects, St Petersburg, Russia.
- 2004 Lopez-Vaamonde, C., Koning, W, Brown, R., Jordan, B., Bourke, A. "Intraspecific social parasitism in bumblebees". Annual Winter Meeting of the British Section of the International Union for the Study of Social Insects. London, UK.
- 2004 Lopez-Vaamonde, C., Koning, W, Jordan, B., Bourke, A. "Relatedness and information in reproductive conflicts in bumble bees". INSECTS network workshop: "Sociobiology revisited: The Scientific Study of Integration in Insect and Human Societies". Helsingor, University of Copenhagen, Denmark.
- 2004 Lopez-Vaamonde, C., Koning, W, Brown, R., Jordan, B., Bourke, A. "Intraspecific social parasitism in bumblebees". 22nd International Congress of Entomology, Brisbane, Australia
- 2004 Lopez-Vaamonde, C., "Timing the origin and diversification of *Phyllonorycter* leaf-mining moths". 22nd International Congress of Entomology, Brisbane, Australia

- 2003 Lopez-Vaamonde, C., Koning, W, Jordan, B., Bourke, A. "A test of information use by reproductive bumblebee workers". Annual Winter Meeting of the British Section of the International Union for the Study of Social Insects. Dublin, Ireland.
- 2003 Lopez-Vaamonde, C. "The evolution of host use and reproductive strategies in *Achrysocharoides* wasps". Royal Entomological Society Symposium: "Insect Evolutionary Ecology", University of Reading, UK.
- 2003 Lopez-Vaamonde, C. "The evolution of host use and reproductive strategies in *Achrysocharoides* wasps". Royal Entomological Society SIG, Parasitoid meeting, London, UK.
- 2002 Lopez-Vaamonde, C. "Worker reproduction in bumblebees". Annual Winter Meeting of the British Section of the International Union for the Study of Social Insects. London.
- 2001 Lopez-Vaamonde, C. "Macroevolutionary patterns of host plant use in leaf-mining moths". 3rd Biennial International Conference of the Systematics Association. London.
- 2000 Lopez-Vaamonde, C. "Evolutionary studies of insect-plant relationships". 2nd Young Systematists Forum, Natural History Museum, London, UK.
- 2000 Lopez-Vaamonde, C. "Using molecular phylogenies to study parallel cladogenesis" Royal Entomological Society SIG Parasitoid meeting. London, UK.
- 2000 Lopez-Vaamonde, C., Rasplus, JY. Weiblen, G. and Cook, J. "Combined nuclear and mitochondrial phylogenies of Australasian pollinating and non pollinating fig wasps: an emerging pattern of parallel cladogenesis?" Sixth International Conference on Fig Biology, Cape Town, South Africa.
- 1999 Lopez-Vaamonde "Using molecular phylogenies to study parallel cladogenesis" 1st Young Systematists Forum, Natural History Museum, London, UK.
- 1999 Lopez-Vaamonde, C., Bull, V., Cook, J. and Rasplus, JY. "Molecular Phylogenies of fig wasps: an emerging pattern of parallel cladogenesis?" 2nd Biennial International Conference of the Systematics Association. Glasgow, UK.

Posters (11)

- 2010 Rougerie R., Smith M.A., Fernandez-Triana J., Lopez-Vaamonde C., Ratnasingham S. and Hebert P.D.N. A new approach towards documenting host-parasitoid relationships through DNA barcoding: Post-metamorphosis persistence of host-DNA in the gut-contents of parasitoid wasps. 2nd symposium on the European Consortium for the Barcode of Life, Braga, Portugal
- 2010 Kawahara, A., Klopstein, S., Ohshima I., Kawakita, A., DePrins, J., Lopez-Vaamonde C. Comparing the phylogenetic utility of 21 protein-coding genes: an empirical study from the leaf-mining moths (Insecta, Lepidoptera, Gracillarioidea). The 59th Annual meeting of the Lepidopterists' Society, Leavenworth, WA USA. (Alexander B. Klots Award for best student poster).
- 2010 Kawahara, A., Klopstein, S., Ohshima I., Kawakita, A., DePrins, J., Lopez-Vaamonde C. "Comparing the phylogenetic utility of 21 protein-coding genes: an empirical study from the leaf-mining moths (Insecta, Lepidoptera, Gracillarioidea)". Annual Congress

of the Society for Molecular Biology and Evolution, Lyon, France.

- 2009 Marí-Mena N, Lopez-Vaamonde C, Auger-Rozenberg MA & Vila M. "Phylogeography of *Graellsia isabelae* (Lepidoptera: Saturniidae)". 2nd European Congress of Conservation Biology, Prague, Czech Republic.
- 2008 Lakatos, F., Augustin, S. & Lopez Vaamonde, C. "Phylogeography of *Phyllonorycter platani* (Lep Gracillariidae) an invasive leaf-miner moth of Mediterranean origin". 23rd International Congress of Entomology, Durban, South Africa.
- 2007 Lopez-Vaamonde C, Vila M. Auger-Rozenberg MA, Marí-Mena N, Goussard, F. "Development of a non-lethal sampling of DNA from an endangered moth for conservation genetics". 11th Congress of the European Society for Evolutionary Biology, Uppsala, Sweden.
- 2005 Lopez-Vaamonde, C., Koning, W, Brown, R., Jordan, B., Bourke, A. "Intraspecific social parasitism in bumblebees". 10th Congress of the European Society for Evolutionary Biology, Krakow, Poland
- 2004 Lopez-Vaamonde C, Shen-Horn, Y., Sims, I., Davis, D., " Evolution of female wing recurrence and case architecture in bagworm moths". 22nd International Congress of Entomology, Brisbane, Australia
- 2003 Lopez-Vaamonde, C., Koning, W, Jordan, B., Bourke, A. "Reproductive bumble bee workers do not reduce the production of new queens". Royal Entomological Society Symposium: "Insect Evolutionary Ecology", University of Reading, UK.
- 2002 Lopez-Vaamonde, C., Koning, W, Jordan, B., Bourke, A. « An Investigation of the Effects of Egg-Laying and Aggression in Bumblebee Workers on New Queen Production". Royal Entomological Society SIG meeting: "Ecology and Evolution of social insects". London, UK.
- 2002 Lopez-Vaamonde, C., Koning, W, Jordan, B., Bourke, A. "Reproductive bumble bee workers do not reduce the production of new queens". XIV International Congress of the International Union for the Study of Social Insects. Hokkaido University, Sapporo, Japan.

Courses & Workshops Attended

Evolution and Phylogenetics

- 7-9 February 2005: "DNA Barcoding of Life". The Natural History Museum, London, UK
- 25 July-6 August 2004: Workshop on "Molecular Evolution". Woods Hole Marine Biological Laboratory, Massachusetts, USA.
- 22-27 April 2001: Workshop in Applied Phylogenetics. Bodega Marine Laboratory, University of Davis, California, USA.
- 24-28 July 2000: Theoretical Genetics and Evolution Summer School, Edinburgh University, UK.

Applied Entomology

- 23-27 September 2005: "Global change and pine processionary moth: a new challenge for integrated pest management" Corsica, Belgodère, Calvi, France,
- 17-19 April 1996: International Course on Integrated Pest Management of Coffee Berry Borer, *Hypothenemus hampei*, (Coleoptera Scolytidae). Centro Nacional de Investigaciones de Café, Cinchiná, Colombia.
- 21-23 September 1995: Course on "Mites of Glasshouses and Nurseries: Identification, Biology and Control". International Institute of Entomology, London, UK
- 3-5 August, 1995: Course on " Whiteflies of Economic Importance and their Natural Enemies". International Institute of Entomology, London, UK.
- 23-30 April 1995: Course on "Taxonomy and Biology of Parasitic Hymenoptera". Imperial College, Silwood Park, UK.
- 12-13 September 1994: Workshop on Integrated Pest Management (IPM) International Institute of Biological Control. European station. Delémont, Switzerland.

Social Insects

- 17-22 September 2003: INSECTS network workshop: "Genomics and Social Insects". University of Lausanne, Switzerland.
- 1-3 November 2002: INSECTS network workshop: "Parasites of Social Insects and Immunology". ETH, Zurich, Switzerland.
- 14-17 February 2002: INSECTS network workshop: "Genetics of Social Insects". Bothnian Bay Research Station, Department of Biology, University of Oulu, Finland.

Fieldwork

Fieldwork	
Bolivia	• 1993 Amazonia Rio Blanco Rio Negro nature reserve
Colombia	• 1996 Central Andes and Choco
Australia	• 1999 Figwasp collection
Papua New Guinea	• 1999 Figwasp collection
Mexico	• 2000 Leaf mine collection
South Africa	• 2010 Leaf mine collection
Greece	• 2008 <i>Cameraria</i> collection in natural stands of horse-chesnuts
Albania	• 2010 <i>Leaf mine</i> collection
Slovenia	
French Guiana	• 2010 Leader of two expeditions to collect leaf miners
Gabon	• 2012 Participate to "Ecole de Terrain en Ecologie Tropicale" at Parc National La Lopé

Teaching

Université des Sciences et Techniques de Masuku de Franceville, Gabon

"Ecole de Terrain dans le Parc National de la Lopé (Gabon): biodiversité, paléoenvironnement et écosystèmes tropicaux ". Teaching Master students of Université des Sciences et Techniques de Masuku de Franceville & Université de Rouen and held by Wildlife Conservation Society. 2 weeks March 2012

University of Orléans, France

Master in "Entomologie Approfondie et gestion des populations d'insectes" (M2)
'Biologie de la Conservation des insectes'. 2h since 2008

University François Rabelais, Tours, France

Master in "Contrôle et conservation des populations d'insectes » (M2)
'Invasions et expansion d'insectes forestiers'. 2h in 2008

Imperial College London, United Kingdom

Course on "Parasitism & Other Life Strategies" (to 2nd year graduate Biology students)
'Social insects, Parasitoids and Predators'. 5 h in 2005

University of Almeria, Spain

Course on "Management of pollination systems" (to biologists and agronomists)
'Behavioural and molecular ecology of the bumblebee *Bombus terrestris*'. 1 h in 2005

University of Sussex, United Kingdom

Course on "Animal Behaviour" (to 3rd year graduate Biology students)
'Evolution of eusociality; Cooperation and conflict in social insects". 6 h in 2004

The Natural History Museum London, United Kingdom

Master in "Advanced Methods in Taxonomy and Biodiversity" (M2)
'Animal-Plant interactions". 7 h from 2001- 2005 (also 12 hours of tutorials)

University College London, United Kingdom

Course on "Wild Animal Biology" (M2)
'Systematics and Conservation". 4 h from 2003- 2004

Research Supervision

In total I have supervised 1 research fellow (Studium); 1 postdoc, 1 PhD, 8 M.Sc. students, 2 technicians and 3 volunteers:

Research Fellow (1)

David C. Lees

INRA Orléans, France

2009-2010 funded by Region Centre « Studium » (co-supervision Sylvie Augustin). Project: « Climate change, demographic expansion and invasion genetics of insect pests ». David is now back back at the Natural History Museum of London, as curator of the Lepidoptera Collection.

Publications:

Lopez-Vaamonde, C., F. C. Breman, D.C Lees, J. Van Houdt & J. De Prins (2012). Analysis of tissue dependent DNA yield for optimal sampling of micro-moths in large-scale biodiversity surveys. **European Journal of Entomology**, 109: 1-6

Hernandez-Lopez A., Rougerie R. Augustin S., Lees D. C., Tomov R., Kenis M., Cota E., Kullaj E., Hansson C., Grabenweger G., Roques A., Lopez-Vaamonde C. (2011). Host tracking or cryptic adaptation? Phylogeography of *Pediobius saulius* (Hymenoptera, Eulophidae), a parasitoid of the highly invasive horse-chestnut leafminer. **Evolutionary Applications** doi: 10.1111/j.1752-4571.2011.00220.x

Lees D.C., Lack, H. W., Rougerie R., Hernandez-Lopez A., Raus, T., Avtzis, N.D., Augustin S. and Lopez-Vaamonde C. (2011) Tracking origins of invasive herbivores using herbaria and archival DNA: the case of the horse-chestnut leafminer. **Frontiers in Ecology and the Environment**, 9 (6): 322-328

Lees D.C., Lopez-Vaamonde C., Augustin S., 2011a. Taxon page for *Cameraria ohridella* Deschka & Dimic 1986. In: *Encyclopedia of Life species*, <http://eolspecies.lifedesks.org/pages/8675>

Lopez-Vaamonde C., Agassiz, D.V.L., Augustin, S., De Prins, J., De Prins, W., Gomboc, S., Ivinskis, P., Karsholt, O., Koutroumpas, A., Koutroumpa, F., Laštůvka, Z., Karsholt, O., Marabuto, E., Olivella, E., Przybyłowicz, L., Roques, A., Ryrholm, N., Šefrová, H., Šima, P., Sims, O., Sinev, S., Tomov, R., Zilli, A. and Lees, D.C., (2010). *Lepidoptera. Chapter 11*. In: Roques A et al. (Eds) *Alien terrestrial arthropods of Europe*. **BioRisk** 4(2): 603–668. doi: 10.3897/biorisk.4.50

Lopez-Vaamonde, C & D.C. Lees. (2010). *Paysandisia archon*, the castniid palm borer (Lepidoptera, Castniidae). In: Roques A et al. (Eds) *Alien terrestrial arthropods of Europe*. **BioRisk** 4(2): 990–991.

Roques A, Kenis M, Lees D, Lopez-Vaamonde C, Rabitsch W, Rasplus Jy, Roy D. 2010. *Alien terrestrial arthropods of Europe*. **BioRisk** Volumes I & II. 1028 pp.

Postdocs (1)

Antonio Hernandez Lopez

INRA Orléans, France

2009 funded by EFPA INRA (co-supervision Sylvie Augustin). He is currently doing a postdoc on speciation of pathogenic bacteria at Didier Raoult's lab at the University of Marseille.

« Génétique des parasites de la mineuse invasive du Marronnier d'Inde »

Publications:

Hernandez-Lopez A., Rougerie R. Augustin S., Lees D., Tomov R., Kenis M., Cota E., Kullaj E., Hansson C., Grabenweger G., Roques A., Lopez-Vaamonde C. (2011). Host tracking or cryptic adaptation? Phylogeography of *Pediobius saulius* (Hymenoptera, Eulophidae), a parasitoid of the highly invasive horse-chestnut leafminer. **Evolutionary Applications** doi: 10.1111/j.1752-4571.2011.00220.x

Lees D.C., Lack, H. W., Rougerie R., Hernandez-Lopez A., Raus, T., Avtzis, N.D., Augustin S. and Lopez-Vaamonde C. (2011) Tracking origins of invasive herbivores using herbaria and archival DNA: the case of the horse-chestnut leafminer. **Frontiers in Ecology and the Environment**, 9 (6): 322-328

Valade R., Kenis M., Hernandez-Lopez A., Augustin S., Mari Mena N., Magnoux E., Rougerie R, Lakatos F., Roques A., Lopez-Vaamonde C., 2009. Mitochondrial and microsatellite DNA markers reveal a Balkan origin for the highly invasive Horse-Chestnut leaf miner *Cameraria ohridella* (Lep. Gracillariidae). **Molecular Ecology**, 18, 3458-3470.

PhD Students (1)

Neus Mari Mena

University of A Coruna, Galicia, Spain

2008-present funded by Spanish Ministry of Science and Education – co-supervision Prof Marta Vila, Université de la Coruna, Espagne)

« Phylogeography and conservation genetics of the protected moth *Graellsia isabellae* (Lepidoptera: Saturniidae)»

Publications:

Mari Mena, N., Lopez-Vaamonde, C, Auger-Rozemberg, MA, Vila, M. (in preparation) Phylogeography of Graellsia isabellae

Millar, J.G., J.S. Mcelfresh, C. Romero, M. Vila, N. Mari Mena & C. Lopez-Vaamonde (2010). Identification of the Sex Pheromone of a Protected Species, the Spanish Moon Moth Graellsia isabellae (Lepidoptera: Saturniidae). Journal of Chemical Ecology, 36 : 923-93

Master Students (8)

Olivier Bouteleux

University François Rabelais, Tours, France

2012 Master in Insect Science (M2) (6 months)

“Rapid inventory via DNA barcoding: cross-lepidopteran diversity survey of Nouragues, French Guiana”

Virginie Gaudin

University François Rabelais, Tours, France

2012 Master in Insect Science (M2) (6 months) co-supervised with David Giron

“Etude populationnelle de l'association hôte-Wolbachia chez la mineuse du pommier *Phyllonorycter blancardella* (Gracillariidae)”

Thibault Andrieux

University François Rabelais, Tours, France

2012 Master in Insect Science (M1) (2 months)

“Use of synthetic pheromone to detect and monitor a protected moth”

Florence Gutzwiller

University François Rabelais, Tours, France

2011 Master in Insect Science (M2) (6 months). Co-supervised with David Giron (IRBI, Tours). She will start a PhD position at Manchester University UK.

“Interactions entre les lépidoptères mineurs de feuilles et leurs endosymbiontes: une approche macroévolutive”

Jean Christophe Bartolucci

University Metz, France

2010 Master in Insect Science (M1) (2 months)

“Mise au point de la phéromone de synthèse de *Graellsia isabellae* (Lepidoptera: Saturniidae)”

Cyril Hemeret

University Orléans, France

2009 Master in Entomology (M1) (2 months)

“Ecologie de la dispersion de *Graellsia isabellae galliaegloria*”

Neus Mari Mena

University of Valencia, Spain

2007 Master in Ecology and Evolution (M2) (6 months). She is currently doing her PhD at A Coruna. “Caracterización de microsatélite polimórficos para el microlepidóptero *Cameraria ohridella* (Gracillariidae)”

Publications:

Mari Mena N., Valade R., Magnoux E., Augustin S., Lopez-Vaamonde 2008. Microsatellites for the highly invasive Cameraria ohridella (Lepidoptera, Gracillariidae) and their amplification in related species. European Journal of Entomology, 105, 945-948.

Romain Valade

University Paris-Sud, France

2006 Master in Ecologie, Biodiversité, Evolution (M2) (6 months). He is currently doing his PhD at INRA Versailles

« Génétique de l'invasion de *Cameraria ohridella* en Europe ».

Publications:

Valade R., Kenis M., Hernandez-Lopez A., Augustin S., Mari Mena N., Magnoux E., Rougerie R, Lakatos F., Roques A., Lopez-Vaamonde C., 2009. Mitochondrial and microsatellite DNA markers reveal a Balkan origin for the highly invasive Horse-Chestnut leaf miner *Cameraria ohridella* (Lep. Gracillariidae). *Molecular Ecology*, 18, 3458-3470.

Technicians

William Koning

Zoological Society of London, UK

2001-2003 "Kin-selected conflict in the bumble bee *Bombus terrestris* (Hymenoptera: Apidae)" (3 years). He then moved to UCL to do his PhD.

Publications:

Lopez-Vaamonde, C., J. W. Koning, W. C. Jordan and A. F. G. Bourke 2003. No evidence that reproductive bumble bee workers reduce the production of new queens. *Animal Behaviour*, 66: 577-584.

Lopez-Vaamonde, C., J. W. Koning, W. C. Jordan & A. F. G. Bourke 2004. A test of information use by reproductive bumblebee workers. *Animal Behaviour*, 68: 611-618.

Lopez-Vaamonde, C., J. W. Koning, R.M. Brown, W. C. Jordan & A. F. G. Bourke. 2004. Social parasitism by male-producing reproductive workers in a eusocial insect. *Nature*, 430: 557-560.

Lopez-Vaamonde, C., N. E. Raine, J. W. Koning, R. M. Brown, J. J. M. Pereboom, T. C. Ings, O. Ramos-Rodriguez, W. C. Jordan & A. F. G. Bourke 2009. Lifetime reproductive success and longevity of queens in an annual social insect. *Journal of Evolutionary Biology*, 22 (5): 983-996.

Ruth Brown

Zoological Society of London, UK

2003-2004 "Kin-selected conflict in the bumble bee *Bombus terrestris* (Hymenoptera: Apidae)" (1 year). She then moved to UCL to do her PhD.

Publications:

Lopez-Vaamonde, C., J. W. Koning, R.M. Brown, W. C. Jordan & A. F. G. Bourke. 2004. Social parasitism by male-producing reproductive workers in a eusocial insect. *Nature*, 430: 557-560.

Lopez-Vaamonde, C. R.M. Brown, E.R. Lucas, J.J.M. Pereboom, W. C. Jordan & A. F. G. Bourke (2007). Effect of the queen on worker reproduction and new queen production in the bumblebee *Bombus terrestris*. *Apidologie*, 38 : 171-180

Lopez-Vaamonde, C., N. E. Raine, J. W. Koning, R. M. Brown, J. J. M. Pereboom, T. C. Ings, O. Ramos-Rodriguez, W. C. Jordan & A. F. G. Bourke 2009. Lifetime reproductive success and longevity of queens in an annual social insect. *Journal of Evolutionary Biology*, 22 (5): 983-996.

Volunteers

Eric Lucas

Zoological Society of London, UK

2004 "Kin-selected conflict in the bumble bee *Bombus terrestris* (Hymenoptera: Apidae)" (1 year). He then moved to University of Sussex, to do his PhD with Jeremy Field on behavioral ecology of wasps.

Publications:

Lopez-Vaamonde, C. R.M. Brown, E.R. Lucas, J.J.M. Pereboom, W. C. Jordan & A. F. G. Bourke (2007). Effect of the queen on worker reproduction and new queen production in the bumblebee *Bombus terrestris*. *Apidologie*, 38 : 171-180

Oscar Ramos

Zoological Society of London, UK

2003-2004 "Kin-selected conflict in the bumble bee *Bombus terrestris* (Hymenoptera: Apidae)" (1 year). He then moved to Queen Mary, University of London, to work as research assistant in Lars Chittka's lab to continue working on bumblebees.

Myriam Smith

Zoological Society of London, UK

2004 "Kin-selected conflict in the bumble bee *Bombus terrestris* (Hymenoptera: Apidae)" (1 year).

Comité de Thèse Doctorat (5)

- Luz Myriam Gómez Piñerez (2008-) Universidad Nacional de Colombia, Sede Medellín. Molecular Ecology of *Hypsipyla grandella* in Cedar plantations in Colombia- COLCIENCIAS fellowship
- Julien Thézé (2011-) Université de Tours, IRBI « Diversification et Adaptation Génomique des Virus Entomopathogènes »
- Adrien Perrard (2009-) UMR5202 OSEB Musée d'Histoire Naturel Paris. « Nervation alaire, taxonomie et phylogénie du genre *Vespa* (Hymenoptera: Vespidae)
- Magally Torres Leguizamon. Université Paris VI. (2007-2010) « Phylogéographie d'un insecte invasif et paradoxe de l'homogénéité génétique »
- Sophie Delamaire. Université d'Orléans (2005-2009). « Structuration génétique des populations de tordeuse du mélèze, *Zeiraphera diniana* (Lepidoptera: Tortricidae), dans l'espace et dans le temps »

Other Activities

Other activities	
Editorial Board	<ul style="list-style-type: none"> • Frontiers in Evolutionary and Population Genetics (2011-) • Nota Lepidopterologica (2007-)
INRA life	<ul style="list-style-type: none"> • Member of “Cellule Web (CW) INRA Orléans” (2006-) • In Charge of web page for URZF INRA Orleans (2006-2011)
Referee for Scientific Journals	<p>81 Manuscripts reviewed for 48 different scientific journals (number of papers reviewed for each journal given between parenthesis): American Midland Naturalist (1); Animal Biodiversity and Conservation (1); Annals of the Entomological Society of America (1); Annals of Forest Science (1); Annales de la Société Entomologique de France (3); Apidology (1); Behavioural Ecology and Sociobiology (5); Biochemical Genetics (1); Biodiversity and Conservation (2); Biological Invasions (1); Biological Journal of the Linnean Society (2); BMC Evolutionary Biology (4); Bulletin of Entomological Research (1); Conservation and Biodiversity (1); Comptes Rendus Academie de Science Série Biologies (1); Diversity and Distributions (1); Ecology Letters (1); Entomologia Experimentalis et Applicata (1); Entomological Science (1); Entomologisk Tidskrift (1); Environmental Entomology (1); Ethology (1); Evolution (7); Evolutionary Applications (1); Evolutionary Ecology (1); Frontiers in Zoology (1); Functional Ecology (1); Insect Conservation and Diversity (2); Insectes Sociaux (1); Israeli Journal of Ecology and Evolution (1); Israel Journal of Plant Sciences (2); Journal of Animal Ecology (1); Journal of Apicultural Research (1); Journal of Biogeography (1); Journal of Ecology and Natural Environment (1); Journal of Ethology (1); Journal of Evolutionary Biology (4); Journal of Insect Science (2); Journal of Medical Entomology (1); Journal of the Royal Society Interface (1); Molecular Ecology (10); Molecular Ecology Ressources (1); Molecular Phylogenetics and Evolution (4); Naturwissenschaften (1); Oecologia (1); PLoS ONE (1), Proceedings of the Royal Society (3), ZooKeys (2).</p>
Grant referee	<ul style="list-style-type: none"> • Royal Society International Outgoing Fellowships (2012) • ANR - Agence Nationale pour la recherche (France): call “jeunes chercheurs” (2011) • South Africa’s National Research Foundation (2006) • BBVA foundation (2007) • Spanish Ministry of Science and Education (2009, 2010, 2011)
PhD Examiner	<ul style="list-style-type: none"> • 2010: Panel of PhD student François Mayer on his MPhil thesis Laboratoire de Lutte biologique de l'ULB. Supervisor : Prof. Jean-Claude Gregoire.
Scientific committee	<ul style="list-style-type: none"> • 2011-2014 : Member of the scientific council of the « Parc naturel régional de la Brenne”. • Referee in panel interview for 2 lectureships at the Natural History Museum Paris (2006) and 1 lectureship (2008).
Scientific	<ul style="list-style-type: none"> • 2005: BBC series “Life in the Undergrowth”. Documentary Chapter

consultancy	5: "supersocieties".
Symposium Organisation	<ul style="list-style-type: none"> • "Insect-plant interactions". Zoological Society of London (2004). • Joint meeting reseaux EFPA "Invasions biologiques" et "Ecologie comportementale": Title: "Comment la dispersion et les mecanismes comportementaux associes peuvent enrichir l'analyse du processus d'invasion biologique?" (2006).
Society Member	<ul style="list-style-type: none"> • Fellow of the Royal Entomological Society (2003-2005) • European Society for Evolutionary Biology (2005) • Society for the Study of Evolution (2005) • Societas Europaea Lepidopterologica (2007-) • The International Union for the Study of Social Insects (2001-2005) • Oreina (2011-) • Société Entomologique Tourangelle et Ligérienne (2011-)

Publications

Peer Reviewed Articles (31)

h-index (calculated by Web of Knowledge 7th February 2012) = 13

(Impact Factor / number of citations based on Google Scholar 7th February 2012) ranking expressed in Quartile

1. **Lopez-Vaamonde, C.**, F. C. Breman, D.C Lees, J.Van Houdt & J. De Prins (2012). Analysis of tissue dependent DNA yield for optimal sampling of micro-moths in large-scale biodiversity surveys. **European Journal of Entomology**, 109: 1-6 (0.945/) Q2
2. Hernandez-Lopez, A., R. Rougerie, S. Augustin, D. Lees, R. Tomov, M. Kenis, E. Cota, E. Kullaj, C. Hansson, G. Grabenweger, A. Roques, **C. Lopez-Vaamonde (2011)** Host tracking or cryptic adaptation? Phylogeography of *Pediobius saulius* (Hymenoptera, Eulophidae), a parasitoid of the highly invasive horse chestnut leafminer. **Evolutionary Applications**. doi: 10.1111/j.1752-4571.2011.00220.x (5.145/) Q1
3. Kawahara, A. Y., I. Ohshima, A. Kawakita, J. C. Regier, C. Mitter, M. P. Cummings, D. R. Davis, D. L. Wagner, J. De Prins, And **C. Lopez-Vaamonde (2011)**. Increased gene sampling provides stronger support for higher-level groups within gracillariid leaf mining moths and relatives (Lepidoptera: Gracillariidae). **BMC Evolutionary Biology**, 11: 182 doi:10.1186/1471-2148-11-182 (3.702/2) Q2
4. Lees, D.C., Lack, H. W., Rougerie, R. Hernandez, A., Raus, T., Avtzis, N.D., Augustin, S. **Lopez-Vaamonde, C.** (2011). Tracking origins of invasive herbivores using herbaria and archival DNA: the case of the horse-chestnut leafminer. **Frontiers in Ecology and the Environment**, 9 (6): 322-328 (8.820/2) Q1
5. Langmaid, J. R., K. Sattler & **C. Lopez-Vaamonde (2011)** Morphology and DNA barcodes show that *Calybites hauderi* (Rebel, 1906) (Lepidoptera: Gracillariidae) does not occur in the British Isles. **Nota Lepidopterologica**, 33 (2): 191-197
6. Rougerie, R., M. A. Smith, J. Fernandez Triana, **C. Lopez-Vaamonde**, S. Ratnasingham, P. D.N. Hebert (2010). Molecular Analysis of Parasitoid Linkages (MAPL): gut-contents of adult parasitoid wasps reveal larval host. **Molecular Ecology**, 20: 179-186. (6.457/5) Q1
7. Millar, J.G., J.S. Mcelfresh, C. Romero, M. Vila, N. Mari Mena & **C. Lopez-Vaamonde (2010)**. Identification of the Sex Pheromone of a Protected Species, the Spanish Moon Moth *Graellsia isabellae* (Lepidoptera: Saturniidae). **Journal of Chemical Ecology**, 36 : 923-932 (2.486/2) Q2
8. Vila, M., N. Mari Mena, S-H. Yen & **C. Lopez-Vaamonde (2010)**. Characterization of ten polymorphic microsatellite markers for the protected Spanish Moon Moth *Graellsia isabellae* (Lepidoptera: Saturniidae). **Conservation Genetics**, 11 (3): 1151-1154 (1.255/2) Q2
9. De Prins, J., R. Mozuraitis, **C. Lopez-Vaamonde** & R. Rougerie (2009). Sex attractant, distribution and DNA barcodes for the Afrotropical leaf-mining moth *Phyllonorycter melanosparta* (Lepidoptera: Gracillariidae). **Zootaxa**, 2281 : 53-67 (0.853/2) Q3
10. Valade, R., M. Kenis, A. Hernandez, S. Augustin, N. Mari Mena, E. Magnoux, R.

- Rougerie, F. Lakatos, A. Roques & **C. Lopez-Vaamonde** (2009) Mitochondrial and microsatellite DNA markers reveal a Balkan origin for the highly invasive Horse-Chestnut leaf miner *Cameraria ohridella* (Lep. Gracillariidae). **Molecular Ecology**, 18 : 3458-3470 (6.457/27) Q1
11. **Lopez-Vaamonde, C.**, N. Wikström, K. M. Kjer, Jy. Rasplus, C. Machado, G. Weiblen & J. M. Cook (2009) Molecular dating and biogeography of fig-pollinating wasps. **Molecular Phylogenetics and Evolution**, 52: 715-726 (3.889/19) Q2
 12. Vilà, M., C. Basnou, P; Pysek, M. Josefsson, P; Genovesi, S. Gollasch, W. Nentwig, S. Olenin, A. Roques, D. Roy, P. Hulme, And Daisie Partners Including Augustin S., Lopez-Vaamonde C. & Yart A., (2009) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. **Frontiers in Ecology and the Environment** 8 (3): 135-144. (8.820/63) Q1
 13. Vila, M., M. A. Auger Rozenberg, F. Goussard & **C. Lopez-Vaamonde** (2009). Effect of non-lethal sampling of DNA on life history traits of the protected moth *Graellsia isabelae* (Lepidoptera: Saturniidae). **Ecological Entomology**, 34 : 356-362. (1.852/7) Q1
 14. **Lopez-Vaamonde, C.**, N. E. Raine, J. W. Koning, R. M. Brown, J. J. M. Pereboom, T. C. Ings, O. Ramos-Rodriguez, W. C. Jordan & A. F. G. Bourke (2009). Lifetime reproductive success and longevity of queens in an annual social insect. **Journal of Evolutionary Biology**, 22 (5): 983-996. (3.656/6) Q2
 15. Kenis, M., M.-A. Auger-Rozenberg, A. Roques, L. Timms, C. Péré, M.J.W. Cock, J. Settele, S. Augustin & **C. Lopez-Vaamonde** (2009). Ecological effects of invasive alien insects. **Biological Invasions**, 11: 21-45. (3.474/95) – Q1
 16. Mari Mena, N., R. Valade, E. Magnoux, S. Augustin & **C. Lopez-Vaamonde** (2008). Microsatellites for the highly invasive *Cameraria ohridella* (Lepidoptera, Gracillariidae) and their amplification in related species. **European Journal of Entomology**, 105 : 945-948 (0.945/3) Q2
 17. Sims & **C. Lopez-Vaamonde** (2008) *Psyche casta* (Pallas) (Lepidoptera: Psychidae) from an Essex saltmarsh; its possible divergence, via ecological specialisation, from inland populations. **British Journal of Entomology and Natural History**, 21: 27-29.
 18. **Lopez-Vaamonde, C.**, R.M. Brown, E.R. Lucas, J.J.M. Pereboom, W. C. Jordan & A. F. G. Bourke (2007). Effect of the queen on worker reproduction and new queen production in the bumblebee *Bombus terrestris*. **Apidologie**, 38 : 171-180 (2.230/9) Q1
 19. **Lopez-Vaamonde, C.**, N. Wikström, C. Labandeira, H. C. J. Godfray, S. J. Goodman & J. M. Cook, (2006). Fossil-calibrated molecular phylogenies reveal that leaf-mining moths radiated several million years after their host plants. **Journal of Evolutionary Biology**, 19: 1314-1326. (3.656/36) Q2
 20. **Lopez-Vaamonde, C.** H. C. J. Godfray, S. West, C. Hansson And J. M. Cook, (2005). The evolution of host use and unusual reproductive strategies in *Achrysocharoides* parasitoid wasps. **Journal of Evolutionary Biology**, 18: 1029-1041. (3.656/19) Q2
 21. **Lopez-Vaamonde, C.**, J. W. Koning, W. C. Jordan & A. F. G. Bourke (2004). A test of information use by reproductive bumblebee workers. **Animal Behaviour**, 68: 611-618. (3.101/7) Q1

22. **Lopez-Vaamonde, C.**, J. W. Koning, R.M. Brown, W. C. Jordan & A. F. G. Bourke. (2004). Social parasitism by male-producing reproductive workers in a eusocial insect. **Nature**, 430: 557-560. (36.104/73) Q1
23. **Lopez-Vaamonde, C.**, J. W. Koning, W. C. Jordan & A. F. G. Bourke (2003). No evidence that reproductive bumble bee workers reduce the production of new queens. **Animal Behaviour**, 66: 577-584. (3.101/19) Q1
24. **Lopez-Vaamonde, C.**, H. C. J. Godfray And J. M. Cook. (2003). Evolutionary dynamics of host plant use in a genus of leaf-mining moths. **Evolution**, 57 (8): 1804-1821. (5.659/60) Q1
25. **Lopez-Vaamonde, C.** D. Dixon, J. M. Cook And J. Y. Rasplus (2002). Revision of the Australian species of *Pleistodontes* (Hymenoptera: Agaonidae) fig-pollinating wasps and their host plant associations. **Zoological Journal of the Linnean Society**, 136: 637-683. (2.319/33) Q1
26. Belshaw, R. **C. Lopez-Vaamonde** , N. Degerli And D.L.J., Quicke (2001).- Paraphyletic taxa and taxonomic chaining: evaluating the classification of braconine wasps (Hymenoptera: Braconidae) using 28S D2-3 rDNA sequences and morphological characters. **Biological Journal of the Linnean Society**, 73: 411-424. (2.166/26) Q3
27. **Lopez-Vaamonde, C.**, G. Weiblen, J. Y. Rasplus And J. M. Cook (2001).- Molecular phylogenies of fig wasps: Partial co-cladogenesis of pollinators and parasites. **Molecular Phylogenetics and Evolution**, 21 (1): 55-71. (3.889/78) Q2
28. Fuester, R. W., M. Kenis, K. S. Swan, P. C. Kingsley, **C. Lopez-Vaamonde** and F. Herard (2001).- Host Range of *Aphantorhaphopsis samarensis* (Villeneuve) (Diptera: Tachinidae), a Larval Parasite of the Gypsy Moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). **Environmental Entomology**, 30: 605-611. (1.534/19) Q2
29. Quicke, D.L.J., R. Belshaw, **C. Lopez-Vaamonde** (1999).- Preservation of hymenopteran specimens for subsequent molecular and morphological study. **Zoologica Scripta**, 28 (1-2): 261-276. (3.091/21) Q1
30. Quicke, D.L.J., **C. Lopez-Vaamonde** and R. Belshaw (1999).- The basal Ichneumonidae (Insecta: Hymenoptera): 28S rDNA considerations of the Brachycyrtinae, Labeninae, Paxylommatinae and Xoridae. **Zoologica Scripta**, 28 (1-2): 203-209. (3.091/17) Q1
31. **Lopez-Vaamonde C.** and D. Moore (1998).- Developing methods for testing host specificity of *Phymastichus coffea* Lasalle (Hym. Tetrastichinae) a potential biological control agent of *Hypothenemus hampei* (Ferrari) (Col. Scolytidae) in Colombia. **Biocontrol Science and Technology**, 8: 397-411. (0.882/19) Q3

Co-editor of books (1)

Roques A, Kenis M, Lees D, **Lopez-Vaamonde C**, Rabitsch W, Rasplus Jy, Roy D. 2010. Alien terrestrial arthropods of Europe. BioRisk Volumes I & II. 1028 pp. Pensoft.

Book Chapters (8)

1. Augustin S., Kenis M., Valade R., Gilbert M., Garcia J., Roques A., **Lopez-Vaamonde C.**, 2010. A Stowaway species from the Balkans, the horse chestnut leafminer, *Cameraria ohridella*. In : Settele, J. et al. (eds.): Atlas of Biodiversity Risks, chapter 6.

Pensoft, Sofia & Moscow. Pp. 160-161.

2. **Lopez-Vaamonde, C.** and Lees, D.C. (2009). *Spodoptera littoralis*, African cotton leaf worm (Lepidoptera, Noctuidae). In: Roques, A., ed. Handbook of alien terrestrial arthropods in Europe page: 339. Pensoft.
3. **Lopez-Vaamonde, C.**, Agassiz, D.V.L., Augustin, S., De Prins, J., De Prins, W., Gomboc, S., Ivinskis, P., Karsholt, O., Koutroumpas, A., Koutroumpa, F., Laštůvka, Z., Karsholt, O., Marabuto, E., Olivella, E., Przybylowicz, L., Roques, A., Ryrholm, N., Šefrová, H., Šima, P., Sims, O., Sinev, S., Tomov, R., Zilli, A. and Lees, D.C., 2010a. Lepidoptera. Chapter 11. In: Roques A et al. (Eds) Alien terrestrial arthropods of Europe. *BioRisk* 4(2): 603–668. doi: 10.3897/biorisk.4.50
4. **Lopez-Vaamonde, C.**, Glavendekic, M. & Santos de Paiva M.R. (2010b) Invaded habitats. Chapter 4. In: Roques A et al. (Eds) Alien terrestrial arthropods of Europe. *BioRisk* 4(1): 45–50. doi: 10.3897/biorisk.4.66
5. **Lopez-Vaamonde, C.** (2010). *Spodoptera littoralis*, African cotton leaf worm (Lepidoptera, Noctuidae). In: Roques A et al. (Eds) Alien terrestrial arthropods of Europe. *BioRisk* 4(2): 1008–1009.
6. **Lopez-Vaamonde, C.** (2010). *Paysandisia archon*, the castniid palm borer (Lepidoptera, Castniidae). In: Roques A et al. (Eds) Alien terrestrial arthropods of Europe. *BioRisk* 4(2): 990–991.
7. Roques A., Rabitsch W, Rasplus JY, **Lopez-Vaamonde C**, Nentwig W, Kenis M, 2009. Alien terrestrial invertebrates of Europe. In W. Nentwig, P. Hulme, P. Pysek, M. Vila (Eds), Handbook of Alien Species in Europe. Springer- Verlag, 63-79.
8. **Lopez-Vaamonde C.**, Augustin S., Roques A., Cota E., Kullaj E., Avtzi N., Tomov R., Naceski S., Papazova I., 2009. Genetic Study of an Invasive Forest Insect and its Parasitoid in the Balkan Region. In: Macháčová J. & Rohsmann K., (eds.): Scientific results of the SEE-ERA.NET Pilot Joint Call. Centre for Social Innovation (ZSI), Vienna, 121-128.

Online Publications (1)

Lees, D., **Lopez-Vaamonde, C.**, Augustin, S., 2011a. Taxon page for *Cameraria ohridella* Deschka & Dimic 1986. In: EOLspecies, <http://eolspecies.lifedesks.org/pages/8675>

Popular Science (2)

Cook J. M. and **C. Lopez-Vaamonde**, (2001).- Fig Biology: Turning over new leaves. *Trends in Ecology & Evolution*, 16 (1): 11-13.

Cook J. M. and **C. Lopez-Vaamonde** (2001).- Figs and fig wasps: evolution in a microcosm. *Biologist* 48 (3): 105-110.

Book Reviews (5)

Lopez-Vaamonde, C. (2004). Bumblebees: Behaviour and Ecology, by Dave Goulson. International Society for Behavioral Ecology Newsletter, 16: 7-8.

Lopez-Vaamonde, C. (2003). Studying antagonistic and mutualistic interactions: Plant-Animal interactions, by Carlos Herrera and Olle Pellmyr (Eds.). Bulletin of the Royal

Entomological Society, *Antenna*, 27, 104-105.

Lopez-Vaamonde, C. (2003). Tangled trees: Phylogeny, Cospeciation and Coevolution, by Rod Page (Ed.). *Bulletin of the Royal Entomological Society, Antenna*, 28: 260-261.

Lopez-Vaamonde, C. (2002). Describing the systematics of Iberian longhorned beetles: Coleoptera Cerambycidae. *Fauna Iberica*, by Eduard Vives. *Bulletin of the Royal Entomological Society, Antenna*, 26, 29-30

Lopez-Vaamonde, C. (2002). Illustrating the diversity of a longhorn beetle genus: Iconografía del género *Iberodorcadion* (Coleoptera, Cerambycidae), by Romero Samper. *Bulletin of the Royal Entomological Society, Antenna*, 27, 330.

Table 1: Publication Subject Categories and Ranking – period 1998-2012

Subject Category	Number of papers	Journals - Quartile (# papers)
Multidisciplinary Sciences	1	Nature - Q1 (1)
Ecology	4	Frontiers in Ecology and the Environment - Q1 (2) Journal of Chemical Ecology – Q2 (1) Biological Invasions – Q1 (1)
Evolutionary Biology	11	Biological Journal of the Linnean Society – Q3 (1) BMC Evolutionary Biology – Q2 (1) Evolutionary Applications - Q1 (1) Evolution - Q1 (1) Journal of Evolutionary Biology- Q2 (3) Molecular Ecology - Q1 (2) Molecular Phylogenetics and Evolution – Q2 (2)
Zoology	6	Animal Behaviour - Q1 (2) Zoological Journal of the Linnean Society – Q1 (1) Zoologica Scripta - Q1 (2) Zootaxa – Q3 (1)
Entomology	6	Apidologie – Q1 (1) Biocontrol Science and Technology – Q3 (1) Ecological Entomology – Q1 (1) Environmental Entomology – Q2 (1) European Journal of Entomology – Q2 (2)
Biodiversity and Conservation	1	Conservation Genetics – Q2 (1)

**Mémoire pour l'obtention de
l'Habilitation à Diriger des Recherches**

**Evolutionary and Ecological studies
of insects**

Résumé

Les interactions entre les organismes jouent un rôle important dans l'organisation de la biodiversité. Toutes les espèces s'engagent d'une manière ou d'une autre dans des interactions interspécifiques. De nombreux caractères évolutifs peuvent être interprétés comme des adaptations aux interactions avec des parasites, compétiteurs, symbiontes, et enfin mutualistes.

Un des objectifs majeur de mes recherches a été l'étude des conflits évolutifs liés aux interactions intra et inter spécifiques et leurs conséquences sur le plan sélectif au niveau des gènes, des individus et des espèces, par l'utilisation d'approches appliquées et fondamentales. Je me suis intéressé en particulier aux conflits pour les ressources liés au parasitisme, au mutualisme entre insectes et plantes et aux conflits liés à la sélection de parentèle chez les insectes sociaux. Plus récemment, j'ai travaillé à l'INRA sur la biologie de l'invasion des mineuses et comment les parasitoïdes natifs s'adaptent à l'arrivée des ces envahisseurs.

Utilisant principalement les outils issus de la phylogénétique, j'ai contribué à la compréhension de l'histoire évolutive des groupes d'insectes sur lesquels j'ai travaillé, notamment les mineuses de la famille Gracillariidae, leurs parasitoïdes et les guêpes des figuiers pollinistricides (Agaonidae) et parasites (Sycoryctinae). Le mémoire est divisé en chapitres correspondants aux questions principales. Les principaux résultats sont résumés ci-après.

1. Travaux pré- doctoraux

Ecologie, systématique et contrôle biologique d'insectes forestiers

Écologie et systématique des Cerambycidae.

Dès mes études de maîtrise, je me suis intéressé à l'écologie et la systématique des insectes forestiers (Lopez-Vaamonde et al. 1993a,b, 1995, 2000). De 1984 à 1992 j'ai étudié les longicornes (Coleoptera, Cerambycidae) de la Galice, région du Nord-ouest de la péninsule ibérique. Un des objectifs principaux de cette étude était d'identifier les conditions d'habitat exigées par les espèces, afin d'établir des recommandations pour leur conservation, et de définir des sites d'importance écologique, en fonction de leur distribution et de leur statut. J'ai compilé une liste récapitulative des 109 espèces de Cerambycidae décrites en Galice. De plus, j'ai recensé la présence des 36 nouvelles espèces pour la Galice. La base de données repose sur les résultats provenant de 516 localités et a été analysée selon un point de vue biogéographique. Le statut de chaque espèce a été examiné selon les critères établis par l'IUCN et une liste rouge comprenant les espèces menacées a été proposée (Lopez-Vaamonde et al., 1993b, 2000). Ce nouveau catalogue établit donc une base à partir de laquelle on pourra détecter les futurs changements d'abondance de certaines espèces. De ce fait, une meilleure gestion des habitats et une stratégie de conservation de cette taxocénose pourrait être envisagée. Le catalogue des Cerambycidae a été mis on-line et il est actualisé régulièrement avec de nouvelles données :

<http://www.aegaweb.com/inventario/index.htm> (aller à Coleoptera puis à Cerambycidae).

Contrôle biologique d'insectes forestiers

Après ma maîtrise, j'ai eu l'opportunité de continuer à cultiver mon intérêt pour les insectes forestiers en travaillant comme ingénieur de recherche dans la section Forêt de CABI Bioscience, station de Delémont en Suisse, sous la direction de l'entomologiste forestier Dr. Marc Kenis. J'étais chargé de collecter et de développer des protocoles d'élevage et des tests de spécificité pour plusieurs insectes parasitoïdes d'insectes forestiers (Kenis and Lopez-Vaamonde, 1997; Fuester et al. 2001).

En 1995-1996, j'ai travaillé pendant 18 mois sur le contrôle biologique du scolyte des baies du caféier à CABI Bioscience à Silwood Park en Angleterre. J'ai importé le parasitoïde *Phymastichus coffea* (Hym. Eulophidae) du Kenya, et développé des protocoles d'élevage et des tests de spécificité en quarantaine au Royaume-Uni et introduit le parasitoïde en Colombie (Lopez-Vaamonde et Moore, 1998). Les derniers résultats montrent que le parasitoïde s'est établi en Colombie et que son impact sur le scolyte est non négligeable.

2. Travaux de Thèse

Évolution des interactions insectes /plantes-hôtes.

Des études sur l'utilisation des plantes-hôtes par les insectes phytophages ont montré quelques patrons macro-évolutifs. Premièrement, les espèces d'insectes taxonomiquement proches ont une tendance à se nourrir de plantes aussi phylogénétiquement proches, bien qu'une concordance entre les phylogénies d'insectes et plantes est plutôt rare et beaucoup de changement d'hôtes entre plantes phylogénétiquement éloignées ont été documentés. Deuxièmement, bien que les insectes herbivores montrent plusieurs degrés de polyphagie, la plupart des espèces sont des spécialistes, qui mangent une espèce de plant-hôte ou bien quelques espèces congénériques.

Les mécanismes responsables de la formation de ces deux patrons macroévolutifs sont toujours à élucider. Par exemple la cospéciation entre insectes et plantes; où le changement sur des nouvelles plantes-hôtes taxonomiquement, écologiquement ou chimiquement similaires aux plantes originelles ont été suggéré comme des mécanismes responsables de ces patrons macroévolutifs. La publication récente des phylogénies de grands clades d'insectes herbivores et de leurs plantes nous permet d'étudier ces mécanismes à un niveau phylogénétique.

Au cours de ma thèse, j'ai étudié les patrons phylogénétiques de l'utilisation des plantes-hôtes chez les microlépidoptères mineuses des feuilles du genre *Phyllonorycter* (Lep. Gracillariidae). J'ai reconstruit les phylogénies moléculaires de 77 espèces de *Phyllonorycter* et de leurs plantes-hôtes. J'ai combiné des données phylogénétiques (insectes et plantes) avec des données écologiques (spectre d'hôte, situation de la mine) pour répondre aux questions suivantes:

(1) Y a-t-il des évidences de cocladogénèse entre les mineuses et leurs plantes-hôtes ?

(2) S'il n'y a pas eu de cocladogénèse, y a-t-il une tendance à coloniser de nouvelles plantes-hôtes phylogénétiquement proches? Ceci démontrerait un conservatisme phylogénétique.

(3) Est-ce que l'évolution de nouveaux moyens d'exploiter la plante-hôte, par exemple, miner la partie supérieure des feuilles par rapport à la partie inférieure, a conduit à une radiation significative dans de nouvelles zones adaptatives ?

Mes études phylogénétiques ont montrées que, malgré leur grande spécificité, les mineuses du genre *Phyllonorycter* n'ont pas cospécié avec leurs plantes-hôtes (Lopez-Vaamonde et al., 2003b; 2006). Les mineuses se seraient diversifiées après la divergence de leurs plantes hôtes (Lopez-Vaamonde et al., 2006). Néanmoins l'évolution de l'utilisation des plantes-hôtes est phylogénétiquement conservée. C'est à dire que la taxinomie des plantes contraint le patron de changements de plantes-hôtes (Lopez-Vaamonde et al., 2003b).

Évolution des interactions tritrophiques: insectes, plantes-hôtes et parasitoïdes

J'ai testé pour la première fois l'hypothèse de la cospéciation entre insectes et plantes au niveau tritrophique (Lopez-Vaamonde et al., 2005). J'ai étudié en particulier les parasitoïdes du genre *Achrysocharoides* (Hym., Eulophidae). Ces guêpes sont endoparasitoïdes des larves de microlépidoptères de la famille des Gracillariidae qui minent les feuilles. De tous les genres de guêpes parasitoïdes qui attaquent les chenilles de *Phyllonorycter*, *Achrysocharoides* est sans doute le plus spécifique. Néanmoins, la plupart des espèces d'*Achrysocharoides* sont aussi spécifiques du point de vue de la plante-hôte. En effet, les *Achrysocharoides* présentent une spécificité d'hôte que l'on peut définir comme "écologique". Ainsi, les *Achrysocharoides* attaquent spécifiquement toutes les chenilles de mineuses du genre *Phyllonorycter* présentes sur un genre d'arbre, indépendamment des relations phylogénétiques des microlépidoptères. Les *Achrysocharoides* semblent être plus spécifique de la plante-hôte que de l'insecte-hôte (*Phyllonorycter*). Cette spécificité écologique est très rare chez les parasitoïdes et suggère que la compétition interspécifique est responsable du partage des niches écologiques dans ce genre. De plus, les guêpes du genre *Achrysocharoides* présentent des stratégies reproductives remarquables. (1) Quelques espèces oviposent un seul oeuf mâle par hôte mais groupent les oeufs femelles par deux ou trois. (2) D'autres espèces déposent des pontes grégaires de mâles ou de femelles ("split sex brood"). (3) Et il y a des espèces qui produisent des pontes mixtes d'oeufs mâles et femelles. Les parasitoïdes non polyembryoniques avec des "split sex broods" sont très rares et presque exclusivement du genre *Achrysocharoides* tandis que les autres stratégies sont plus communes.

Reconstruire la phylogénie moléculaire des 15 espèces d'*Achrysocharoides* m'a permis d'étudier trois questions:

1. -J'ai examiné l'évolution des différentes stratégies reproductives: 1) solitaire, 2) groupes grégaires mixtes, 3) pontes grégaires séparées (« split sex broods »). Mes résultats suggèrent que la stratégie de groupes grégaires séparés a évolué deux fois et qu'il y a eu une transition de la stratégie solitaire à la stratégie de pontes grégaires mixtes, via la stratégie de pontes grégaires séparées comme la théorie le prédit.

2.-J'ai étudié l'évolution de l'utilisation des hôtes insecte et plante en comparant la phylogénie des parasitoïdes avec celles des hôtes: mineuses et plantes-hôtes (Lopez-Vaamonde et al., 2005). Ce papier présente la première étude publiée de phylogénétique au niveau tri-trophique. J'ai aussi montré que les parasitoïdes n'ont pas cospécié mais radié plus récemment (ou plus rapidement) que leurs insectes-hôtes (mineuses *Phyllonorycter*)

(Lopez-Vaamonde et al., 2005). Par ailleurs, les parasitoïdes montrent un patron phylogénétiquement conservé de l'utilisation des genres de plantes-hôtes. Pour resumer, mes résultats montrent que les plantes jouent un plus grand rôle que les insectes herbivores dans la radiation des parasitoïdes

3.-Finalement, j'ai testé des hypothèses taxinomiques. Le genre *Achrysocharoides* a fait l'objet de plusieurs révisions taxinomiques, dû à l'existence de complexes d'espèces difficiles à étudier morphologiquement. Ma phylogénie moléculaire est congruente avec la classification classique basée sur des caractères morphologiques.

Évolution des interactions entre les guêpes pollinisatrices et parasites des figuiers

Il existe environ 700 espèces de figuiers. Chaque espèce est généralement pollinisée par une seule espèce de guêpe agaonide. La nature intime et spécifique de ce mutualisme obligatoire suggère que les figuiers et leurs guêpes pollinisatrices ont coévolué (Cook & Lopez Vaamonde 2001 a,b). Actuellement, de nombreux travaux de recherche tentent de tester l'hypothèse de coévolution par la reconstruction d'arbres phylogénétiques. Les premiers résultats indiquent qu'il y a eu un nombre significatif d'événements de cospéciation entre les figuiers et leurs guêpes pollinisatrices et aussi entre certains groupes de guêpes parasitiques et les pollinisateurs. J'ai choisi d'étudier les interactions coévolutives entre les figuiers Australiens de la section *Malvanthera*, leurs guêpes pollinisatrices (*Pleistodontes*) et leurs guêpes parasitiques (*Sycoscapter*).

Pour tester des hypothèses de cospéciation il est indispensable de définir dès le départ le nombre d'espèces appartenant au groupe étudié ainsi que d'établir toutes les associations et leur spécificité. Quand j'ai commencé ma thèse, une révision des figuiers *Malvanthera* était en cours par Dale Dixon (Université Townsville, Australie). Ce travail a mis à jour la nécessité de réviser la taxonomie des pollinisateurs. Pendant cette révision, j'ai trouvé sept espèces nouvelles qui ont été décrites et publiées (Lopez Vaamonde et al. 2002). Dans cet article, les associations avec les plantes hôtes ont aussi été révisées et nous avons trouvé trois exceptions à la règle d'une seule espèce de pollinisateur pour une seule espèce de figuier : (1) La coexistence sympatrique de deux pollinisateurs ; (2) un cas de ségrégation géographique où une espèce de figuier est pollinisée par deux espèces de pollinisateurs ; et (3) deux espèces de figuiers qui sont pollinisées par une seule espèce de pollinisateur. Malheureusement, je n'ai pas pu compléter la révision systématique des guêpes parasitiques (*Sycoscapter*) à cause de leur grande similarité morphologique. Jean Yves Rasplus est actuellement en train de compléter cette révision.

Une fois que la révision taxonomique des pollinisateurs a été achevée, il a été possible de commencer la reconstruction de leurs phylogénies moléculaires (Lopez Vaamonde et al. 2001). J'ai utilisé trois marqueurs, deux nucléaires : 28S et ITS et un mitochondrial: Cyt *b*, pour 20 espèces de *Pleistodontes* et 16 espèces de *Sycoscapter*. J'ai reconstruit les phylogénies moléculaires pour les deux genres de guêpes et comparé leurs topologies. Les résultats ont montré un niveau significatif de co-cladogénèse. Cependant celle-ci n'est pas parfaite ce qui indique des changements d'hôtes au cours de l'évolution de ces interactions.

En conclusion, mes travaux sur la taxonomie et la phylogénie ont confirmé la grande spécificité du système figuier, mais ont aussi révélé quelques exceptions à la règle. De plus, en utilisant des données moléculaires j'ai montré que des co-pollinisateurs d'un seul figuier

sont des espèces soeurs, ce qui suggère que certaines lignées de guêpes montrent une tendance à spécié indépendamment et plus rapidement que leurs hôtes, les figuiers (Lopez Vaamonde et al. 2001).

Finalement, dans une étude publiée récemment (le dernier article de ma thèse) je montre que l'origine du mutualisme entre figuiers et pollinisateurs est probablement asiatique mais les techniques moléculaires de datation ne permettent pas de dater avec certitude l'origine des agaonides (Lopez Vaamonde et al. 2009a).

3. Travaux post-doctoraux

Écologie moléculaire et comportementale du bourdon terrestre

Après ma thèse, j'ai travaillé comme chercheur postdoctoral à l'Institut de Zoologie, à la Société Zoologique de Londres pendant trois ans (2001-2004). Mon projet consistait à tester plusieurs hypothèses sur la sélection de parentèle chez le bourdon terrestre *Bombus terrestris*. Les méthodes utilisées incluent la manipulation de colonies en conditions de laboratoire, l'observation du comportement d'individus marqués, et le typage génétique par microsatellites de plusieurs milliers d'individus (Lopez Vaamonde *et al.* 2003a; 2004a,b; 2007; 2009b).

Le bourdon terrestre est un excellent modèle pour étudier des hypothèses de sélection de parentèle en raison de leur régime de reproduction. Les colonies sont fondées par une seule reine, qui s'est accouplée avec un seul mâle. Il en résulte que les reines sont plus apparentées avec leurs fils (niveau de parenté, $r = 0.5$) qu'avec les fils des ouvrières ($r = 0.25$). En comparaison, les ouvrières sont plus apparentées avec leurs propres fils ($r = 0.5$) et les fils d'autres ouvrières ($r = 0.375$) qu'avec les fils de reines ($r = 0.25$). Dans ce genre de situations, la théorie de la sélection de parentèle prévoit un conflit potentiel pour la production des mâles. Les reines devraient favoriser l'élevage de leurs fils, tandis que les ouvrières devraient favoriser l'élevage de mâles produits par des ouvrières.

J'ai testé l'hypothèse que les ouvrières expriment leurs propres intérêts génétiques en produisant des fils. En génotypant 1563 jeunes mâles adultes produits par 32 colonies semi-naturelles avec 2.5 loci microsatellite en moyenne par individu, et en génotypant la reine, sa spermatèque et les ouvrières de la même colonie j'ai démontré que les ouvrières produisent 4.3% des mâles. Par conséquent, j'ai confirmé que les ouvrières arrivent à s'échapper au contrôle de la reine et expriment leurs intérêts de parentèle en produisant des mâles adultes, bien que le pourcentage de mâles adultes produits par les ouvrières est très bas (Lopez-Vaamonde et al., 2004b).

Le résultat le plus important de ma recherche postdoctorale a été publié dans le journal Nature (Lopez-Vaamonde et al., 2004b). J'ai découvert que quelques ouvrières de *B. terrestris* s'introduisent dans des colonies conspécifiques et non apparentées dans lesquelles elles produisent des mâles adultes. Ces ouvrières agissent comme parasites sociaux et sont significativement plus reproductives et se comportent plus agressivement que les ouvrières résidentes. Ceci implique que l'usage de la sélection de parentèle pour expliquer le niveau de reproduction des ouvrières ne requiert pas seulement les intérêts de parentèle des ouvrières résidentes. Il faudra aussi connaître toutes les options reproductives disponibles aux ouvrières en tenant en compte du parasitisme social intraspécifique.

Dans une étude récente, nous avons montré que 3% des ouvrières des colonies de *B. terrestris* prélevées dans la nature sont originaires d'autres colonies conspécifiques et que des ouvrières peuvent envahir d'autres colonies situées jusqu'à 60 mètres de distance (Zanette et al soumis).

Cette découverte suggère que chez *B. terrestris* et peut être aussi chez d'autres abeilles et guêpes sociales quelques ouvrières se comportent comme parasites sociales intraspecificque. Ce résultat a attiré l'attention des moyens de communication et a été présenté dans la série de documentaires de la BBC, dirigé par David Attenborough "Life In the Undergrowth" (chapitre 5 sur les sociétés d'insectes « supersocieties »).

En conclusion, si la théorie de sélection de parentèle a été avancée pour expliquer la fondation des sociétés de vertébrés et d'invertébrés, il reste encore à démontrer quel rôle elle joue dans leur fonctionnement.

4. Travaux Chargé de Recherche

Depuis mon recrutement à l'INRA en Juillet 2005, mon activité principale de recherche a été centrée sur l'étude de la diversité génétique des insectes forestiers concentrée principalement sur cinq thématiques:

- Traçage génétique de l'origine géographique d'espèces invasives et étude de leurs parasitoïdes
- Inventorier les espèces exotiques d'insectes en Europe
- Développement de bases de données code barre ADN et de phylogénies moléculaires
- Conservation des espèces menacées d'insectes forestiers
- Evolution et signification adaptative du mode de vie endophyte chez les insectes

Traçage génétique de l'origine géographique d'espèces invasives et étude de leurs parasitoïdes

Les invasions biologiques sont des processus d'évolution rapide au cours desquels les populations souffrent d'un effet de fondation suivi d'une expansion rapide. Ainsi les populations des fronts d'expansion sont souvent génétiquement moins variables que les populations d'origine. Connaître l'origine géographique des espèces invasives est essentiel pour déterminer quels sont leurs ennemis naturels qui pourraient être utilisés dans la lutte biologique (Vilà et al 2009).

La mineuse du marronnier, *Cameraria ohridella*, est un microlépidoptère qui a été observé pour la première fois en Macédoine en 1984. Depuis, elle a colonisé progressivement l'Europe Centrale et Occidentale à une vitesse alarmante. Elle a envahi toute la France en seulement quatre ans. Les larves sont des mineuses de feuilles et s'attaquent principalement au marronnier d'Inde, *Aesculus hippocastanum*, espèce endémique des Balkans mais utilisé à des fins ornementales en milieu urbain partout en Europe. Les larves de *C. ohridella* provoquent le brunissement des feuilles pouvant aller jusqu'à leur chute prématurée en été. Les dégâts sont souvent spectaculaires provoquant l'inquiétude du public et des responsables locaux. Les rares forêts naturelles de marronniers qui survivent dans les Balkans sont elles aussi très attaquées et leur futur semble compromis (Lees et al 2009 ; Lopez Vaamonde et al 2009c).

La lutte contre ce ravageur est très difficile car elle fait face à un accroissement rapide des populations, une grande disponibilité de la plante hôte, un traitement chimique difficile et très coûteux en milieu urbain et une absence de prédateurs et de parasitoïdes spécifiques.

Les objectifs de ce projet sont doubles:

- Tracer génétiquement l'origine de cette espèce pour trouver des ennemis naturels spécifiques dans un but de lutte biologique.
- Etudier l'écologie et la systématique des parasitoïdes qui attaquent *Cameraria* pour leur possible utilisation en lutte biologique.

Identification de l'aire d'origine de *Cameraria ohridella*

Le contrôle biologique classique de *C. ohridella* est considéré comme l'unique option valable à long terme, mais nécessite de trouver des prédateurs et/ou des parasitoïdes spécifiques. Ceci implique de trouver au préalable l'origine géographique de *C. ohridella*. Les scientifiques ont longtemps débattu pour déterminer si l'invasion de la mineuse était le fruit d'une introduction à partir de l'Asie du Sud ou d'une acquisition d'aptitude invasive à la suite d'un récent changement de plante hôte, depuis l'érable sycomore ou un autre érable (Augustin et al 2010).

Nous avons d'abord développé une approche génétique pour trouver l'origine géographique de *C. ohridella*. Avec Neus Mari Mena pendant son projet de Master 2, nous avons développé des marqueurs moléculaires polymorphes microsatellites (Mari Mena et al 2008) pour étudier la génétique des populations de l'espèce.

Avec Romain Valade, un étudiant de Master 2, nous avons collecté et séquencé des échantillons pris dans différents sites nouvellement colonisés (parcs et jardins) par *C. ohridella* en Europe. Nous avons analysé les données génétiques (COI + microsatellites) et comparé à des populations prélevées dans les forêts naturelles de marronniers dans les montagnes des Balkans. L'analyse de marqueurs mitochondriaux et nucléaires (microsatellites) a été réalisée sur près de 500 individus provenant de populations récoltées dans toute l'Europe en fonction de la date d'apparition de l'insecte. De manière convergente, ces deux marqueurs montrent une origine balkanique de l'insecte. Une très forte diversité génétique des populations d'insectes est observée dans les peuplements forestiers de marronniers d'Inde du sud des Balkans (Albanie, Macédoine, Grèce). Cette diversité est considérablement réduite au niveau des populations échantillonnées dans le reste de l'Europe mais aussi des populations urbaines des Balkans. Ces résultats ont été publiés dans le journal *Molecular Ecology* (Valade et al 2009).

Dans une nouvelle étude avec David Lees (chercheur associé au Musée d'Histoire Naturelle de Londres) dans le cadre du projet STUDIUM, nous avons examiné des spécimens d'herbier de marronnier d'Inde de plusieurs institutions botaniques à travers l'Europe. De nombreuses chenilles de mineuse de marronniers ont été trouvées, involontairement pressées dans les feuilles des marronniers d'Inde. La plus ancienne chenille a été trouvée dans un spécimen d'herbier recueilli en 1879 en Grèce, soit plus d'un siècle avant que l'on ne soupçonne l'existence du genre *Cameraria* en Europe. Par l'analyse moléculaire de l'ADN mitochondrial et nucléaire des chenilles anciennes, nous avons confirmé l'identité de la mineuse du marronnier. Nous avons également pu comparer la diversité génétique parmi les populations actuelles du papillon et les spécimens des herbiers

historiques. Les données génétiques recueillies à partir de spécimens d'herbier révèlent que la mineuse du marronnier est, dans les Balkans, encore plus génétiquement diversifiée que précédemment rapporté. En effet, l'analyse de ces insectes prélevés dans les échantillons d'herbier a permis de découvrir des éléments génétiques non observés jusqu'alors.

Cette étude montre aussi que des pullulations de la mineuse du marronnier remontent au moins à 1961. Le désenclavement récent des Balkans, accompagné du développement d'infrastructures routières, pourrait avoir accéléré la propagation des populations de mineuses, qui vivaient auparavant dans des canyons isolés. La mineuse du marronnier est capable de voyager comme passagère clandestine des véhicules, et l'amélioration des voies de communication a favorisé sa mobilité entre les marronniers naturels et ornementaux.

Cette étude démontre également que les herbiers sont largement sous-utilisés dans les études sur les interactions plantes-insectes, la biodiversité des herbivores, l'origine des espèces envahissantes, et pour documenter les distributions passées. Les herbiers sont une source pertinente d'informations pour résoudre des problèmes modernes, y compris des espèces envahissantes nuisibles et des maladies, et pour apprécier les changements temporels dans la biodiversité. Ces résultats ont été publiés dans la revue « *Frontiers in Ecology and the Environment* » (Lees et al 2011). Cet article a fait l'objet de plusieurs articles dans la presse : BBC, The Scientist., Science daily. Les deux articles (Valade et al 2009 ; Lees et al 2011) ont également fait l'objet de communiqués de presse placés sur le site web national de l'INRA.

Identification d'une population balkanique du parasitoïde *Pediobius saulius* comme possible candidat contre la lute biologique de *Cameraria ohridella*

La découverte de l'aire d'origine de *C. ohridella* ouvre de nouvelles perspectives pour la lutte biologique contre *Cameraria* en zone urbaine. La connaissance de l'aire d'origine devrait permettre de trouver des ennemis naturels spécifiques pour développer des stratégies de contrôle.

Les recherches menées pendant les 10 dernières années sur le complexe parasitaire de *C. ohridella* ont montré que le complexe parasitaire dans les Balkans est composé par des espèces plus ou moins polyphages qui attaquent habituellement des mineuses vivant sur d'autres essences et que la principale différence entre les populations des Balkans et du reste de l'Europe est la prépondérance de *Pediobius saulius* (Hymenoptera, Chalcidoidea) dans les Balkans. Dans le but de trouver un moyen de lutte contre la mineuse du marronnier nous avons orienté nos recherches sur cette espèce.

P. saulius est un parasitoïde de pupes avec une large gamme d'hôtes, y compris la mineuse du marronnier d'Inde *C. ohridella*. En Europe centrale et occidentale, il attaque de nombreuses mineuses mais rarement *C. ohridella*. Ceci suggère que *P. saulius* pourrait être un complexe d'espèces avec une race spécifique de *C. ohridella* dans les Balkans. Avec Antonio Hernandez Lopez, postdoc EFPA, nous avons mené des études génétiques pour tester cette hypothèse.

Nous avons complété une étude phylogéographique en séquençant le gène mitochondrial COI pour 146 individus provenant de 10 pays européens et neuf hôtes différents. Nous avons trouvé des preuves de divergence mitochondriale associée aux hôtes, ce qui suggère une base génétique pour l'utilisation d'hôte qui peut limiter l'expansion de spectre d'hôtes chez les parasitoïdes. La divergence pour le COI (jusqu'à 8%) suggère

l'existence d'espèces cryptiques, bien que ce ne soit pas confirmé par la divergence nucléaire (28SrRNA et ITS2), ni par la morphologie (SEM, morphométrie). La présence potentielle d'une race d'hôte spécialisé sur *C. ohridella* dans les Balkans, ouvre la possibilité d'autres études pour évaluer l'utilisation de *P. saulius* comme agent de lutte biologique contre cet insecte envahissant (Hernandez-Lopez et al. 2011).

Finalement, nous avons récemment publié une synthèse de tous les travaux publiés sur *C. ohridella* pour « l'Encyclopedia of Life »: <http://eolspecies.lifedesks.org/pages/8675> (Lees et al 2009).

Cette recherche a été financée par trois projets :

- 2007-2008: Pilot Joint Call for Research and Thematic Network Projects with the Western Balkan Region (SEE-ERA.NET). Project: "Genetic survey of an invasive forest insect and its parasitoids in the Balkan region" (Project number: 10627RP). Project Leaders: Carlos Lopez-Vaamonde et Sylvie Augustin.
- 2006: Department EFPA, INRA. Project: "Genetics of invasion of the horse chest nut leaf miner *Cameraria ohridella* (Lepidoptera, Gracillariidae)". Project Leaders: Carlos Lopez-Vaamonde et Sylvie Augustin.
- 2004-2009: Integrated EU Project Alarm " Assessing large-scale environmental risks with tested methods"
- Nous avons obtenu deux financements pour recruter contractuellement deux chercheurs étrangers sur cette thématique:
 - Un poste de chercheur contractuel confirmé pour 2 ans (2009-2010) sur un financement Studium de la Région Centre, complété par des crédits INRA EFPA, pour travailler sur le traçage génétique de l'origine de la mineuse invasive du Marronnier d'Inde (David Lees).
 - Un poste de post-doctorant de 12 mois (2008-2009) sur crédits INRA EFPA pour travailler sur la génétique des parasites de la mineuse invasive du Marronnier d'Inde (Antonio Hernandez Lopez). Antonio fait actuellement un postdoc à l'Université de Marseille.

Inventorier les espèces exotiques d'insectes en Europe

Jusqu'au début des années 2000, les études menées au plan européen sur les invasions d'insectes n'ont concerné que des cas d'espèces, et aucune liste des organismes exotiques déjà établis n'existait ni en France, ni au niveau du continent dans son ensemble. La même situation prévalait à l'échelle mondiale même si des inventaires partiels pouvaient exister pour certains groupes. L'enjeu de disposer de tels inventaires, surtout au plan continental, est de pouvoir analyser rétrospectivement les voies et vecteurs d'invasion, caractériser les éventuels traits spécifiques facilitateurs pouvant être prédictifs des risques d'établissement, et apprécier la vulnérabilité/ invasibilité des écosystèmes aux invasions. Un autre enjeu est de pouvoir comparer à une échelle globale les patrons d'invasion des différents taxa animaux et végétaux.

L'objectif de ce projet est d'élaborer un inventaire pour les insectes exotiques introduits et d'en dégager de premiers éléments d'analyse sur les facteurs sous-tendant ces invasions, l'origine des envahisseurs, les habitats envahis, l'impact de ces espèces, et de confronter ces données à celles des collègues travaillant sur d'autres groupes.

Mon unité l'URZF a assuré la coordination de l'activité « invertébrés terrestres » dans ce

projet et généré, la première liste des invertébrés terrestres exotiques établis en Europe. Un total de 1650 espèces, incluant 1590 arthropodes dont 1390 insectes a été identifié (Roques et al 2008; 2010). Nous avons montré que le nombre d'espèces exotiques d'insectes nouvellement observées chaque année en Europe a augmenté de manière exponentielle depuis le début du 20ème siècle, avec une notable accélération due à la globalisation et à l'arrivée prédominante d'espèces phytophages liées aux échanges horticoles. Nous avons aussi montré que l'Asie était désormais la source dominante des espèces envahissantes (>30%) au détriment de l'Amérique du Nord autrefois majoritaire. De nouvelles voies d'invasions ont été mises en évidence comme le commerce des bonsaïs qui peuvent abriter une faune diversifiée

L'édition en 2010 de l'ouvrage 'Alien arthropods in Europe', coordonnée par l'URZF a permis de mettre à disposition de toute la communauté scientifique, sous forme téléchargeable gratuitement, l'ensemble des résultats obtenus (Roques et al 2010). J'ai été co-éditeur de cet ouvrage et coordinateur du chapitre sur les lépidoptères non natifs en Europe publié dans *Biorisks*.

Le projet européen DAISIE (<http://www.europe-aliens.org/>) a regroupé des équipes concernant tous les taxa d'animaux et plantes et couvrait toute l'Europe. Pour le chapitre sur lépidoptères sous ma coordination j'ai rassemblé 23 lépidoptéristes de 16 pays européens (Lopez Vaamonde et al 2010).

Cette recherche a été financée par le projet européen : 6ème PCRD-STREP--DAISIE Delivering Alien Invasive Species Inventories for Europe ; 01/02/2005- 31/01/2008.

Développement de bases de données code barre ADN et de phylogénies moléculaires

L'identification taxonomique et la délimitation des espèces occupent une position centrale dans les études de biodiversité, en particulier dans le contexte des invasions où la majorité des individus arrive à l'état immature. De plus, cette identification est rendue difficile chez les insectes phytophages, le plus souvent oligo- ou polyphages, pour lesquels il existe des complexes d'espèces sœurs, génétiquement proches et des espèces cryptiques, non décelables morphologiquement. A l'URZF nous utilisons une approche multidisciplinaire combinant des méthodes traditionnelles et classiques (connaissances de terrain, morphologie, comportement) et des méthodes plus innovantes (génétique moléculaire) de type code barre (fragment du gène de la Cytochrome Oxydase I de l'ADN mitochondrial) pour identifier les espèces d'insectes invasifs ou potentiellement invasifs en Europe.

Le code barre ADN est un nouvel outil efficace pour accélérer les identifications d'espèces connues et la découverte de celles qui ne le sont pas. Il s'agit d'une technique rapide et à haut débit offrant un moyen robuste et objectif pour explorer et documenter la richesse spécifique à un rythme sans précédent. Les codes barres peuvent être utilisés pour caractériser des unités opérationnelles utilisables comme des proxy pour les espèces dans les groupes où la taxonomie est incertaine. Ils offrent ainsi un moyen unique de documenter la part inconnue de la biodiversité de notre planète.

Les objectifs de ce projet sont doubles :

- Développement de bases de données code barres ADN et de phylogénies moléculaires

pour des familles d'insectes comprenant un grand nombre d'envahisseurs comme la famille des micro-lépidoptères Gracillariidae.

- Utilisation de bases de données code barres ADN pour répondre à des questions écologiques: i) structure des réseaux trophiques, ii) estimation de la biodiversité en milieu tropical.

Code Barre ADN et phylogénomique des mineuses Gracillariidae

Une base de donnée ADN codes de barres a été créée pour 220 espèces de Gracillariidae sur les 256 espèces connues pour l'Europe. Cette base de donnée nous permet d'identifier des stades immatures de ces microlépidoptères ainsi qu'à confirmer la distribution de certaines espèces (Langmaid et al 2011). Ce travail a été accompli avec la collaboration de plusieurs collègues notamment Zdenek Lastuvka (Mendel University, République Tchèque), Peter Huemer (Natural History Museum Innsbruck, Autriche), Christian Wieser (Natural History Museum Carinthia).

En collaboration avec Jurate & Willy De Prins (Museum of Central Africa, Belgique) nous étudions la faune afrotropicale de Gracillariidae (De Prins et al 2009). En Mars 2012 je participe à une école de terrain (ECOTROP) dans le Parc national de la Lopé au Gabon organisée par l'Université des Sciences et Techniques de Masuku de Franceville, l'Institut de Recherche pour le Développement (IRD) et l'Université de Rouen. L'objectif est de former des étudiants de Master gabonais et français sur l'étude du fonctionnement des écosystèmes tropicaux. J'ai formé des étudiants sur les techniques de collectes, élevage et préparation des microlépidoptères en générale, et mineuses Gracillariidae en particulier.

Nous avons aussi reconstruit une phylogénie moléculaire de la superfamille Gracillarioidea en utilisant jusqu'à 21 gènes. Nous avons démontré qu'une augmentation partielle du nombre des gènes utilisés augmente le niveau de résolution et support statistique des noeuds profonds d'une phylogénie. En revanche une augmentation du nombre de taxa sans augmentation du nombre des gènes provoque une diminution du niveau de support (Kawahara et al 2011). Cette étude a été financée par le National Science Foundation en collaboration principale avec Akito Kawahara (Université de Floride). Un projet NSF a été soumis avec Kawahara pour améliorer les connaissances systématiques de la famille Gracillariidae dans la région neotropicale.

Code Barre ADN et Réseaux trophiques

L'étude des réseaux trophiques est un élément fondamental des sciences écologiques. Elle permet notamment de mieux comprendre le fonctionnement ou le dysfonctionnement des communautés, en documentant les interactions et les interdépendances entre organismes. Connaître les relations prédateur/proie, hôte/parasite, ou plante-hôte/herbivore est ainsi à la base d'applications en lutte biologique, ou plus généralement en production agricole. Chez les insectes à métamorphose complète (holométaboles), nos connaissances sur les ressources employées aux différents stades du développement de l'insecte sont généralement fragmentaires. Pour la plus grande part, les informations disponibles résultent d'observations de terrain ou d'élevage, et dans l'ensemble la nourriture des insectes adultes est beaucoup mieux connue que celle des larves, simplement du fait que les stades précoces du développement sont le plus souvent cachés.

Avec les récents développements et les progrès des méthodes moléculaires pour la détection et l'identification d'organismes, la dernière décennie a vu croître un vif

engouement pour l'analyse moléculaire des contenus digestifs. Nous avons récemment développé une approche moléculaire originale qui permet, pour la première fois, de documenter à partir d'hyménoptères parasitoides adultes la source de nourriture utilisée lors de leur développement larvaire, avant métamorphose. Cette méthode baptisée MAPL (Molecular Analysis of Parasitoid Linkages; Rougerie *et al.*, 2010) est basée sur la persistance dans le contenu digestif de la guêpe adulte, après métamorphose, de l'ADN de l'hôte ingéré par sa larve. Son application chez d'autres insectes holométaboles pourrait être extrêmement intéressante, mais elle n'a pas encore été testée.

Code Barre DNA et mesure de la richesse spécifique en région tropicale

Les invertébrés sont les organismes les plus diversifiés sur Terre, avec un nombre d'espèces estimé à près de 30 millions, dont seule une faible proportion (probablement moins de 20%) a été jusqu'à présent décrite ou découverte. L'urgence est maintenant d'accélérer la caractérisation, la description et l'identification de cette biodiversité, ceci dans le but de produire les connaissances fondamentales nécessaires à une meilleure compréhension de sa dynamique sous l'impact des activités humaines.

En utilisant le code barre ADN, nous avons étudié la diversité de lépidoptères de la réserve des Nouragues en Guyane (<http://www.nouragues.cnrs.fr/>). Les échantillons ont été barcodés de façon systématique et 5644 séquences ont été obtenue pour ~2800 espèces. Un travail parallèle a été réalisé dans des collections publiques de façon à compléter l'échantillonnage taxonomique et à mesurer pour chacun de ces groupes le ratio entre espèces connues et inconnues, ceci afin de mettre en évidence la diversité cryptique révélée par nos résultats. Nous avons constitué ainsi une bibliothèque de référence permanente et publique de façon à pérenniser l'expertise taxonomique investie dans le projet et à la rendre largement accessible. Nous utilisons des techniques de raréfaction pour calculer des estimateurs de richesse spécifique à partir de l'inventaire complet de toutes les espèces (connues et inconnues) collectées sur le terrain.

Nous avons aussi développé une technique pour prélever des microlépidoptères en milieu tropical pour des études moléculaires (ie. codes barres) et au même temps préserver les spécimens pour des études morphologiques (Lopez Vaamonde et al 2011).

Je collabore avec David Lees (URZF), Rodolphe Rougerie & Thibaud Decaens (Université Rouens), Jérôme Barbut & Antoine Leveque (Musée d'Histoire Naturelle Paris) sur le barcode de la faune des lépidoptères de la réserve des Nouragues, Guyane.

Cette recherche a été financée par les projets :

- CNRS Research Grant Program Nouragues- Exploring tropical diversity and host plant interactions of leaf-mining moths: tapping into a megadiverse insect group; 1/10/2009- 30/09/2010. Coordinateur: Carlos Lopez-Vaamonde.
- Belgian Science Policy Research Programmes for the Federal Scientific Institutions. "Biodiversity and molecular evolutionary studies of leaf mining moths in the Afrotropical region (Lepidoptera, Gracillariidae); 1/09/2008- 30/12/2010. Coordinateur: Marc De Meyer (Museum of Central Africa, Belgique).
- Le séquençage de tout le matériel est fait en collaboration avec le Biodiversity Institute of Ontario, University of Guelph et financée par GENOME Canada.

Conservation des espèces menacées d'insectes forestiers.

Un objectif de listes rouges est la documentation du status des espèces menacées. Les insectes sont mal représentés dans la dernière version de la liste rouge du « World conservation Union ». Cette absence n'est pas due à des niveaux de menace faibles mais à un défaut de connaissances sur leur écologie et génétique. Ce manque de données représente actuellement un obstacle important pour la conservation de beaucoup d'espèces invertébrés.

Nous avons centré nos études sur le statut de conservation d'un insecte forestier protégé: *Graellsia isabellae* (Graëlls, 1849) (Lepidoptera: Saturniidae) qui vit dans les forêts de conifères du centre et de l'est de l'Espagne, ainsi qu'en France et dans les Alpes Suisse entre 100 et 1800 m. *G. isabellae* a une chenille sédentaire, non grégaire et se développe en cinq stades. Les larves se nourrissent de plusieurs espèces de pin : *Pinus sylvestris*, *P. uncinata* et *P. nigra laricio* de juin à août avant de se métamorphoser en chrysalide. C'est une espèce univoltine qui vole au crépuscule, d'avril jusqu'en juin. Ce grand papillon de nuit est l'un des insectes européens les plus emblématiques. En raison de sa beauté, sa taille et sa distribution géographique restreinte, il est devenu un symbole pour plusieurs organisations entomologiques et de conservation.

G. isabellae est protégée par la directive d'habitat (Initiative de la Communauté Européenne pour un réseau écologique de régions protégées spéciales, plus connue en tant que : "Natura 2000"), la convention de Bern, le « Red Book of Lepidoptera » ainsi que d'autres catalogues nationaux. En dépit de cette législation protectrice, la dernière liste rouge de l'IUCN considère que le *G. isabellae* comme « pas assez documenté » (IUCN 2006). Effectivement, il y a des données actualisées sur la distribution actuelle de *G. isabellae* et aucune donnée sur la génétique, indispensables pour déterminer le niveau précis de menace sur cette espèce.

Le but principal de nos études est de réunir des données écologiques et génétiques afin d'évaluer le statut de conservation de *Graellsia isabellae*.

Nous réalisons des expériences de capture, de marquage et de libération pour évaluer les densités de populations sauvages dans les Alpes françaises.

À l'INRA nous avons maintenu une colonie de laboratoire de *G. isabellae* depuis 1990. Cet élevage nous a permis d'identifier récemment la phéromone sexuelle de *Graellsia* (Millar et al 2010). Cette publication a fait la couverture du Journal of Chemical Ecology.

Nous avons récemment développé une méthode non létale d'échantillonnage pour extraire et amplifier par PCR l'ADN des queues des ailes de *G. isabellae* (Vila et al 2009) et nous avons caractérisé dix microsatellites polymorphes pour étudier la génétique des populations de l'espèce (Vila et al. 2010). Plusieurs manuscrits sur la phylogéographie et génétique de la conservation de *G. isabellae* sont en cours de préparation.

Cette recherche a été financée principalement par un projet du ministère espagnol d'Education et Science : 2008-2010: Spanish Ministry of Science and Education. Project: "Conservation genetics of a protected moth, *Graellsia isabellae* (Lepidoptera, Saturniidae)" coordinateurs : Marta Vila Taboada (University of La Coruna, Spain); Carlos Lopez-Vaamonde (Co PI).

Nous avons aussi eu deux autres projets financés:

- Programme Egide/ Picasso 2008. Project: "Assessment of the conservation status of a protected forest insect, *Graellsia isabelae* (Lepidoptera, Saturniidae)" Project coordinateurs : Carlos Lopez-Vaamonde et Marta Vila
- 2007: Department EFPA, INRA. Project: "Development of a DNA non-lethal sampling method from adult moths for conservation genetics" coordinateurs : Marie-Anne Auger-Rozenberg & Carlos Lopez-Vaamonde.

Evolution et signification adaptative du mode de vie endophyte chez les insectes

Chaque organisme végétal est confronté à de nombreuses pressions évolutives imposées en particulier par les insectes phytophages et les phytopathogènes. Le mode de vie sédentaire des arthropodes endophytes (cad. vivant au sein des tissus végétaux) et leur association intime avec le végétal constituent des éléments clés pour aborder les mécanismes écologiques et évolutifs liés à la phytophagie. Ce projet vise à comprendre les mécanismes qui sont à la base de ce mode de vie endophyte. Ceci implique une étude des mécanismes moléculaires, biochimiques et physiologiques utilisés par les insectes mineurs de feuilles (Gracillariidae) pour manipuler leur environnement végétal, mais également des conséquences en termes de succès reproducteur ("fitness") pour l'insecte.

Un des signes caractéristiques des manipulations induites par les insectes mineurs de feuilles peut se manifester de façon très explicite à l'automne. En effet, lors de la sénescence de la feuille, la photosynthèse s'arrête et une partie des nutriments contenus dans le tissu foliaire est réallouée dans la plante (en particulier au niveau des racines). Pour la larve enclose dans la feuille, cette diminution de quantité de nutriment peut s'avérer délétère si son développement n'est pas achevé. Chez certaines espèces, la zone minée reste verte durant le jaunissement du reste de la feuille donnant naissance à un phénotype qualifié d' « **île verte** ». C'est le cas pour *Phyllonorycter blancardella* (Lepidoptera, Gracillariidae) un microlépidoptère minant les feuilles de pommier. Dans l'îlot vert, la concentration de cytokinines s'est avérée bien plus élevée que dans le reste de la feuille et parfois plus élevée que dans les feuilles vertes non minées. L'origine de cette forte concentration d'hormone n'est pas encore connue, mais un médiateur bactérien semble jouer un rôle prépondérant dans l'induction du phénomène d'île verte chez *Phyllonorycter blancardella*. La bactérie *Wolbachia*, apparaît comme un candidat privilégié dans ce phénotype étendu d'île verte. En effet, *Wolbachia* est la seule bactérie qui a été détectée à partir des mineuses de cette espèce. De plus, si l'on traite les mineuses avec des antibiotiques, les larves asymbiotiques ne forment pas d'îles vertes et le taux d'émergence des adultes chute drastiquement.

L'induction d'une île verte procure certains avantages aux larves de *Phyllonorycter blancardella*. En effet, elle leur permet de continuer à se développer sur la feuille jaunissante dans un microenvironnement favorable d'un point de vue énergétique jusqu'à atteindre le stade adulte. De plus, cela permet alors d'effectuer une génération supplémentaire par an. Néanmoins, l'association étroite entre l'insecte et une bactérie symbiotique peut également avoir un coût lors d'association avec des bactéries de type parasite comme cela est généralement le cas avec *Wolbachia*. Si l'île verte est bien associée à la présence de *Wolbachia*, on peut s'interroger sur la balance bénéfice/coût et les implications dans l'évolution et la diversification des mineuses.

Afin de savoir si le rôle de *Wolbachia* dans la formation d'îles vertes est envisageable chez d'autres espèces de mineuses, il est intéressant d'étudier la distribution de *Wolbachia* et la

corrélation avec la présence d'îles vertes chez d'autres espèces mineuses et en particulier au sein de la famille des Gracillariidae.

Les objectifs du projet sont : i) Développer un protocole permettant de détecter *Wolbachia* à partir de quantités très faibles de tissus comme les premiers stades larvaires de microlépidoptères permettant ainsi une analyse sur un plus grand nombre d'échantillons. ii) De tester la validité du « DNA barcoding » comme outil pour identifier au niveau de l'espèce différents stades de Gracillariidae. iii) D'évaluer l'étendue de l'association *Wolbachia*/mineuses de feuilles/île verte, en investiguant la présence de *Wolbachia* et des îles vertes pour 162 microlépidoptères dont 142 Gracillariidae.

De la variabilité dans la distribution des caractères d' « île verte » et de « *Wolbachia* » a pu être observé au niveau intra et interspécifique. La corrélation entre la présence d'îles vertes et de *Wolbachia* a pu être validée. On peut donc envisager un rôle clé de la bactérie dans le phénotype « île verte » chez plusieurs espèces. Cependant, certains individus forment des îles vertes mais, d'après les tests fiables, ne sont pas infectés par *Wolbachia* suggérant que d'autres mécanismes doivent être envisagés.

Cette recherche est financée par le Conseil Régional Centre- ENDOFEED- Evolution et Signification Adaptative du mode de vie Endophyte chez les Insectes ; 29/01/2010-30/01/2013 ; 28 000 € (coordinateur: David Giron, IRBI. Je suis coordinateur du workpackage V).

HDR Thesis

Foreword

As an entomologist, my interests range far and wide in Evolutionary Biology, Systematics and Ecology of insects.

Much of my research has been centered on molecular phylogenetics and I have seen the development of this field since the early days of manual sequencing in the 90s to the boom of phylogenetic data in the last 10 years. My interest in molecular phylogenies is mainly driven by questions on how some particular ecological, morphological, biogeographical and behavioural traits have evolved. It is the combination of DNA sequence data and ecology (ie. host use, behavior,..) that has allowed me to address interesting questions about the ecology and evolution of a wide range of insects from fig wasps, leaf-mining moths and their parasitoids, to bumblebees and wild silk moths.

I have made substantial contributions to the fields of systematics, evolutionary ecology, social behaviour and invasion biology and I am keen to build on this progress. It is only now, with the explosion of new high-throughput, second-generation sequencing approaches, that we have the tools necessary to address fundamental questions about the evolutionary ecology of non-model insects. My long-term goal is to establish a research group investigating evolutionary ecology and systematics across a range of insect groups using a variety of approaches, including laboratory experimentation and observation, fieldwork, genetic analyses and modeling.

I have divided this report into chapters named after the different periods of my career. I highlight the main results for each period and the path that I have followed over the years to try to understand insect diversity, how it is organized and how it has originated.

1. Predoctoral Studies

I have been interested in the ecology and systematics of forest insects since I was an undergraduate. From 1984 till 1992 I carried out systematic studies of longhorn beetles (Cerambycidae) in the north west of the Iberian Peninsula (Galicia). After my degree, I had the opportunity to pursue my interests on forest insects by working as research assistant at the Forest section, CABI Bioscience Station in Switzerland, under the supervision of Dr. Kenis.

Ecology and Faunistics of forest insects

From 1984 till 1992, I carried out systematic studies of longhorn beetles (Cerambycidae) in the north west of the Iberian Peninsula (Galicia). During this period, 516 different localities were visited, 5743 specimens of 109 species with 36 new species for the region were collected and many private and public collections that hold Galician material were studied. The main aim of the study was to use some Cerambycidae species as bioindicators to identify areas of highest diversity for saproxylophagous beetles, to help establish conservation areas of ancient woodlands. This study is being up dated regularly on line:

<http://www.aegaweb.com/inventario/index.htm> (go to link: Coleoptera and then to Cerambycidae). This web page contains faunistic information and photos of the 109 species of longhorned beetles recorded from Galicia.

During this period of time, I also published a series of papers and notes in Spanish on faunistics of several remarkable species of Coleoptera and Lepidoptera for Galicia (Estevez et al 1989, Fernandez Vidal et al 1992, Lopez-Vaamonde et.al. 1988, 1989a,b, 1991, 1992a,b,c, 1993a,b, 1994, 1995, 2000). This work is based on hundreds of fieldtrips across some remote mountainous areas of Galicia. The region has changed much over the last 20 years and the faunistic data collected in the 80s and 90s will be of great value to assess impact of habitat and climate change on insects. I still collaborate with people working on faunistics and conservation of insects in Galicia (Pino et al 2009).

Publications:

- Estévez Rodríguez, R.; **López Vaamonde, C.** & Pino Pérez J. J. 1989. Descubrimiento de *Parnassius apollo* (Linne) en Galicia. *Boletín Auriense.*, (1988-1989): 379-381.
- Lopez Vaamonde, C.**; Estévez Rodríguez, R. & Iglesias Garrote, J. L. 1988. *Zerynthia rumina* (Linnaeus, 1758) en las Islas Cíes (Pontevedra) (Lepidoptera: Papilionidae). *SHILAP Revista Lepid.* 16(62): 97-100
- Lopez Vaamonde, C.**; Estévez Rodríguez, R. & Pino Pérez, J. J. 1989a. Contribución al conocimiento lepidopterológico de Galicia (I). Una colonia de *Parnassius apollo* (Linnaeus, 1758) en Ancares (Lugo) (Lepidoptera: Papilionidae). *SHILAP Revista Lepid.* 17(66): 209-215.
- Lopez Vaamonde, C.**; Estévez Rodríguez, R. & Pino Pérez, J. J. 1991. Datos corológicos de interés faunístico para la lepidopterología gallega. *SHILAP Revista Lepid.* 19(76): 300-303.
- Lopez Vaamonde, C.** & Pino Pérez, J. J. 1992a. Primera cita de *Hyponephele lupina* (Costa, 1836) para Galicia. *SHILAP Revista Lepid.* 20(78): 189.
- Lopez Vaamonde, C.** & Pino Pérez, J. J. 1992b. Confirmación de la presencia de *Erebia euryale* (Esper, 1805) en Lugo y primera cita para Galicia de *Strymonidia w-album* (Knoch, 1782). *SHILAP Revista Lepid.* 20: 405-406.
- Lopez Vaamonde, C.**; Estévez Rodríguez, R. & Pino Pérez, J. J. 1992c. Distribución de *Maculinea alcon* (Denis & Schiffermuller, 1775) en Galicia y Portugal. *SHILAP Revista Lepid.* 20(80): 406.
- Fernández Vidal, E. H.; **López Vaamonde, C.** & Pino Pérez, J. J. 1992. Contribución al conocimiento de los Ártidos de Galicia. (Lepidoptera: Arctiidae). *SHILAP Revista Lepid.* 20(77): 51-91.
- Lopez-Vaamonde, C.**, J.J. Pino-Perez, A. Martinez-Fernandez Y S. Devesa-Regueiro 1993a. *Sinodendron cylindricum* (Linneo, 1758) y *Pseudolucanus barbarossa* (Fabricius, 1801) en Galicia (Coleoptera, Lucanoidea, Lucanidae). *Boletín de la Asociación Española de Entomología*, 17 (2): 349-350.
- Lopez-Vaamonde, C.**, J.J. Pino-Perez, A. Martinez-Fernandez, J.C. Fernandez-Abelleira and S. Devesa-Regueiro 1993b. A contribution to the knowledge of forest insects: Cerambycidae Latreille, 1804 (I): *Morimus asper* (Sulz., 1776) in Galicia (Coleoptera, Polyphaga). *Proceedings: 1st Spanish Forestry Convention. Vol. III. Spain*
- Lopez Vaamonde, C.**; Pino Pérez, J. J. & Martínez Fernández, A. 1994. Presencia de *Cupido osiris* (Meigen, 1829) en Galicia (Lepidoptera: Lycaenidae). *Bol. Asoc. Esp. Entomol.* 18(3-4): 100-101.
- Lopez Vaamonde, C.**; Pino Pérez, J. J. & Martínez Fernández, A. 1995. Distribución de *Pheosia gnoma* (Fabricius, 1777), *Clostera curtula* (L., 1758) y *Drymonia dodonaea* (Denis & Schiffermüller, 1775) en el Noroeste peninsular ibérico (Lepidoptera: Notodontidae). *Bol. Asoc. Esp. Entomol.* 19(1-2): 314-315.
- Lopez-Vaamonde, C.**, J.J. Pino, S. Devesa 2000. Distribución y estatus de conservación de la familia Cerambycidae Latreille, 1804 (Insecta, Coleoptera) de Galicia (Noroeste de la península Iberica). *Boletín de la Real Sociedad Española de Historia Natural (Sec. Biología)*, 96 (1-2): 125-137.
- Pino Pérez, J. J.; **López Vaamonde C.**; Garrido González J.; Rodríguez Gracia, V.; Martínez Fernández, A.; Camaño Portela, J. L. & Pino Pérez, R. (2009) Catálogo de los Sphingidae (Lepidoptera) de Galicia BIGA. *Boletín nº 6*: 131-144. http://www.biga.org/Boletin_BIGA/Boletin_BIGA6/IC_Sphingidae/index.html

Classical Biocontrol

Biocontrol of Canadian forest pests using European parasitoids

After my degree, I had the opportunity to pursue my interests on forest insects by working as research assistant at the Forest section, CABI Bioscience Station in Switzerland, under the supervision of Dr. Marc Kenis. My work consisted of collecting natural enemies of forest insects in Alpine areas (Alps and Jura Mountains). I was in charge of setting up procedures to rear them in the laboratory and test their host specificity to send them to Forestry Canada for release against pests in North America as an environmentally friendly alternative to chemical control. I worked on the following projects:

- Biocontrol of the spruce weevil *Pissodes strobi*, (Col. Curculionidae) by the parasitoids: *Eubazus semirugosus* and *Coeloides sordidator* (Hym. Braconidae)
- Biocontrol of gypsy moth, *Lymantria dispar* (Lep. Lymantriidae) by the parasitoid *Aphantorhaphopsis samarensis* (Dip. Tachinidae).
- Biocontrol of the spruce budworm, *Choristoneura fumiferana* (Lep. Tortricidae)
- Biocontrol of the spruce seed moth, *Cydia strobilella*, (Lep. Tortricidae) and the spruce cone maggots *Strobilomyia neanthracina* (Dip. Anthomyidae).
- Study of the parasitoid complex of *Agriopsis aurantaria* and *Epirrita autumnata* (Lep. Geometridae) feeding on of larch (*Laryx*).
- Biocontrol of the spruce budmoth *Zeiraphera canadensis* (Lep. Tortricidae) by parasitoids of European *Zeiraphera* spp.
- Biocontrol of birch leaf-mining sawflies *Fenusa pusilla* and *Profenusa thomsoni* (Hym. Tenthredinidae).
- Biocontrol of the pine false webworm *Acantholyda erythrocephala* (Hym. Pamphiliidae).

Particularly interesting was the study of the parasitoid complex of gypsy moth at low densities. We would expose larvae for a few weeks and then bring them back to the lab to rear the parasitoids, in particular the tachinid fly *Aphantorhaphopsis samarensis* (Kenis & Lopez Vaamonde 1997). We also studied the natural host range of this tachinid collecting native Lepidoptera larvae in France and Switzerland but also by artificially infecting larvae of several Lepidoptera species in the lab (Fuester et al 2001).

Publications:

- Fuester, R. W. M. Kenis, K. S. Swan, P. C. Kingsley, C. Lopez-Vaamonde and F. Herard 2001. Host Range of *Aphantorhaphopsis samarensis* (Villeneuve) (Diptera: Tachinidae), a Larval Parasite of the Gypsy Moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). *Environmental Entomology*, 30: 605-611.
- Kenis, M. and C. Lopez-Vaamonde 1997. Classical biological control of the gypsy moth, *Lymantria dispar* (L.) in North America: prospects and new strategies. In McManus, M. (Ed.) *Proceedings: IUFRO Conference on Population Dynamics and Integrated Management of Forest Defoliating Insects in Banska Stiavnica, Slovak Republic*, 1-9.

Biocontrol of coffee berry borer in Colombia using an African parasitoid

In 1995-1996, I went to work as research assistant for CABI at Silwood Park in the UK on biocontrol of coffee berry borer (*Hypothenemus hampei*, Col., Scolytidae) (CBB). The aim of the project was: 1) to import CBB infested coffee berries from Kenya into the UK; 2) to set up a rearing protocol under quarantine conditions of the adult endoparasitoid *Phymastichus coffea* (Hym. Eulophidae) (Fig. 1); 3) to test its host specificity and export the parasitoid to Colombia to set up a mass rearing and release it against CBB (Lopez-Vaamonde et Moore,

1998). This work was done under the supervision of both Dave Moore and Mathew Cock (CABI, UK). After spending most of 1995 in a quarantine setting up the rearing protocol, I was more than happy to go to Colombia in 1996 where I spent 5 months under the supervision of both Drs. Peter Baker (CABI) and Reinaldo Cardenas (Centro Nacional de Investigaciones del Café, CENICAFE, Chinichina) to continue the host specificity tests of *Phymastichus coffea* using native Colombian bark beetles.

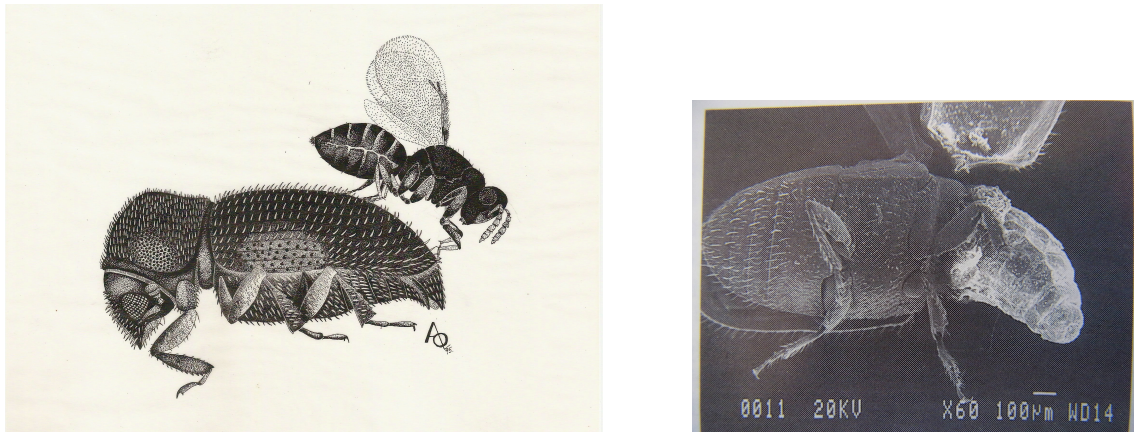


Figure 1 *P. coffea* is the only known parasitoid to attack adults of coffee berry borer. a: The host is stung dorsally by a pore of the elytra (drawing by Aquilino Martinez); b: Coffe berry borer dissected to reveal a late-instar larva of *P. coffea* (photo Dr Arroyave)

During the host specificity tests of *Phymastichus coffea*, along with Reinaldo Cardenas we collected several hundred specimens of 47 species of Scolytidae from the coffee-growing area of Colombia. The material was sent to Prof. Stephen Lane Wood (Monte L. Bean Life Science Museum, Brigham Young University) who identified the specimens and included the information in his monumental monograph of 900 pages on 1339 South American species bark and ambrosia beetles of South America (Wood 2007).

P. coffea was finally released in Colombia and Mexico and it has been shown that using *P. coffea* at a density of 1 parasitoid per 10 hosts results in a 3- to 5.6-fold decrease in CBB damage to the coffee seeds when compared to the control (Espinoza et al 2009). *P. coffea* is now an important biocontrol agent against CBB, in combination with other parasitoids (Bethylidae) as a component of integrated pest management.

Publication:

Lopez-Vaamonde, C. and D. Moore 1998. Developing methods for testing host specificity of Phymastichus coffea Lasalle (Hym. Tetrastichinae) a potential biological control agent of Hypothenemus hampei (Ferrari) (Col. Scolytidae) in Colombia. Biocontrol Science and Technology, 8: 397-411.

Biodiversity studies on Colombian butterflies

During those five months, I also carried out some biodiversity studies on the Lepidoptera fauna of the central Andean Massif. I recorded in a small patch of rainforest (4 hectares) right at the top of the hill called Planalto near the Institute over 250 butterfly species (Lopez Vaamonde & Cardenas Murillo, 2002). The specimens were all deposited at CENICAFE and it was the start of an insect reference collection, which over the years it has been greatly expanded to other insect groups and is being well curated. During this period, I collaborated with Julian Salazar at the local Natural History Museum of the University of Caldas,

Manizales (Salazar & Lopez Vaamonde 1996) and described a new species of Morphinae, *Antirrhea weymeri* (Salazar et al. 1998) (Figure 2). I also had the great opportunity to participate to an expedition to the Choco, in the West Andes of Colombia (upper Garrapatas valley) where we found an outstanding diversity of Lepidoptera with over 375 butterfly species for the studied region (Salazar & Lopez Vaamonde 2002).

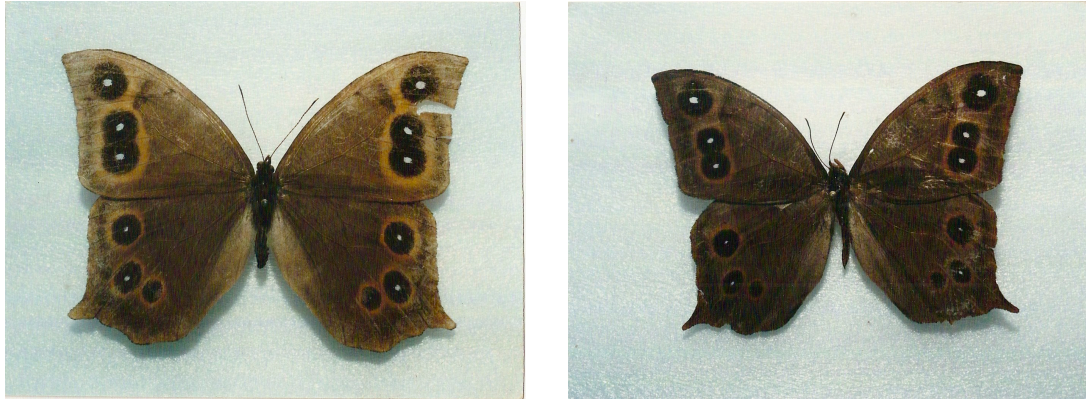


Figure 2: *Antirrhea weymeri* Salazar, Constantino & Lopez-Vaamonde 1998, female (left) and male (right). A rare species endemic to the cloud forests of West Andes of Colombia (photo Julian Salazar).

Publications:

Lopez-Vaamonde, C., & Cardenas Murillo, R., 2002. *Composicion faunistica de las comunidades de mariposas diurnas de un bosque subandino tropical, Colombia (Lepidoptera, Rhopalocera) Parte 1.* Boletin científico Museo de Historia Natural Universidad de Caldas, 6: 45-71.

Salazar, J.A. & **Lopez Vaamonde, C.** 1996. *Gibbonota, Nuevo género de mariposas listadas tropicales de América (Lepidoptera Lycaenidae).* Boletin científico Museo de Historia Natural Universidad de Caldas, 1: 22-26.

Salazar, J.A., Constantino. L.M. & **Lopez Vaamonde, C.** 1998. *Estudio faunistico y ecologico de los géneros Antirrhea Hübner 1822 y Caeoris Hübner 1819 en Colombia (Lepidoptera Nymphalidae, Morphinae).* Boletin científico Museo de Historia Natural Universidad de Caldas, 2: 59-99.

Salazar, J.A. & **Lopez Vaamonde, C.** 2002. *Predicting the overall butterfly species richness in a tropical montane rain forest in the Colombian Choco.* Boletin científico Museo de Historia Natural Universidad de Caldas, 6: 111-145.

Molecular and morphological phylogenetics: a combined approach

After my work at CABI on biocontrol, I went back to the university.

Phylogenetics of Agaonidae fig pollinating wasps

I did a Master degree on “Advanced Methods in Taxonomy and Biodiversity” organized by the Natural History Museum and the Imperial College London in 1996-1997. I did my four month practical project at Silwood Park under the supervision of Dr James Cook and a short stay in Montpellier under the supervision of Dr Jean Yves Rasplus. A morphological phylogeny of 17 *Pleistodontes* (Agaonidae) fig-pollinating wasps (Fig. 3a) of figs of the section Malvanthera (Fig 3b) based on 34 adult female and male morphological characters was reconstructed. I also obtained Cytb and 28S sequence data for both *Pleistodontes* and non-pollinating fig wasps of the genus *Sycoscapter* (Figure 3c) and carried out cospeciation tests. To my knowledge my MSc thesis was the first time anyone had applied a cladistics analysis to reconstruct a morphological phylogeny of fig wasps (Lopez Vaamonde 1997).



Figure 3a: female of *Pleistodontes imperialis* 3b. Leaves and syconia of *Ficus watkinsiana* 3c. female of *Sycoscapter* sp.

Master Thesis:

Lopez Vaamonde, C. 1997. *A combined Morphological and Molecular Phylogeny for Pleistodontes Pollinator Fig Wasp (Hymenoptera; Agaonidae)*. Master Thesis in "Advanced Taxonomy and Biodiversity". Imperial College London & Natural History Museum.

Phylogenetics of Braconidae and Ichneumoidae parasitoids

After my M.Sc., I worked as research assistant for over a year at Silwood under the supervision of Drs. Donald Quicke and Robert Belshaw on molecular phylogenetics of Braconid and Ichneumonid wasps. It was a great opportunity to get more experience in the lab and learnt about parasitoid evolution. I sequenced hundreds of braconid wasps comparing the sequencing success rate using several preservation methods (Quicke et al 1999a). The newly generated DNA sequence data was also used to reconstruct the basal interrelationships of basal Ichneumonids (Quicke et al 1999b) and parasitoids of the subfamily Braconinae (Belshaw et al 2001).

Publications:

Belshaw, R. **C. Lopez-Vaamonde**, N. Degerli and D.L.J., Quicke 2001.- *Paraphyletic taxa and taxonomic chaining: evaluating the classification of braconine wasps (Hymenoptera: Braconidae) using 28S D2-3 rDNA sequences and morphological characters*. *Biological Journal of the Linnean Society*, 73: 411-424.

Quicke, D.L.J., R. Belshaw and **C. Lopez-Vaamonde** 1999.- *Preservation of hymenopteran specimens for subsequent molecular and morphological study*. *Zoologica Scripta*, 28 (1-2): 261-276.

Quicke, D.L.J., **C. Lopez-Vaamonde** and R. Belshaw 1999.- *The basal Ichneumonidae (Insecta: Hymenoptera): 28S rDNA considerations of the Brachycyrtinae, Labeninae, Paxylommatinae and Xoridae*. *Zoologica Scripta*, 28 (1-2): 203-209.

2. Doctoral Studies: Macroevolution of insects-plant interactions

Associations between insects and plants are remarkably diverse, ranging from antagonism to mutualism. During my doctorate, I studied coevolutionary interactions between phytophagous insects and their host plants using molecular phylogenies in two model systems. The first one was the obligate mutualism between figs (*Ficus*) and their pollinators (Hymenoptera, Agaonidae); the second was focused on the antagonistic relationship between leaf-mining moths (Lep. Gracillariidae), their associated parasitoid wasps *Achrysocharoides* (Hym. Eulophidae) and their host plants. Here there are some of the main results:

PhD Thesis:

Lopez Vaamonde, C. 2002. Macroevolutionary studies of two insect-host plant systems. PhD Thesis. Imperial College London, UK. 288 pp

Taxonomy, Host specificity, Cospeciation and Biogeography

Taxonomy of pollinators and host specificity breakdown

Evolutionary as well as ecological studies rely on “**good taxonomy**”. In my studies, I emphasize the importance of accurate identification and the need for thorough taxonomic revision if we want to get a clear picture of the level of host specificity.

Ficus is one of the largest genera of terrestrial plants, with 807 *Ficus* species described (figweb.org). Each fig (*Ficus*) species is generally pollinated by its own unique pollinator microwasp species (Hymenoptera: Agaonidae), whose larvae also feed and develop within the syconia (fig fruits) of the host plant (Cook & Lopez Vaamonde 2001a,b). The intimate fig-pollinator wasp association is an obligate mutualism and has been the subject of many behavioural, ecological, and coevolutionary studies. However, despite the status of this mutualism as a model system for testing evolutionary and ecological hypotheses, fig wasp communities are poorly known taxonomically, and even the pollinators of many figs remain undescribed.

Indeed, at present, there are 366 described species of Agaonidae, but we know that this is an underestimate of the true number for two reasons. First, there are 807 *Ficus* species described and most *Ficus* species have unique pollinators (see Machado et al. 2005 for discussion of exceptions). This suggests that there could be at least 807 pollinator species. Second, there are many examples where one *Ficus* species supports two (or occasionally more) host-specific pollinators (Kerdelhué et al., 1997; Michaloud et al., 1985) and it has been suggested that 25-50% of fig species may have multiple pollinators (Cook and Rasplus, 2003; Machado et al., 2005). Consequently, if we multiply the average number of pollinating wasps per fig species (1-1.8) by the total number of fig species the estimated total number of Agaonid wasps is over 1000 species. That means that more than 600 pollinating fig wasps await description (Cruaud et al. 2009).

My modest contribution to the titanic task of describing the worldwide diversity of fig-pollinating wasps was a revision of the taxonomy of the Australian species of *Pleistodontes*. All species of this genus are known to pollinate fig species of the section Malvanthera. (Figure 4).

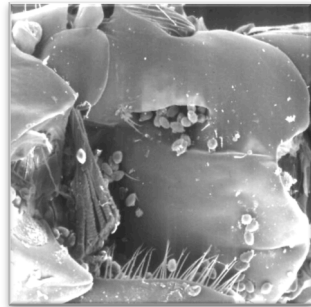


Figure 4: *Pleistodontes* figwasps and *Ficus*; a: Female of *Pleistodontes imperialis* the pollinator of *Ficus rubiginosa*. Female wasps enter receptive syconia (figs) through a narrow tunnel called the ostiole and then pollinate the female flowers; b: *Ficus crassipes* with its large brownish cylindrical syconia (photo James Cook); c: Females have elongate heads and mandibular appendages with many transverse combs of teeth that they use to progress down the ostiole; d: Some agaonid species pollinate passively, carrying pollen dispersed on their bodies and lacking specialized behaviour. However females of *P. imperialis* actively use coxal combs (on their legs) to collect pollen into special thoracic pollen pockets and later deposit it into receptive flowers (photos Jean Yves Rasplus).

In Australia, 14 species of *Malvanthera* figs were known. From these figs, we recorded 17 species of *Pleistodontes*, of which seven species were described as new to science (Lopez Vaamonde et al. 2002) (Figure 5).

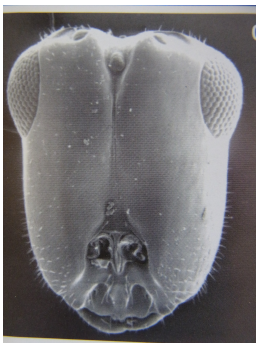


Fig. 5a

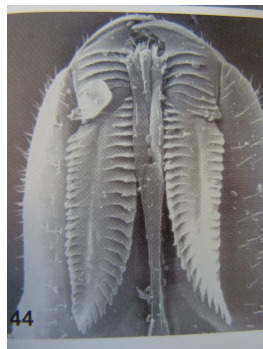


Fig. 5b

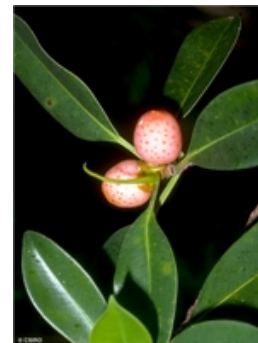


Fig. 5c

Figure 5a: Head of female of the micro hymenoptera *Pleistodontes schizodontus* Lopez-Vaamonde, Dixon, Cook & Rasplus 2002. Fig. 5b: The species name is derived from Greek *schizo* (=cut) and *odontes* (=teeth), in reference to the shape of the lamellae of the mandibular appendages. Fig. 5c: Its host *Ficus triradiata* is a beautiful species with peach to apricot coloured figs and is endemic to a small mountain region of north-eastern Queensland. The pollinator has so far only been recorded from Mount Windsor (photos 3a,b: after (Lopez Vaamonde et al. 2002); 3c: CSIRO).

This large paper was done under the supervision of the world-leading taxonomist on fig wasps Dr Jean Yves Rasplus and in collaboration with the Australian botanist Dr Dale Dixon. Dale did his PhD on the revision of Australian Malvantheran figs. Dale's (2003) revision of Australian malvantheran figs clarified the species delimitation in this group. Simultaneous collection of wasps by Dale from authenticated plant specimens, along with more secure identification of *Ficus* species in other new collections, allowed me to re-examine the host relationships of *Pleistodontes* species with much greater confidence. In most cases we found a one-to-one correspondence of *Ficus* and pollinator species. However, we showed three new notable exceptions to the one to one specificity rule between figs and their pollinators. These were cases of two pollinator wasps per fig helping to reconstruct the true pattern of host associations by repeated sampling of pollinator wasps from their fig hosts. Furthermore, using molecular data, I also showed that some of these co-pollinators of a single fig are sister species (Lopez Vaamonde et al 2001). This opens the interesting hypothesis that some lineages of fig wasps might show a tendency to speciate independently and more rapidly than their host figs.

But how general is this pattern of host specificity breakdown? Recent molecular studies have reported cases of local coexistence of several pollinators on individual *Ficus* species (Molbo et al., 2003; Haine et al., 2006) and pollinator sharing among multiple fig species (Molbo et al., 2003; Machado et al., 2005; Marussich & Machado, 2007; Su et al., 2008; Moe et al 2011). Molecular evidence of hybridization among fig species has also been documented (Parrish et al., 2003; Machado et al., 2005; Renoult et al., 2009). Therefore it has been suggested that cryptic co-occurring species may be more frequent among agaonid wasps than previously thought and that the sharing of pollinating fig wasps and hybridization between closely related *Ficus* species may be an important process generating the high diversity of figs and fig wasps (Machado et al. 2005; Herre et al 2008). However, this view is based on Neotropical figs and remains to be seen whether other biogeographical regions show similar patterns of high levels of fig hybridization, « cryptic » speciation and sharing of their pollinators. In fact a recent study has shown that a widely distributed fig (*Ficus racemosa*) is pollinated by a single pollinator species across continental South-East Asia (Kobmoo et al 2010).

More studies on the phylogeography of figs and their associated fig wasps are needed and the debate will no doubt continue in the future.

Publications:

Cook J. M. & C. Lopez-Vaamonde, 2001a. *Fig Biology: Turning over new leaves. Trends in Ecology & Evolution, 16* (1): 11-13.

Cook J. M. & C. Lopez-Vaamonde, 2001b. *Figs and fig wasps: evolution in a microcosm. Biologist 48* (3): 105-110.

Lopez-Vaamonde, C., D. Dixon, J. M. Cook and J. Y. Rasplus 2002. *Revision of the Australian species of Pleistodontes (Hymenoptera: Agaonidae) fig-pollinating wasps and their host plant associations. Zoological Journal of the Linnean Society, 136: 637-683.*

Non pollinating fig wasps and cospeciation

Figs are also exploited by several clades of non-pollinating fig wasps (NPFW), which are parasites of the mutualism, and whose patterns of speciation have received little attention. The diversity of NPFW is enormous with thousands of new species to be described (Figure 6). One species of fig can host up to 30 species of NPFW. In my Ph.D. thesis, I followed up

my work during my M.Sc. thesis and focused on the genus *Sycoscapter* (Pteromalidae, Sycoryctinae).



Figure 6. Most Non Pollinating Figwasps lineages are not closely related to the pollinators and have evolved convergent adaptations such as long ovipositors to penetrate the syconium and lay eggs such as this female of *Apocrypta robusta* (photo Jean Yves Rasplus)

Sycoscapter female wasps lay eggs into the galls of fig-pollinating wasps, or more rarely other gall-inducing fig wasps, and kill their hosts directly as parasitoids (Tzeng et al. 2008).

I obtained data from nuclear and mitochondrial DNA regions to estimate the phylogenies of 20 species of *Pleistodontes* pollinating wasps and 16 species of *Sycoscapter* non-pollinating wasps associated with *Ficus* species in the section *Malvanthera*. I compare the phylogenies of 15 matched *Pleistodontes* / *Sycoscapter* species pairs and show that the level of cospeciation is significantly greater than expected by chance. However, I also show that there is not perfect congruence of pollinator and parasite phylogenies (for any substantial clade), and argue that host plant-switching is likely to be less constrained for *Sycoscapter* parasites than for *Pleistodontes* pollinators (Lopez Vaamonde et al 2001).

Interestingly, a recent study has also found significant levels of cospeciation between non pollinating Otiteselline fig wasps and their associated pollinators suggesting that both groups have cospeciated with their host figs or at least that host association is phylogenetically conserved (Jousselin et al. 2005).

Publication:

Lopez-Vaamonde, C., G. Weiblen, J. Y. Rasplus et J. M. Cook. 2001. Molecular phylogenies of fig wasps: Partial co-cladogenesis of pollinators and parasites. Molecular Phylogenetics and Evolution, 21: 55-71.

A Cretaceous/Gondwanan origin for fig-pollinating wasps?

Fig trees are a diverse and ubiquitous component of tropical rain forests and are keystone resources for many fruit-eating vertebrates. Consequently, the fig-pollinator mutualism is central to the evolutionary history of tropical ecosystems. But when and where did this obligate mutualism originate? We used a combination of phylogenetic and biogeographical data to infer the age, the major period of diversification, and the geographic origin of pollinating fig wasps.

Rønsted et al. (2005) used a double dating (independent dating of two associated lineages) approach and considered fig wasps (Agaonidae) to have co-diverged with their associated hosts (*Ficus*) during the last 60 million years. However our results show that the crown group of Agaonidae could have originated anytime between 54 and 216 MYA. This

wide error margin partly originates from differences between molecular-dating methods (Lopez Vaamonde et al 2009a). This makes it difficult to assess with any certainty the Cretaceous/Gondwanan origin of agaonids.

Our ancestral area analyses favor an Asian origin for fig wasps, in sharp contrast to previous studies which have suggested a South American origin for the mutualism, on the basis that the basalmost lineages of extant figs (Pharmacosyceae) and associated extant fig wasps (*Tetrapus*) occur only in South America (Lopez Vaamonde et al 2009a).

Interestingly, using a similar approach of molecular dating and ancestral state reconstruction Simon Segar, a PhD student of Prof. James Cook (my former PhD supervisor), shows that the non-pollinating subfamily Sycoryctinae also originated in Asia some 54 million years ago. This makes the Sycoryctinae a considerably later invasion when compared with the pollinating wasps and suggest that phylogenetic tracking may have played an important role in their speciation (Segar et al submitted).

In another recent global phylogeny of the mostly gall-inducing non pollinating fig wasps that form the subfamily Sycophaginae suggests a different evolutionary history for this group compared to the pollinators, with a more recent (ca. 45 Ma) origin on Australia, followed by global radiation through dispersal (Cruaud et al 2010).

Publications:

Lopez-Vaamonde, C. N. Wikström, K. M. Kjer, J.Y. Rasplus, C. Machado, G. Weiblen & J. M. Cook (2009a)
Molecular dating and biogeography of fig-pollinating wasps. Molecular Phylogenetics and Evolution, 52: 715-726

Segar, S.T., Lopez Vaamonde, C., Rasplus, J-Y and Cook, J.M. submitted. *The global phylogeny of the subfamily Sycoryctinae (Pteromalidae): Parasites of an obligate mutualism. Molecular Phylogenetics and Evolution.*

Co-diversification, host shifts and ecological specificity of tritrophic interactions

Herbivores and flowering plants constitute a very large proportion of all species. Excluding algae, fungi and microbes, it has been estimated that nearly 50% of the biota are green plants and herbivorous insects (Price 2002). A key aim to understand global patterns in terrestrial biodiversity is to understand how phytophagous insects have diversified.

The notion that coevolution between insects and plants might explain species diversity was first proposed by Ehrlich and Raven (1964). They noticed that phylogenetically related butterflies tended to have as hosts phylogenetically related plants. They argued that this pattern of host use arose as a result of a kind of arms race scenario between herbivores and plants. This model is known as “escape and radiation” coevolution (Thompson 1988).

In the last couple of decades there has been a series of phylogenetic studies trying to test macroevolutionary predictions from this model. A key prediction of the escape and radiate hypothesis is that host plant lineages, after gaining a new defense that gave them protection from herbivores, would undergo rapid range expansion and radiation due to the competitive advantage inherent in being able to withstand attack from specialist enemies (Ehrlich and Raven 1964). Insects would eventually counteradapt and be able to circumvent these defenses and would enjoy a competitive advantage and potential free enemy space leading to their own species radiation. Thus, it is expected that plant radiations should predate herbivorous insect radiations and the parasitoids, a “speciation cascade” whereby the diversification of lower trophic levels spur radiation in a higher level (Nyman et al. 2007).

Timing the diversification of leaf-mining micromoths

Leaf miners are an ideal group to study plant-insect interactions in a historical context because their mines (as part of their host plant) are preserved together as fossils dating back millions of years ago allowing an excellent opportunity to calibrate divergence times and test co-evolutionary hypotheses.

During my Ph.D., I used a combination of fossil, molecular and ecological data (host plant use) to show that the radiation of a genus of gracillarid leaf-mining micromoths, *Phyllonorycter*, occurred millions of years after the diversification of their host plants (Lopez-Vaamonde et al. 2006) (Figure 7). I also showed that the phylogenies of *Phyllonorycter* moths and their host plants were not congruent (Lopez-Vaamonde et al. 2003). However, *Phyllonorycter* species feeding of the same host-plant genus frequently form a monophyletic clade. This phylogenetic conservatism of host use whereby closely related moth species often feed on closely related plants, is interpreted as due to host switching (colonization followed by speciation) being more likely to happen amongst phylogenetically related plants (Lopez-Vaamonde et al. 2003b).



Figure 7a. The markings and striking metallic ground coloration of the forewings of *Phyllonorycter* micromoths make this genus an attractive group for amateur microlepidopterists to study and, consequently, the faunistics, alpha taxonomy, and autecology of these moths are quite well known, at least for the Holarctic region. 7b. The early instars mine the epidermal cells of leaves or young bark as sap feeders and, after the second or third ecdysis, the larvae undergo hypermetamorphosis to become tissue feeders, mining the parenchyma (photos Carlos Lopez Vaamonde).

We suggested that this scenario of asynchronous radiations, high phylogenetic conservatism of host plant use and lack of parallel cladogenesis might apply to other predominantly monophagous insect-plant systems. It has recently been shown that conservatism of plant higher taxon use seems to be ubiquitous in phytophagous insects (Winkler & Mitter, 2008). Recent studies also show that major radiations within beetles likely predated the angiosperms (Gómez-Zurita et al. 2007, Hunt et al. 2007, McKenna et al. 2009). Thus, the null hypothesis, that insect herbivore and angiosperm diversification is uncoupled, garners support.

Publications:

Lopez-Vaamonde, C., H. C. J. Godfray and J. M. Cook. 2003b. Evolutionary dynamics of host plant use in a genus of leaf-mining moths. Evolution, 57 (8): 1804-1821.

Lopez-Vaamonde, C. N. Wikström, C. Labandeira, H. C. J. Godfray, S. J. Goodman & J. M. Cook (2006). Fossil-calibrated molecular phylogenies reveal that leaf-mining moths radiated several million years after their host plants. Journal of Evolutionary Biology, 19: 1314-1326.

Ecological specificity and split sex ratios in parasitoids of leaf-mining micromoths

Studies have focused on the radiation of herbivorous insect lineages over terrestrial plant taxa, but far less is understood about the speciation of their parasitoid natural enemies (Godfray 1994). Indeed, few studies have compared radiation across multiple trophic levels (Lopez-Vaamonde et al. 2005; Stireman et al. 2006; Nyman et al. 2007).

Leaf miners have an extraordinary diversity of parasitoids. Eulophid micro-parasitoids of the genus *Achrysocharoides* are larval endoparasitoids of leaf mining moths in the family Gracillariidae, in particular they have mainly been recorded attacking larvae of the leaf mining moth genus *Phyllonorycter* (Figure 8).

Figure 8. Male *Achrysocharoides*. There are 48 species described from temperate areas. The ecology of *Achrysocharoides* species is reasonably well understood and there are host records for most species (photo John Lasalle).



Achrysocharoides parasitoids represents an interesting unique case of “ecological specificity”, that is its host range is restricted to a taxonomically defined-range of host plants. Thus, most species attack *Phyllonorycter* moths confined to single-host plant genera.

I studied the tritrophic interactions between Gracillariid moths, their host plants and their *Achrysocharoides* parasitoids and showed that the *Achrysocharoides-Phyllonorycter*-host plant system is more shaped by host shifts, through colonization and specialization than by parallel cladogenesis. The radiation of *Achrysocharoides* appears to be more constrained by the host plant phylogeny than the host insect phylogeny (Lopez-Vaamonde et al. 2005).

No study so far has tested the hypothesis that parasitoid diversification has substantially postdated the diversification of their herbivorous insect hosts. A phylogenetic approach, with *Achrysocharoides* fossil-calibrated phylogenies could be used to test this hypothesis and shed some light on the role that coevolutionary arms races play in the evolution of diversity at three trophic levels.

We also examined the evolution of clutch size and sex allocation of these parasitoids. *Achrysocharoides* contains gregarious species with mixed and split sex broods, whilst species in closely related genera are solitary. Separate (split) sex broods are very rare and virtually restricted to *Achrysocharoides*. Our phylogeny suggests that split sex broods have evolved twice and provides evidence for a transition from solitary to mixed sex broods, via split sex broods.

Publication:

Lopez-Vaamonde, C. H. C. J. Godfray, S. West, C. Hansson And J. M. Cook, (2005). The evolution of host use and unusual reproductive strategies in Achrysocharoides parasitoid wasps. Journal of Evolutionary Biology, 18: 1029-1041.

3. Post-Doctoral Studies: Behavioural Ecology of Bumblebees

The study of the evolutionary ecology of social behaviour is a long-standing source of discovery and ideas in evolutionary biology. Traditionally, social insect societies were regarded as cooperative with the workers acting for the 'good of the colony'. However, it is now widely understood that the non-clonal kin structure of insect societies results in potential conflict among individuals or groups of individuals over reproduction. Kin selection theory states that individuals value one another in proportion to their genetic relatedness. Therefore, potential within-group conflict arises when different parties are unequally related to offspring. Studies of social insects provide some of the most powerful tests of kin selection theory.

My postdoctoral research involved experiments on captive bumblebee (*Bombus terrestris*) colonies (Figure 9), and microsatellite analyses, to investigate the role of relatedness and information availability in social evolution. My research has yielded some insights into how relatedness, information use and novel worker behaviours interact to affect social evolution. Below, I summarise some highlights of my findings and publications:

Figure 9. We conducted all our experiments using colonies of *B. terrestris* obtained from a commercial supplier (Koppert Biological Systems, and kept them in wooden nestboxes (20*30 cm and 17 cm high) and bees were fed with thawed fresh pollen supplied by Koppert and 50% sugar solution provided ad libitum (photo Carlos Lopez Vaamonde).



Kin conflict over reproduction

One of the most important potential conflicts within animal societies arises over who gets to reproduce. In many animal societies, reproduction is monopolized by one or a few individuals. Understanding the factors that give an individual or a group the ability to manipulate reproduction is a fundamental aspect of the functioning and internal organization of animal societies.

Measuring colony level costs of worker reproduction

Workers of many species of social Hymenoptera are capable of laying unfertilized haploid eggs that develop into males. Under conditions of monogyny and single queen mating, kin selection theory predicts that, workers gain greater inclusive fitness from rearing sons (relatedness, $r = 0.5$) or the sons of other workers (nephews, $r = 0.375$) rather than the queen's male offspring (brothers, $r = 0.25$), whereas the queen gains greater inclusive fitness from the rearing of sons ($r = 0.5$) rather than workers' male offspring (grandsons, $r = 0.25$) (Hamilton, 1964). Therefore, there is a potential kin-selected conflict between queens and workers over male parentage (Hammond & Keller 2004) (Figure 10).

Workers should raise worker-produced males. However, there are many species in which a lower level of worker male-production occurs than is predicted (Bourke 2005). This could be due to costs of worker male-production to colony-level productivity, since reproductive workers tend to work less than non-reproductive ones.

Figure 10: Kin selection theory predicts potential conflict over male parentage, with queens favouring the rearing of queen-produced males, and workers favouring the rearing of worker-produced males (preferentially their own sons). Consistent with this expectation, ovary-activated workers in mature colonies of *Bombus terrestris* attempt to replace queen-laid eggs with their own eggs and attack the queen and one another. Here a worker is eating eggs laid by another worker (photo Will Koning).



Few studies have tried to measure the costs of worker reproduction at colony level (Bourke 2011). In a series of experiments we showed that by removing aggressive, reproductive workers from colonies and comparing colony productivity with that of control colonies, that there is no detectable cost of worker reproduction to the production of new queens in the bumble bee *Bombus terrestris* (Lopez-Vaamonde *et al.*, 2003a). A recent study has also failed to detect significant costs of worker male-production in leafcutter ants (Dijkstra & Boomsma, 2007). More studies are needed to see whether workers restraint from reproducing due to colony level costs.

Publication:

Lopez-Vaamonde, C., J. W. Koning, W. C. Jordan and A. F. G. Bourke 2003a. No evidence that reproductive bumble bee workers reduce the production of new queens. Animal Behaviour, 66: 577-584.

Kin conflict and information use

Whether kin-selected conflict is expressed may depend on individuals' ability to obtain and use information about their social environment to make decisions affecting their fitness.

We investigated whether bumblebee workers use information on age of male larvae to start reproducing. We show that workers have access to information (presence of male brood) but do not act on it by commencing egg-laying. We concluded that either the kin-selection interpretation of the workers' behaviour is wrong, or workers are constrained from acting in their self-interest (Lopez-Vaamonde *et al.*, 2004a).

So, what does determine the timing of the start of worker aggression in *B. terrestris* colonies? In a separate study we tested the hypothesis that a queen signal (cessation of a non-volatile pheromone production) to female larvae to start development as queens could trigger worker reproduction (Lopez-Vaamonde *et al.*, 2007).

Publications:

Lopez-Vaamonde, C., J. W. Koning, W. C. Jordan & A. F. G. Bourke 2004a. A test of information use by reproductive bumblebee workers. Animal Behaviour, 68: 611-618.

*Lopez-Vaamonde, C. R.M. Brown, E.R. Lucas, J.J.M. Pereboom, W. C. Jordan & A. F. G. Bourke (2007). Effect of the queen on worker reproduction and new queen production in the bumblebee *Bombus terrestris*. **Apidologie**, 38: 171-180*

Intraspecific social parasitism

In a novel discovery, published in *Nature* (Lopez Vaamonde et al 2004), we show that some bumblebee workers enter unrelated, conspecific colonies in which they then produce adult male offspring, and that these socially parasitic workers reproduce earlier and are significantly more reproductive and aggressive than resident reproductive workers. We also showed that, only a small percentage of males (3.6%), were produced by workers in queenright conditions. This discovery of an alternative reproductive tactic among bumblebee workers created an unanticipated new aspect to kin-selected conflict over male parentage, with potentially important implications that require investigation. First, most radically, it suggested that, in *B. terrestris* and possibly other social bees and wasps, worker reproduction by resident workers may not be a function of the genetic structure of the workers' natal colony, as kin selection theory predicts, but may instead be a by-product of workers' capacity for intraspecific social parasitism.

It is important to determine the frequency of intraspecific social parasitism by workers in natural colonies of eusocial Hymenoptera to improve our understanding of social evolution (Beekman & Oldroyd, 2008). Since the publication of my paper, several studies have shown drifting and intraspecific social parasitism by workers in several species of honey bees (Nanork et al. 2005, 2007; Chapman et al. 2010) and bumble bees (Birmingham et al. 2004; Lefebvre and Pierre 2007; Takahashi et al. 2010).

In a recent field experiment we show that workers of *B. terrestris* travelled to, and became accepted in, conspecific nests up to 60 m away (Zanete et al submitted). We also show using microsatellite genotyping that up to 3% of workers in field-collected nests are not full sisters of nestmate workers and are likely to be drifters. Therefore, worker drifting is not artefactual (due to high density of experimental nests), is likely to be countered by nestmate recognition, and, contrary to existing models, potentially transmits pollen and pathogens directly to conspecific nests at relatively high rates over substantial distances (Zanete et al submitted).

Publications:

*Lopez-Vaamonde, C., J. W. Koning, R.M. Brown, W. C. Jordan & A. F. G. Bourke. 2004b. Social parasitism by male-producing reproductive workers in a eusocial insect. **Nature**, 430: 557-560.*

*Zanette, L. R. S., S. M. Miller, C. Faria, C. Lopez-Vaamonde & A. F. G. Bourke (submitted). Spatial ecology of drifting bumble bee workers in field conditions. *Oecologia**

Life-History Evolution

Although central to understanding life-history evolution, we know very little about what social, ecological, and genetic factors affect breeding success and survival in animals (Clutton-Brock & Sheldon 2010).

Social insects represent important subjects for the study of life history. However, the study of life-history evolution in social insects lags behind that in unitary organisms. This is partly because many social insects form perennial colonies with long-lived queens, and in

these taxa the estimation of basic life-history parameters such as longevity or lifetime reproductive success is practicable only in rare cases. One solution to this problem is to investigate social insects with annual colonies such as bumblebees.

We characterized the overall demography of colony growth and production, we measured queen longevity, the extent of worker reproduction, and the relative masses of queen- and worker-produced males from samples of colonies reared from wild-caught queens of the bumble bee *Bombus terrestris audax*. We demonstrated for the first time in social insects, that queens achieve reproductive success in proportion to their longevity (Lopez-Vaamonde et al. 2009b). This is a novel result of general interest in the field of life history evolution because, it shows for the first time that sociality in insects has allowed a life history to evolve in which the negative relationship between fecundity and longevity found in most non-social insects is reversed. Indeed, in many nonsocial insects, lifetime reproductive success and longevity show a negative relationship (high female reproductive success comes at the cost of reduced longevity: « live fast, die young »). However, a positive relationship does occur in semelparous nonsocial Hymenoptera with parental care. Therefore, we suggested that annual social Hymenoptera may have inherited a positive relationship of lifetime reproductive success and longevity from their nonsocial ancestors showing parental care, and maintained it because queens are buffered by their workforce against extrinsic mortality.

To date, this paper remains one of the very few attempts at testing life history theory with social insects as models (Clutton-Brock & Sheldon 2010).

Finally, as shown above, there is a large amount of behavioural and genetic information about the species *B. terrestris*. However, we know very little about the behavioural ecology of other bumblebee species. More studies are needed to see the extent to which kin selection theory successfully predicts the internal organization of bumblebee societies.

Publication:

Lopez-Vaamonde, C. , N. E. Raine, J. W. Koning, R. M. Brown, J. J. M. Pereboom, T. C. Ings, O. Ramos-Rodriguez, W. C. Jordan & A. F. G. Bourke (2009b). Lifetime reproductive success and longevity of queens in an annual social insect. Journal of Evolutionary Biology, 22 (5): 983-996.

4. Work at INRA: Evolutionary ecology of insects

Since 2005 I have been working at INRA Orléans as entomologist on the genetic diversity of forest insects. My main research is focused on three main areas:

- Invasion biology of forest insects
- Molecular systematics and DNA barcoding
- Conservation biology of forest insects

Invasion biology

Tracking the origin of the horse-chestnut leaf-mining moth

Determining the origin of alien invasive species is crucial to developing invasive species management strategies (Roques et al 2010). However, the origin of many alien species remains uncertain because of the lack of historical data. For instance, the moth *Cameraria ohridella* (Gracillariidae) was described in 1986, as a genus new to Europe and had managed to invade almost all Europe since 1989 (Augustin et al 2010) (Figure 11a). Its larvae are leaf miners on the white flowering horse-chestnut (*Aesculus hippocastanum*), causing significant damage to their summer foliage (Figure 11b). The fact that the appearance of *C. ohridella* in much of Western Europe has been so recent and dramatic, without earlier detection by entomologists, has made its origin a subject of debate (Lees et al 2011a). Scientists had been long debating whether the moth was a possible introduction from Southeast Asia or an example of a recent host switch from sycamore or maple trees (Lopez Vaamonde 2009c).

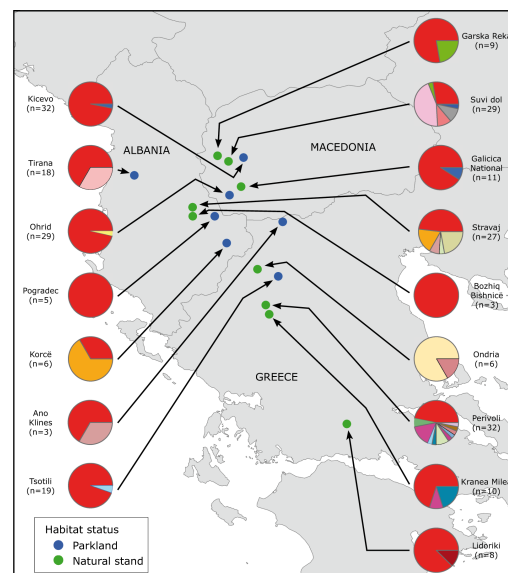


Figure 11a: adult of the micromoth *C. ohridella* (photo David Lees) b). Fig. 11b : larvae cause significant damage to their summer foliage. Fig. 11c: Haplotype diversity was higher in natural stands (on the right) than in parks (on the left). Notice that in an isolated remote canyon in Perivóli, Central Greece we found 11 haplotypes (after Valade et al 2009)

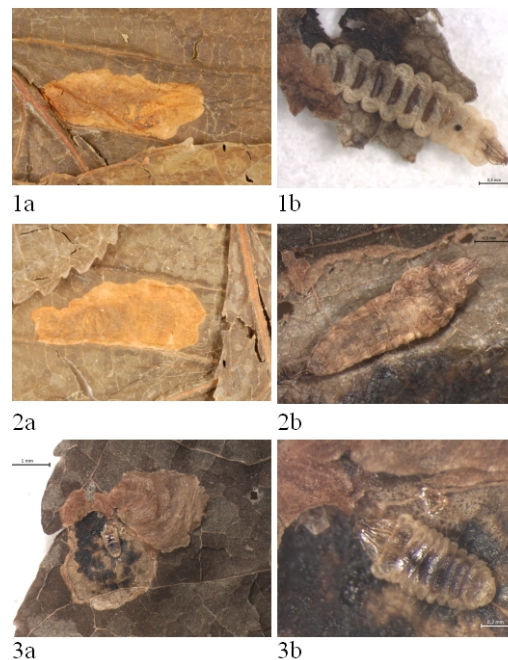
By using a combination of mitochondrial and microsatellite data we showed an unexpected high genetic diversity for such a recently invasive herbivore. Romain Valade, a Master Student, found twenty-five mitochondrial cytochrome c oxidase subunit 1 [COI] haplotypes – each differing by at least one single nucleotide mutation (Valade et al., 2009). We noted that only three haplotypes have invaded western and eastern Europe in the past quarter century. Indeed, most COI haplotypes of *C. ohridella* were either endemic or very narrowly distributed among natural horse-chestnut populations in the Balkans (Figure 11c).

We also examined nuclear genetic variations using six microsatellite loci developed for *C. ohridella* by another Master student, Neus Mari Mena (Mari Mena et al. 2008). Consistent with the COI trend, these data showed a decrease in diversity away from the Balkans and from natural to ornamental populations.

The key question posed by Valade et al. (2009) was that, if *C. ohridella* was Balkan in origin, why had the modern explosion apparently been delayed until two decades ago?

David Lees from the Natural History Museum London, who was working with us at INRA as a Studium fellow, suggested to me that there should exist an historical trace of *C. ohridella* in herbarium collections of *A. hippocastanum* given a Balkan origin and a quarter-century record of outbreaks. David searched horse-chestnut collections of seven historic European herbaria for leaf mines of *C. ohridella*. David found that almost half of 71 sheets had leaf mines with larvae/pupae inside (Fig 12).

Figure 12: Larvae and leaf mines from natural populations in Albania and Greece and dated from 1981 back to 1879. Therefore, the horse-chestnut leaf miner appeared to be living on native stands of the horse-chestnut in Greece by 1879 and was already present in the Balkans more than a century before its scientific description (after Lees et al 2011).



DNA from 54 archival larvae was extracted and used five COI minibarcode primer pairs developed specifically by David for *C. ohridella*. We successfully amplified DNA minibarcode fragments from 10 larvae extracted from herbarium specimens from 1936 to 1981. These archival sequences confirmed an identity and Balkan origin for *C. ohridella* and the herbarium data set its history back by over a century. Our study resolved a two decade-long debate about origin and invasion of the horse-chestnut leaf miner. These results were

published in *Frontiers in Ecology and the Environment*, the scientific journal of the Ecological Society of America (Lees et al. 2011) and attracted media attention (BBC, The Scientist, Science daily).

Our study demonstrates that herbaria are greatly underutilised in studies of invasive species origins, herbivore biodiversity and insect-plant interactions.

Publications:

Augustin S., Kenis M., Valade R., Gilbert M., Garcia J., Roques A., **Lopez-Vaamonde C.**, 2010. A Stowaway species arriving from the Balkans, the horse chestnut leafminer, *Cameraria ohridella*. pp. 160-161 In : Settele, J. et al. (eds.) : Atlas of Biodiversity Risks. Pensoft publishers, Sofia, Bulgaria.

Lees D.C., **Lopez-Vaamonde C.**, Augustin S., 2011a. Taxon page for *Cameraria ohridella* Deschka & Dimic 1986. In: EOLspecies, <http://eolspecies.lifedesks.org/pages/8675>.

Lees D.C., Lack, H. W., Rougerie R., Hernandez-Lopez A., Raus, T., Avtzis, N.D., Augustin S. and **Lopez-Vaamonde C.** (2011b) Tracking origins of invasive herbivores using herbaria and archival DNA: the case of the horse-chestnut leafminer. *Frontiers in Ecology and the Environment*, 9 (6): 322-328.

Lopez-Vaamonde C., Augustin S., Roques A., Cota E., Kullaj E., Avtzis N., Tomov R., Naceski S., Papazova I., (2009c). Genetic Study of an Invasive Forest Insect and its Parasitoid in the Balkan Region. In: Macháčová J. & Rohsmann K., (eds.): Scientific results of the SEE-ERA.NET Pilot Joint Call. Centre for Social Innovation (ZSI), Vienna, 121-128.

Mari Mena N., Valade R., Magnoux E., Augustin S., **Lopez-Vaamonde C.** 2008. Microsatellites for the highly invasive *Cameraria ohridella* (Lepidoptera, Gracillariidae) and their amplification in related species. *European Journal of Entomology*, 105, 945-948.

Valade R., Kenis M., Hernandez-Lopez A., Augustin S., Mari Mena N., Magnoux E., Rougerie R., Lakatos F., Roques A., **Lopez-Vaamonde C.**, 2009. Mitochondrial and microsatellite DNA markers reveal a Balkan origin for the highly invasive Horse-Chestnut leaf miner *Cameraria ohridella* (Lep. Gracillariidae). *Molecular Ecology*, 18, 3458-3470.

A parasitoid cryptic host race from the Balkans as potential biocontrol?

C. ohridella is an urban pest and as such its control is achieved by destroying fallen leaves (containing overwintering pupae) every Autumn. However this control measure is labour intensive and expensive. Classical biocontrol with either enrichment of local native parasitoids or introduction of a new biocontrol agent remains the best option. The identification of the native area of *C. ohridella* opens the possibility to look for specific natural enemies that could potentially be used in biocontrol.

Until now, surveys in the Balkans have failed to identify specific natural enemies that could be used as biological control agents, in particular parasitoids, and parasitism rates are lower than those usually observed in native leaf miners. Research on parasitoid complexes of *C. ohridella* conducted during the past 10 years shows significant differences between the Balkans and the rest of Europe in the prevalence of *Pediobius saulius* (Eulophidae). This pupal parasitoid is fairly polyphagous and the dominant species in both artificial (gardens and parks) and natural horse-chestnut populations where *C. ohridella* occurs in the Balkan, while in central and western Europe, *P. saulius* is a common parasitoid of other leaf miners but rarely attacks *C. ohridella* (Figure 13).

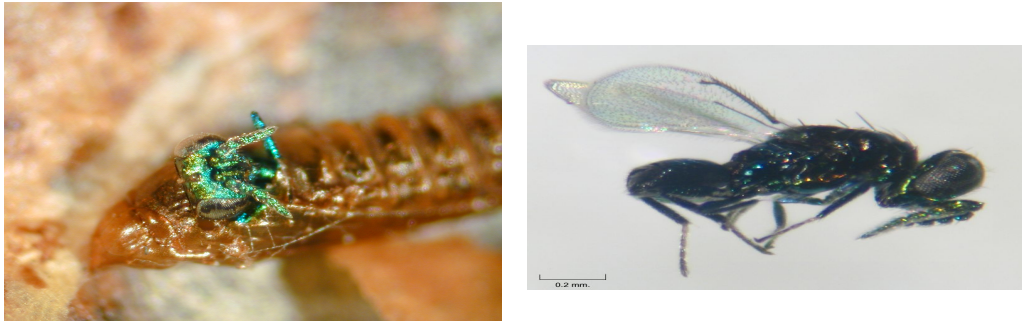


Figure 13a: a male of *Pediosbius saulius* emerging from a pupa of *Cameraria ohridella* (left) and a female of *P. saulius* (right). It is thought to be very polyphagous attacking 76 species of Lepidoptera (59 species of Gracillariidae), 20 species of Hymenoptera and 11 Coleoptera (photos Rumen Tomov).

It has been suggested the possible existence of cryptic host-differentiated races or sibling species of the wasp, based on the observation of high parasitism of *P. saulius* on the plane leaf miner *Phyllonorycter platani*, while *P. saulius* was totally absent from sympatric populations of *C. ohridella* in Switzerland.

Antonio Hernandez a postdoc that worked with me at INRA, used mitochondrial data to show the existence of at least five highly differentiated parasitoid complexes, within two of which clades with differing degrees of host specialization were found: a Balkan clade that mainly (but not only) attacks *C. ohridella* and a more generalist European group that attacks many hosts, including *C. ohridella*. The divergence in COI (up to 7.6%) suggests the existence of cryptic species, although this is neither confirmed by nuclear divergence (ITS, 28S) nor morphology (Hernandez et al 2011). We plan to use microsatellites in the future to see whether we can reveal some nuclear variation and whether there is congruence with mitochondrial differentiation.

The higher parasitism rates observed in the Balkans and the scarcity of the Balkan *Cameraria* haplotypes out of the Balkans, open the possibility of using these Balkan haplotypes as biological control agents of *C. ohridella* elsewhere in Europe.

Publication:

Hernandez-Lopez A., Rougerie R., Augustin S., Lees D., Tomov R., Kenis M., Cota E., Kullaj E., Hansson C., Grabenweger G., Roques A., Lopez-Vaamonde C. (2011). Host tracking or cryptic adaptation? Phylogeography of *Pediosbius saulius* (Hymenoptera, Eulophidae), a parasitoid of the highly invasive horse-chestnut leafminer. *Evolutionary Applications* doi: 10.1111/j.1752-4571.2011.00220.x

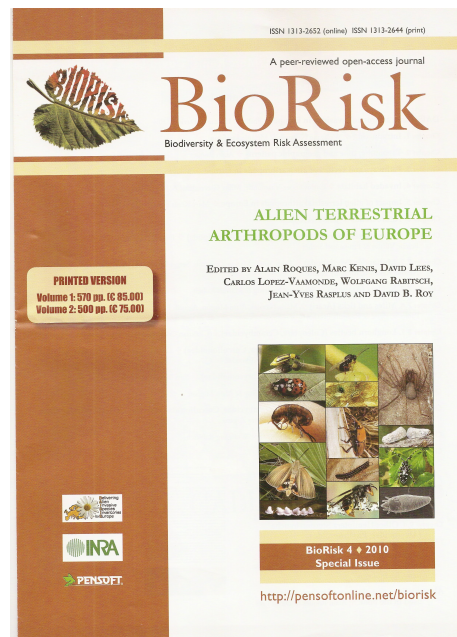
Inventory of alien insects established in Europe and their ecological impacts

Unlike other groups of animals and plants, no checklist of alien terrestrial invertebrates was available in any of the European countries until recently. Thus, estimating the importance of terrestrial alien invertebrates at the European level remained impossible. By gathering taxonomists specialized on most invertebrate taxa with ecologists collaborators working at the national level in 35 European countries, the DAISIE (Delivering Alien Invasive Species Inventories in Europe (<http://www.europe-aliens.org/>) European project intended to fill this gap.

Our research unit at URZF, lead by Alain Roques, has coordinated the work at DAISIE on alien terrestrial invertebrates. The work revealed a huge list of 1650 species of terrestrial

invertebrates, including 1590 arthropods and 1390 insects (Roques et al 2008). The enormous amount of information on all those alien species was published in two volumes (Roques et al., 2010) (Figure 14).

Figure 14: This book is the first comprehensive review of the fauna of alien terrestrial arthropods that have colonized the European continent. It is the result of the joint work of 89 authors from 27 different European countries. For each species all key information is provided, feeding regime, data and country of first record in Europe, invaded countries, invaded habitats, plant or animal host. Detailed factsheets are provided for 80 species considered to be the most representative of the different pathways of introduction, and of the diversity of impacts on ecosystems, economic activities and human and animal health. All chapters can be freely downloadable at: <http://www.pensoft.net/journals/biorisk/issue/4/>



A temporal analysis shows that the arrival of alien invertebrates has increased exponentially since the 15th century but a significant acceleration was observed during the second half of the 20th century. As a probable result of globalization, this trend is still increasing with an average of 19.1 alien species newly reported per year in Europe between 2000 and 2007. Asia has contributed the most alien invertebrates occurring in Europe (29% of the species of identified origin), followed by North America (20%).

The data base and results of the analysis were published in 2010 in two volumes ‘Alien arthropods in Europe’, freely downloadable online (Roques et al 2010). I was co-editor of these books and leading author of the chapter on alien Lepidoptera published with the contribution of 23 lepidopterists from 16 different European countries (Lopez Vaamonde et al 2010).

Ecological impacts of alien invertebrate species have been much less investigated than their economic or human health impacts (Vila et al 2009). In a recent worldwide review by Kenis et al. (2009) we identified several types of ecological impacts for alien insects. Alien invertebrates can affect the native biodiversity through direct interactions, e.g. hybridization with native related species, feeding on native plants, preying or parasitizing native species. They can also affect native species and ecosystems indirectly, through cascading effects, or through various mechanisms, e.g. by competing for food or space, carrying diseases, or sharing natural enemies with native species. In Europe, only a handful of examples of terrestrial invertebrates showing a clear impact on native biodiversity or ecosystems have been identified so far.

Publications:

Kenis, M., M.-A. Auger-Rozenberg, A. Roques, L. Timms, C. Péré, M.J.W. Cock, J. Settele, S. Augustin & C. Lopez-Vaamonde (2009). Ecological effects of invasive alien insects. Biological Invasions, 11: 21-45.

- Lopez-Vaamonde, C.** and Lees, D.C. (2009). *Spodoptera littoralis*, African cotton leaf worm (Lepidoptera, Noctuidae). In: Roques, A., ed. Handbook of alien terrestrial arthropods in Europe page: 339. Pensoft.
- Lopez-Vaamonde, C.**, Agassiz, D.V.L., Augustin, S., De Prins, J., De Prins, W., Gomboc, S., Ivinskis, P., Karsholt, O., Koutroumpas, A., Koutroumpa, F., Laštůvka, Z., Karsholt, O., Marabuto, E., Olivella, E., Przybylowicz, L., Roques, A., Ryrholm, N., Šefrová, H., Šima, P., Sims, O., Sinev, S., Tomov, R., Zilli, A. and Lees, D.C., 2010a. Lepidoptera. Chapter 11. In: Roques A et al. (Eds) Alien terrestrial arthropods of Europe. *BioRisk* 4(2): 603–668. doi: 10.3897/biorisk.4.50.
- Lopez-Vaamonde, C.**, Glavendekic, M. & Santos de Paiva M.R. (2010b) Invaded habitats. Chapter 4. In: Roques A et al. (Eds) Alien terrestrial arthropods of Europe. *BioRisk* 4(1): 45–50. doi: 10.3897/biorisk.4.66
- Lopez-Vaamonde, C.** (2010). *Spodoptera littoralis*, African cotton leaf worm (Lepidoptera, Noctuidae). In: Roques A et al. (Eds) Alien terrestrial arthropods of Europe. *BioRisk* 4(2): 1008–1009.
- Lopez-Vaamonde, C** & D.C. Lees. (2010). *Paysandisia archon*, the castniid palm borer (Lepidoptera, Castniidae). In: Roques A et al. (Eds) Alien terrestrial arthropods of Europe. *BioRisk* 4(2): 990–991.
- Roques A., Rabitsch W, Rasplus JY, **Lopez-Vaamonde C**, Nentwig W, Kenis M, 2009. Alien terrestrial invertebrates of Europe. In W. Nentwig, P. Hulme, P. Pysek, M. Vila (Eds), Handbook of Alien Species in Europe. Springer-Verlag, 63-79.
- Roques A, Kenis M, Lees D, **Lopez-Vaamonde C**, Rabitsch W, Rasplus Jy, Roy D. 2010. Alien terrestrial arthropods of Europe. *BioRisk Volumes I & II*. 1028 pp.
- Vilà, M., C. Basnou, P; Pys̃Ek, M. Josefsson, P; Genovesi, S. Gollasch, W. Nentwig, S. Olenin, A. Roques, D. Roy, P. Hulme, And Daisie Partners Including Augustin S., **Lopez-Vaamonde C.** & Yart A., (2009) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* 8 (3): 135-144.

Molecular Systematics and DNA barcoding

An accurate taxonomic identification and delimitation of species is crucial for an early detection of alien species. Indeed, alien insect species often arrive as immature stages and are difficult to identify using morphology. At URZF we use an integrative approach combining detailed morphological studies with DNA barcoding (De Prins et al 2009, Langmaid et al 2011).

We are currently developing DNA barcoding libraries for rapid and accurate identification of insect groups that have a high number of invasive species such as the family of leaf-mining moths Gracillariidae. I am also interested in the potential of DNA barcoding to estimate species diversity in relatively unknown tropical faunas and looking at the structure and complexity of host-parasitoid food webs. See below an outline of my latest work on this area of research:

DNA barcoding and Phylogenomics of Gracillariidae leaf-mining moths

Moths in the family Gracillariidae constitute one of the primary groups of plant-mining microlepidoptera. While the majority of species are leaf miners, the family shows a diversity of other life-history strategies, such as fruit mining, stem mining, leaf rolling, boring, and galling. Many species are highly invasive and serious pests of agricultural and ornamental plants. Gracillariids include 1855 described species of which 256 have been recorded in Europe. We have obtained barcodes for more than 2000 specimens for 219 species representing 85.5% of the European fauna. Preliminary results show that barcoding is capable of unambiguously discriminating ~97% of the species investigated so far, including some of closely related species notoriously difficult to identify. Our comprehensive DNA

barcode library for Gracillariidae leaf-mining micromoths will make identification more straightforward in particular larvae and light trapped specimens for which no host plant data is known. This work is being done in collaboration with 16 lepidopterists from 10 different European countries. This research highlights the importance of international cooperation among European entomologists to complete the barcoding of all the Lepidoptera of Europe. A paper is currently under preparation.

In collaboration with Jurate & Willy De Prins (Museum of Central Africa, Belgique) we are also developing a DNA barcoding library for Afrotropical Gracillariidae (De Prins et al 2009). In March 2012, I will be participating in a course on tropical Biology on the National park of La Lopé (Gabon) to teach Master students about fieldwork in the tropics. I will be showing them how to collect, rear and prepare micromoths for further morphological and molecular studies as described in a recent paper Lopez Vaamondet et al (2012).

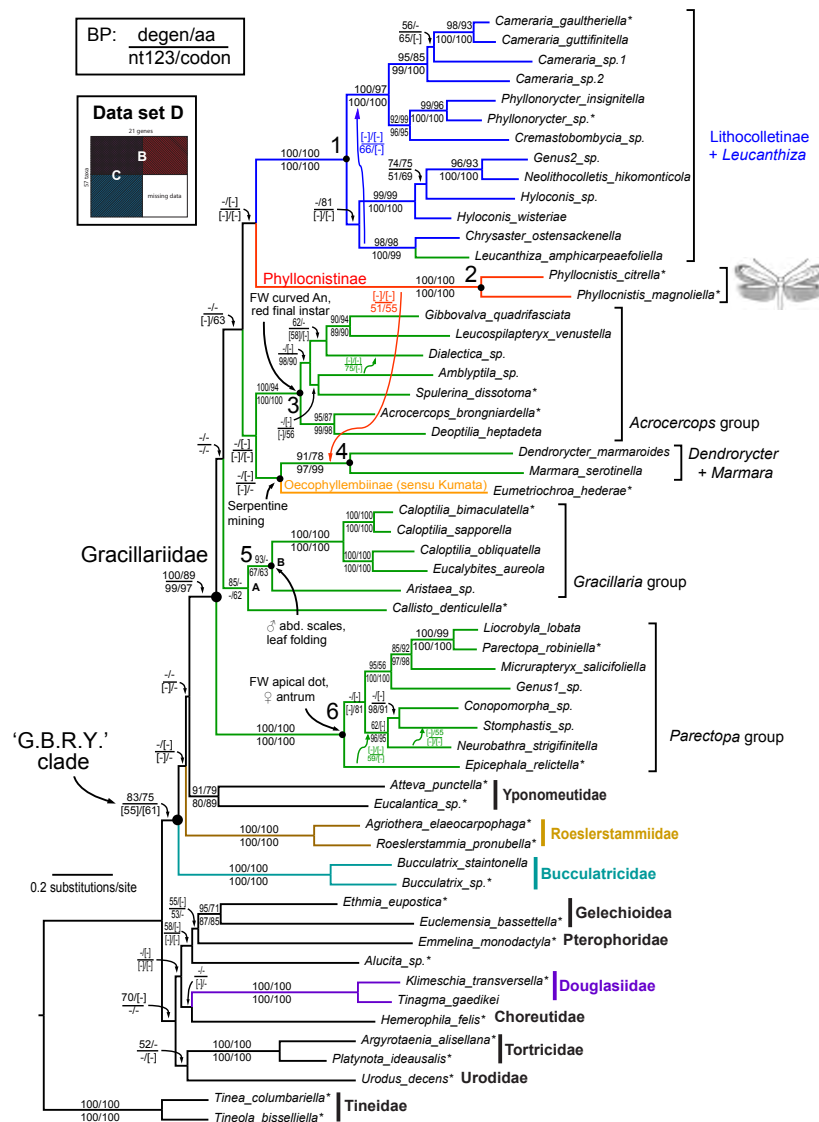


Figure 15: Phylogeny of Gracillarioidea (after Kawahara et al. 2011). Gracillarioidea, as defined by Davis and Robinson (1998), clearly do not include Douglasiidae and changes to the current classification have been done accordingly (see Nieukerken et al 2011).

Building up on my PhD work on Gracillariidae phylogenetics (Lopez Vaamonde et al 2003b, 2006) we have now reconstructed a molecular phylogeny for the superfamily Gracillarioidea using up to 21 genes (Figure 15).

In this study we show that by partially increasing the number of genes the level of resolution and statistical support of deep nodes increases. On the other hand an increase in the number of taxa included in the analysis without an increase in number of genes causes a decrease in level of support (Kawahara et al 2011). A comparison of 21 genes reveals the superiority of CAD to others in recovering deep relationships in Gracillarioidea. We predict that CAD would be a better choice for reconstructing both shallow and deep nodes in Insecta than many other genes currently available. In addition, we show that Gracillariidae is monophyletic and Bucculatricidae is difficult to place when both non-synonymous and synonymous characters are analyzed together. We tentatively conclude that the Bucculatricidae is closely related to Gracillariidae+ Roeslerstammidae + Yponomeutidae.

While we were able to get some relationships resolved within Gracillariidae, relationships among the deepest part of the tree still remain tentative, even after sequencing 14811 bp. In collaboration with Prof. Akihiro Kawahara (Florida University) and Prof. Issei Ohshima and Prof. Atsushi Kawakita (University of Kyoto, Japan) we are now sequencing the transcriptomes of several Gracillariids (*Cameraria ohridella* included) using next generation sequencing (Illumina HiSeq 2500) that we hope will help to resolve the deepest nodes of the Gracillariidae phylogeny, which will be to look at the evolution of host use and other interesting ecological traits.

Publications:

De Prins, J. R. Mozuraitis, C. Lopez-Vaamonde & R. Rougerie 2009. Sex attractant, distribution and DNA barcodes for the Afrotropical leaf-mining moth Phyllonorycter melanosparta (Lepidoptera: Gracillariidae). Zootaxa, 2281 : 53-67.

Kawahara, A., I. Ohshima, A. Kawakita, J. C. Regier, C. Mitter, M. P. Cummings, D. R. Davis, D. L. Wagner, J. De Prins, and C. Lopez-Vaamonde (2011). Increased gene sampling provides stronger support for higher-level groups within gracillariid leaf mining moths and relatives (Lepidoptera: Gracillariidae). BMC Evolutionary Biology, 11: 182

Langmaid, J. R., K. Sattler & C. Lopez-Vaamonde (2011) Morphology and DNA barcodes show that Calybites hauderi (Rebel, 1906) (Lepidoptera: Gracillariidae) does not occur in the British Isles. Nota Lepidopterologica, 33 (2): 191-197

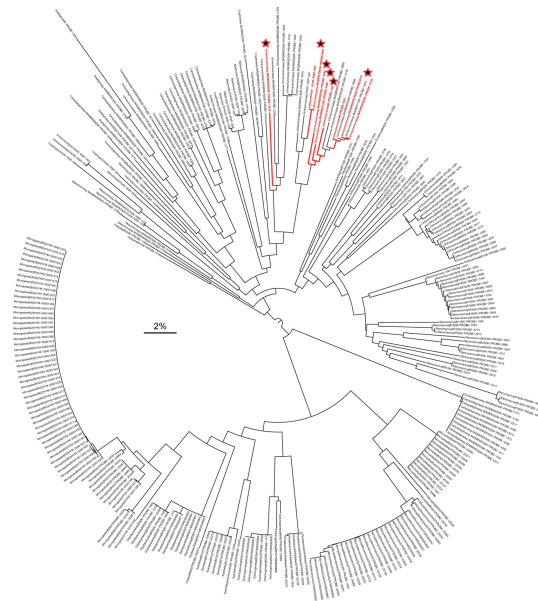
Food-webs and DNA barcoding of gut-contents of parasitoids

Although the use of molecular approaches to document food-webs is developing quickly, it has not yet provided significant benefits to some very ecologically and economically important groups of organisms such as parasitoid wasps. These megadiverse insects have a complex biology, and their concealed larval stages, within the body of their host, have considerably limited the documentation of their life-histories, only accessible through field observations, rearing or dissections

In a recent study, we addressed the question of the persistence – in the gut-contents of the adult parasitoid wasp – of DNA from tissues ingested by the wasp's larva before its metamorphosis. In other words, when collecting an adult parasitoid wasp whose host is completely unknown, can we identify what this host was by analyzing the wasp's guts?

In a recent study, we developed a new molecular protocol and demonstrated that the DNA of the host used by a parasitoid wasp during its larval development can be detected when sequencing genomic DNA extracts made from abdominal contents of the adult wasp (Rougerie et al 2010). Indeed, using parasitoid wasps (ie. *Pediobius saulius*) reared from known hosts (ie. Gracillariidae micromoths) and targeting a portion of the mitochondrial genome used as a standard animal DNA barcode, we show that through the strategic selection of exclusionary primers, host-DNA can be selectively amplified and sequenced from wasp abdomens (Figure 16). This represents a completely new method to associate parasitoids and their hosts

Figure 16: Only 9 (highlighted terminals) out of 297 samples of parasitoid wasps were successfully amplified and sequenced using primer MLepR1 associated to a universal forward primer. The Neighbour-Joining (NJ) tree was built with the 297 DNA barcodes generated from leg-derived DNA extracts amplified with universal insect primers (after Rougerie et al 2010)



Considering the global diversity, and economic importance, of parasitoid wasps, and of their hosts, we in fact know very little about the relationships between them. Our findings provide a way to document these relationships at a much faster pace, more comprehensively and with higher accuracy. We expect this will result in the generation of a large amount of new data with immediate impact in all fields of biology where host-parasitoid relationships are studied, in particular in ecology and in evolutionary biology.

Finally, our discovery that DNA from ingested tissues persists in adult parasitoids' guts through metamorphosis has led us to try to expand the study to other groups such as Diptera and Lepidoptera. Indeed, we have just received funding from the department EFPA at INRA for a "projet innovant" in which we will use the abdomens of adult Lepidoptera to amplify the DNA of the host plant on which the larval stages have fed. This study is being done in collaboration with Rodolphe Rougerie (University Rouen).

Publication:

Rougerie, R., M. A. Smith, J. Fernandez Triana, C. Lopez-Vaamonde, S. Ratnasingham, P. D.N. Hebert (2010). Molecular Analysis of Parasitoid Linkages (MAPL): gut-contents of adult parasitoid wasps reveal larval host. *Molecular Ecology*, 20: 179-186

Rapid biodiversity assessments using DNA barcoding

DNA barcoding is a powerful new taxonomic tool that promises to speed up the identification of known species and the discovery of new ones. As a technically fast and

high-throughput method, it also offers a new robust and objective way to explore and document species richness at an unequalled pace. Barcodes can characterize operational units and be used as proxy for species in groups with no available taxonomy. As such, they offer a unique way toward documenting these unknowns of the biodiversity of our planet.

We twice visited Nouragues inselberg nature reserve (<http://www.nouragues.cnrs.fr/>), French Guiana, in two different seasons (January/February and September, 2010), attempting to barcode representatives of all light-attracted moths. We focused on focusing on Gracillariidae and have recently described a protocol for sampling micromoths for morphological and barcoding analysis in rapid biodiversity surveys (Lopez Vaamonde et al 2012).

For all trips, 5644 specimens have already been collected and identified to the extent of available expertise and processed systematically for DNA barcoding. The MSc student, Olivier Bouteleux (co-supervisor Rodolphe Rougerie), is currently doing his project in our lab analysing this large barcode data set of Lepidoptera from Nouragues. Olivier is using a barcode clustering system (Barcode index number system, BINS) tallying well with morphologically reliably identified control groups, to provide uniquely numbered units for faunal analysis. He is also using rarefaction techniques to infer estimates of species richness based on the exhaustive census of all species (known and unknown) collected in the field.

Publication:

Lopez-Vaamonde, C., F. C. Breman, D.C Lees, J.Van Houdt & J. De Prins (2012). Analysis of tissue dependent DN A yield for optimal sampling of micro-moths in large-scale biodiversity surveys. European Journal of Entomology, 109: 1-6

Interactions between leaf-mining moths and endosymbionts

Leafminers are excellent examples of how insects can manipulate the plant physiology to their own advantages. For example, some species are able to keep the mined area green leading to a phenomenon called “green island”, photosynthetically active patches of the leaf around a mine that remain green even after the rest of the leaf has turned yellow/brown (Figure 17). This remarkable process by which these moths can delay plant aging is still poorly understood, but it has been shown that in *Phyllonorycter blancardella* (Gracillariidae), the *Wolbachia* bacterial endosymbiont appears to play an important role in the formation of the « green island » phenotype.

In a project funded by the Region centre and lead by Dr David Giron at IRBI, Tours we are currently looking at the specific role played by endosymbiotic *Wolbachia* of the leafminers in host plant manipulation both at the nutritional and the defensive levels. In particular the MSc student Florence Gutzwiller, has evaluated how widespread the *Wolbachia* /leafminer/ green island relation is by screening the presence of green islands and *Wolbachia* in 162 microlepidoptera including 142 leaf-mining Gracillariidae micromoth. Significant correlation was found between the evolution of both characters, so *Wolbachia* is likely to have played an important role in the evolution of green island phenotype, not only in *P. blancardella* but in leaf-mining moths in general and Gracillariidae micromoths in particular. However, according to the high reliability of our PCR assay, some individuals are able to make green islands without being infected by *Wolbachia*, which means that other mechanisms have to be considered. This study opens new perspectives for the understanding of the mechanisms underlying host plant manipulation by endophagous insects and the *Wolbachia*/leafminer

interactions. A manuscript is currently under preparation.



Figure 17: The apple leaf miner *Phyllonorycter blancardella* relies on bacterial endosymbionts, most likely *Wolbachia*, to manipulate the physiology of its host plant resulting in the 'green-island' phenotype (right). Curing leaf-miners of their symbiotic partner with antibiotics resulted in the absence of green-island formation on leaves (left), increased compensatory larval feeding and higher insect mortality (after Kaiser et al, 2010).

Conservation Biology

The conservation of biodiversity is a priority that has led to the elaboration of multiple Red Lists in an effort to document the status of endangered species. Invertebrates are badly underrepresented in the last version of the Red list of the World Conservation Union not because of lower threat levels but for lack of information on their ecology and genetics. This lack of data currently represents a major obstacle to conservation of many invertebrate species.

We focus on *Graellsia isabellae* (Graëlls, 1849) a moth (Saturniidae) distributed mainly in Spain, with a few small populations in France and Switzerland. Five subspecies have been described based on morphology. It lives in conifer forests of Eastern and central Spain and in French and Swiss Alps between 100 and 1800 m (Figure 18).



Figure 18: This large moth is one of the most emblematic European insects. Due to its size, attractive wing patterns and restricted geographical distribution it has become a symbol for several entomological and conservation organizations. The larva feeds mainly on *Pinus sylvestris* but can also be found on *P. nigra laricio* in southern Spain (Sierra Cazorla). (Photo credits: larva: Carlos Lopez Vaamonde, adult moth: Josep Ylla)

G. isabellae is protected by the Habitats Directive (the European Community initiative for an ecological network of special protected areas, known as "Natura 2000"), Bern Convention, Red Book of Lepidoptera, and other national catalogues. Despite this protective legislation, the latest Red list of the IUCN considered *G. isabellae* as "insufficiently documented" (IUCN 2006). Indeed, there is updated data on *G. isabellae*'s current distribution, and no data at all on genetics, all of which are indispensable to determine the precise level of threat on this species.

However, there is neither genetic nor population data which would allow to set up a suitable conservation plan for this species. We have recently developed a non lethal sampling method to extract and PCR amplify DNA from the hind wing tails of adults of *Graellsia isabellae* (Vila et al 2009). We have also identified its sexual pheromone (Millar et al 2010) (Figure 19), which we use in field surveys to update the distribution range of this species. We have also developed polymorphic microsatellite markers (Vila et al 2010).

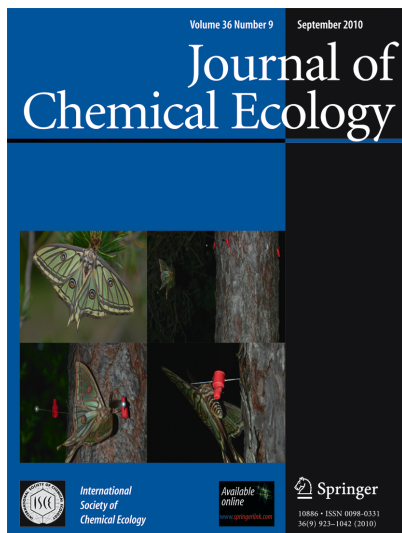


Fig. 19: the pheromone of *G. isabellae* proved to be a triunsaturated aldehyde, (4E,6E,11Z)-hexadecatrienal. The paper made the front cover of Chemical Ecology showing how males are highly attracted to the synthetic pheromone lures nailed to trunks.

The Ph.D. student Neus Mari Mena (co-supervised with Prof. Marta Vila from University A Coruna, Spain) has used all those newly generated methods/molecular markers to sample and obtained DNA sequence data for over 878 individuals from 32 populations across the whole distribution range of the species. The aims of Neus' thesis are: (i) to define Evolutionary Significant Units by studying intraspecific genetic variability, population genetic structure and divergence, (ii) to assess the validity of the five different described subspecies, (iii) to trace the origin of the controversial French subspecies *galliaegloria*, (iv) to measure the level of genetic diversity of the recently introduced Swiss population, (v) to study the phylogeography and postglacial history of the species, and (vi) to estimate demographic parameters such as effective population size and gene flow between populations.

This genetic survey of Iberian, French and Swiss populations of *Graellsia isabellae* will allow us to identify which units should be focus of a higher degree of protection, as from their genetic diversity and divergence. Neus is currently analysing the genetic data and

writing up her thesis. A manuscript on the phylogeography of the species is about to be submitted.

With the help of the new synthetic sexual pheromone new populations have been discovered well beyond the previously known limits of its range. This « newly » discovered populations raise the question of whether the species is expanding its distribution range or those are isolated populations that had been overlooked. This Spring in collaboration with the French Lepidoptera conservation group "Proserpine" and Master student Thibault Andrieux, we will use the synthetic sex pheromone to test the potential presence of the species in an area of the « Alpes de Haute Provence". Historical data of the occurrence of the species for this alpine area has been collected over the last ten years by members of "Proserpine". The project will involve setting up pheromone traps to document the presence or absence of the species along several transects in areas where the species could potentially occur. This work will be a good example of how the use of pheromones can be a practical and efficient method of detecting and monitoring the temporal population dynamics of protected species.

Publications:

Millar, J.G. J.S. Mcelfresh, C. Romero, M. Vila, N. Mari Mena & **C. Lopez-Vaamonde** (2010). Identification of the Sex Pheromone of a Protected Species, the Spanish Moon Moth *Graellsia isabellae* (Lepidoptera: Saturniidae). *Journal of Chemical Ecology*, 36 : 923-932

Vila, M., Auger-Rozenberg, M.A., Goussard, F., **Lopez-Vaamonde, C.** (2009). Effect of non-lethal sampling on life history traits of the protected moth *Graellsia isabellae* (Lepidoptera: Saturniidae). *Ecological Entomology*, 34 : 356-362.

Vila, M., Mari Mena, N., Yen, S-H. & **Lopez-Vaamonde, C.** (2010). Characterization of ten polymorphic microsatellite markers for the protected Spanish Moon Moth *Graellsia isabellae* (Lepidoptera: Saturniidae). *Conservation Genetics*, 11 (3): 1151-1154.

People

Biocontrol - CABI period

Working with Marc Kenis, I discovered biocontrol and the biology and natural history of parasitoids. I had a wonderful time looking for parasitoids in the Alps!

Silwood Times

Being at Silwood as a student is a great experience, with its seminar series every Thursday given by some of the best ecologists and evolutionary biologists in the world. As a PhD student in Cook's lab I enjoyed teaching molecular techniques to a long series of Master students that came to do their projects. I also enjoyed giving tutorials and teaching to the Master students at the Natural History Museum in London.

Institute of Zoology

After my doctoral studies, I had the opportunity to spend three years in Andrew Bourke's lab at the Institute of Zoology, Zoological Society of London as a postdoctoral research associate. Working at IoZ was a great experience and particularly enjoyed working with my technician Will Koning who after this job went on to do a PhD at UCL.

INRA times

These six years working at URZF have been really interesting. After three years working in CT rooms under red light watching bumblebees, I was more than happy to go back to the Alps and Spanish Sierras with Francis Goussard, Neus Mari Mena and Marta Vila to study the magnificent *Graellsia isabellae*. I have particularly enjoyed continuing my phylogenetic work on leaf-mining moths in collaboration with Akito Kawahara and studying the invasion biology of *Cameraria ohridella* with Sylvie Augustin, Romain Valade, David Lees, and Antonio Hernandez.

References

En bleu : étudiants/scientifiques, techniciens encadrés ou co-encadrés directement.

- Augustin S., Kenis M., **Valade R.**, Gilbert M., Garcia J., Roques A., **Lopez-Vaamonde C.**, 2010. A Stowaway species arriving from the Balkans, the horse chestnut leafminer, *Cameraria ohridella*. pp. 160-161 In : Settele, J. et al. (eds.) : Atlas of Biodiversity Risks. Pensoft publishers, Sofia, Bulgaria.
- Beekman M, Oldroyd BP (2008) When workers disunite: intraspecific parasitism by eusocial bees. *Annu Rev Entomol* 53:19-37
- Birmingham AL, Hoover SE, Winston ML, Ydenberg RC (2004) Drifting bumble bee (Hymenoptera: Apidae) workers in commercial greenhouses may be social parasites. *Can J Zool* 82:1843-1853
- Bourke, A.F.G. 2005. Genetics, relatedness and social behaviour in insect societies. In M. D.E. Fellowes, G.J. Holloway and J. Rolff, eds. *Insect Evolutionary Ecology*, pp. 1-30. CABI Publishing Wallingford.
- Bourke, A.F.G. 2011. Principles of Social Evolution. Oxford Series in Ecology and Evolution. 267 pp.
- Chapman NC, Beekman M, Oldroyd BP (2010a) Worker reproductive parasitism and drift in the western honeybee *Apis mellifera*. *Behav Ecol Sociobiol* 64:419-427
- Clutton-Brock, T. & Sheldon, B. 2010. The seven ages of *Pan*. *Science*, 327 : 1207-1208
- Cruaud, A., Jabbour-Zahab, R., Genson, G., Couloux, A., Yan-Qiong, P., Da Rong, Y., et al. (2011). Out of Australia and back again: the world-wide historical biogeography of non-pollinating fig wasps (Hymenoptera: Sycophaginae). *J. Biogeogr.* 38, 209–225
- Cook J. M. & **C. Lopez-Vaamonde**, 2001a. Fig Biology: Turning over new leaves. *Trends in Ecology & Evolution*, 16 (1): 11-13.
- Cook J. M. & **C. Lopez-Vaamonde**, 2001b. Figs and fig wasps: evolution in a microcosm. *Biologist* 48 (3): 105-110.
- Cook J. M. & Rasplus J-Y., 2003. Mutualists with attitude: coevolving fig wasps and figs. *Trends in Ecology & Evolution*, 18 (5): 241-248.
- Cruaud, A., Jabbour-Zahab, R., Genson, G., Cruaud, C., Couloux, A., Kjellberg, F., van Noort, S. & Rasplus, J.-Y. (2010) Laying the foundations for a new classification of Agaonidae (Hymenoptera: Chalcidoidea), a multilocus phylogenetic approach. *Cladistics*, 26, 359–387.
- Davis DR, Robinson GS: The Tineoidea and Gracillarioidea. In *Lepidoptera, moths and butterflies 1: Evolution, Systematics and Biogeography.. 35 edition*. Edited by: Kristensen NP. Berlin, New York: De Gruyter; 1998:91-117, 4. Arthropoda: Insecta, Part.
- De Prins, J. R. Mozuraitis, **C. Lopez-Vaamonde** & R. Rougerie 2009. Sex attractant, distribution and DNA barcodes for the Afrotropical leaf-mining moth *Phyllonorycter melanosparta* (Lepidoptera: Gracillariidae). *Zootaxa*, 2281 : 53-67.
- Dijkstra, M.B. & Boomsma, J.J. 2007. The economy of worker reproduction in *Acromyrmex* leafcutter ants. *Animal Behaviour*, 74, 519-529.
- Dixon, D. J. 2003. A taxonomic revision of the Australian *Ficus* species in the section *Malvanthera* (*Ficus* subg. *Urostigma*: Moraceae). *Telopea* 10 (1): 125-153.
- Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18: 586–608.
- Estévez Rodríguez, R.; **López Vaamonde, C.** & Pino Perez J. J. 1989. Descubrimiento de *Parnassius apollo* (Linne) en Galicia. *Boletín Auriense.*, (1988-1989): 379-381.
- Godfray, H.J.C. 1994. *Parasitoids: Behavioural and Evolutionary Ecology*. Princeton University Press, Princeton, New Jersey.

- Gómez-Zurita, J., Hunt, T., Kopliku, F., Vogler, A., 2007. Recalibrated tree of leaf beetles (Chrysomelidae) indicates independent diversification of angiosperms and their insect herbivores. *PLoS ONE* 2: e360
- Haine, E.R., Martin, J., Cook, J.M., 2006. Deep mtDNA divergences indicate cryptic species in a fig-pollinating wasp. *BMC Evol. Biol.* 6, 83.
- Hamilton WD (1964) The genetical evolution of social behaviour, I, II. *J Theor Biol* 7: 1–52.
- Hammond, R. & Keller, L. 2004. Conflict over male parentage in social insects. *PLOS Biology* 2(9): e248.
- Hernandez-Lopez A., Rougerie R., Augustin S., Lees D., Tomov R., Kenis M., Cota E., Kullaj E., Hansson C., Grabenweger G., Roques A., Lopez-Vaamonde C. (2011). Host tracking or cryptic adaptation? Phylogeography of *Pediobius saulius* (Hymenoptera, Eulophidae), a parasitoid of the highly invasive horse-chestnut leafminer. *Evolutionary Applications* doi: 10.1111/j.1752-4571.2011.00220.x
- Herre EA, Jander C, Machado CA (2008) Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. *Annual Review of Ecology, Evolution and Systematics*, 39, 439–458.
- Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., St. John, O., Wild, R., Hammond, P.M., Ahrens, D., Balke, M., Caterino, M.S., Gómez-Zurita, J., Ribera, I., Barraclough, T.G., Bocakova, M., Bocak, L., Vogler, A.P., 2007. A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science* 318, 1913-1916.
- Jousselin E, Van Noort S, Rasplus JY, Greeff JM 2006. Patterns of diversification of Afrotropical Otiteselline fig wasps: phylogenetic study reveals a double radiation across host figs and conservatism of host association. *Journal of Evolutionary Biology*, 19, 253–266.
- Kaiser, E. Huguet, J. Casas, C. Commin and D. Giron. 2010. Plant green-island phenotype induced by leaf-miners is mediated by bacterial symbiont. *Proceedings of the Royal Society*, 277: 2311-2319.
- Kawahara, A., I. Ohshima, A. Kawakita, J. C. Regier, C. Mitter, M. P. Cummings, D. R. Davis, D. L. Wagner, J. D. e Prins, and C. Lopez-Vaamonde (2011). Increased gene sampling provides stronger support for higher-level groups within gracillariid leaf mining moths and relatives (Lepidoptera: Gracillariidae). *BMC Evolutionary Biology*, 11: 182
- Kenis, M. and C. Lopez-Vaamonde 1997. Classical biological control of the gypsy moth, *Lymantria dispar* (L.) in North America: prospects and new strategies. In McManus, M. (Ed.) *Proceedings: IUFRO Conference on Population Dynamics and Integrated Management of Forest Defoliating Insects in Banska Stiavnica, Slovak Republic*, 1-9.
- Kenis, M., M.-A. Auger-Rozenberg, A. Roques, L. Timms, C. Péré, M.J.W. Cock, J. Settele, S. Augustin & C. Lopez-Vaamonde (2009). Ecological effects of invasive alien insects. *Biological Invasions*, 11: 21-45.
- Kerdelhué, C., Hochberg, M., Rasplus, J.Y., 1997. Active pollination of *Ficus sur* by two sympatric fig wasp species in West Africa. *Biotropica* 29, 69-75.
- Kobmoo, N., Hossaert-Mckey, M., Rasplus, J-Y., and Kellberg, F. 2011. *Ficus racemosa* is pollinated by a single population of a single agaonid wasp species in continental South-East Asia. *Molecular Ecology*, 19: 2700-2712.
- Langmaid, J. R., K. Sattler & C. Lopez-Vaamonde (2011) Morphology and DNA barcodes show that *Calybites hauderi* (Rebel, 1906) (Lepidoptera: Gracillariidae) does not occur in the British Isles. *Nota Lepidopterologica*, 33 (2): 191-197
- Lees D.C., Lopez-Vaamonde C., Augustin S., 2011a. Taxon page for *Cameraria ohridella* Deschka & Dimic 1986. In: EOLspecies, <http://eolspecies.lifedesks.org/pages/8675>.
- Lees D.C., Lack, H. W., Rougerie R., Hernandez-Lopez A., Raus, T., Avtzis, N.D., Augustin S. and Lopez-Vaamonde C. (2011b) Tracking origins of invasive herbivores using herbaria and archival DNA: the case of the horse-chestnut leafminer. *Frontiers in Ecology and the Environment*, 9 (6): 322-328.
- Lefebvre D, Pierre J (2007) Demographic consequences of drift in contiguous hives of *Bombus terrestris*. *J Econ Entomol* 100:1756-1763
- Lopez-Vaamonde, C., G. Weiblen, J. Y. Rasplus et J. M. Cook. 2001. Molecular phylogenies of fig wasps: Partial co-cladogenesis of pollinators and parasites. *Molecular Phylogenetics and Evolution*, 21: 55-71.

- Lopez Vaamonde, C.** 2002. Macroevolutionary studies of two insect-host plant systems. PhD Thesis. Imperial College London, UK. 288 pp
- Lopez-Vaamonde, C.,** D. Dixon, J. M. Cook and J. Y. Rasplus 2002. Revision of the Australian species of *Pleistodontes* (Hymenoptera: Agaonidae) fig-pollinating wasps and their host plant associations. *Zoological Journal of the Linnean Society*, 136: 637-683.
- Lopez-Vaamonde, C., J. W. Koning,** W. C. Jordan and A. F. G. Bourke 2003a. No evidence that reproductive bumble bee workers reduce the production of new queens. *Animal Behaviour*, 66: 577-584.
- Lopez-Vaamonde, C.,** H. C. J. Godfray and J. M. Cook. 2003b. Evolutionary dynamics of host plant use in a genus of leaf-mining moths. *Evolution*, 57 (8): 1804-1821.
- Lopez-Vaamonde, C., J. W. Koning,** W. C. Jordan & A. F. G. Bourke 2004a. A test of information use by reproductive bumblebee workers. *Animal Behaviour*, 68: 611-618.
- Lopez-Vaamonde, C., J. W. Koning,** R.M. Brown, W. C. Jordan & A. F. G. Bourke. 2004b. Social parasitism by male-producing reproductive workers in a eusocial insect. *Nature*, 430: 557-560.
- Lopez-Vaamonde, C.** H. C. J. Godfray, S. West, C. Hansson And J. M. Cook, (2005). The evolution of host use and unusual reproductive strategies in *Achrysocharoides* parasitoid wasps. *Journal of Evolutionary Biology*, 18: 1029-1041.
- Lopez-Vaamonde, C.** N. Wikström, C. Labandeira, H. C. J. Godfray, S. J. Goodman & J. M. Cook (2006). Fossil-calibrated molecular phylogenies reveal that leaf-mining moths radiated several million years after their host plants. *Journal of Evolutionary Biology*, 19: 1314-1326.
- Lopez-Vaamonde, C.** R.M. Brown, E.R. Lucas, J.J.M. Pereboom, W. C. Jordan & A. F. G. Bourke (2007). Effect of the queen on worker reproduction and new queen production in the bumblebee *Bombus terrestris*. *Apidologie*, 38 : 171-180
- Lopez-Vaamonde, C.** N. Wikström, K. M. Kjer, J.Y. Rasplus, C. Machado, G. Weiblen & J. M. Cook (2009a) Molecular dating and biogeography of fig-pollinating wasps. *Molecular Phylogenetics and Evolution*, 52: 715-726
- Lopez-Vaamonde, C.,** N. E. Raine, J. W. Koning, R. M. Brown, J. J. M. Pereboom, T. C. Ings, O. Ramos-Rodriguez, W. C. Jordan & A. F. G. Bourke (2009b). Lifetime reproductive success and longevity of queens in an annual social insect. *Journal of Evolutionary Biology*, 22 (5): 983-996.
- Lopez-Vaamonde C.,** Augustin S., Roques A., Cota E., Kullaj E., Avtzis N., Tomov R., Naceski S., Papazova I., (2009c). Genetic Study of an Invasive Forest Insect and its Parasitoid in the Balkan Region. In: Macháčová J. & Rohsmann K., (eds.): Scientific results of the SEE-ERA.NET Pilot Joint Call. Centre for Social Innovation (ZSI), Vienna, 121-128.
- Lopez-Vaamonde C.,** Agassiz, D.V.L., Augustin, S., De Prins, J., De Prins, W., Gomboc, S., Ivinskis, P., Karsholt, O., Koutroumpas, A., Koutroumpa, F., Laštůvka, Z., Karsholt, O., Marabuto, E., Olivella, E., Przybyłowicz, L., Roques, A., Ryrholm, N., Šefrová, H., Šima, P., Sims, O., Sinev, S., Tomov, R., Zilli, A. and Lees, D.C., (2010). Lepidoptera. Chapter 11. In: Roques A et al. (Eds) Alien terrestrial arthropods of Europe. *BioRisk* 4(2): 603–668. doi: 10.3897/biorisk.4.50
- Lopez-Vaamonde, C.,** F. C. Breman, D.C Lees, J.Van Houdt & J. De Prins (2012). Analysis of tissue dependent DNA yield for optimal sampling of micro-moths in large-scale biodiversity surveys. *European Journal of Entomology*, 109: 1-6
- Machado, C.A., Robbins, N., Gilbert, M.T.P., Herre, E.A., 2005. Critical review of host specificity and its coevolutionary implications in the fig/fig-wasp mutualism. *Proc. Natl. Acad. Sci. U.S.A.* 102, 6558-6565.
- Mari Mena N., Valade R.,** Magnoux E., Augustin S., **Lopez-Vaamonde** 2008. Microsatellites for the highly invasive *Cameraria ohridella* (Lepidoptera, Gracillariidae) and their amplification in related species. *European Journal of Entomology*, 105, 945-948.
- Marussich WA, Machado CA. 2007. Host-specificity and coevolution among pollinating and nonpollinating New World fig wasps. *Molecular Ecology* 16: 1925–1946.
- McKenna, D.D., Sequeira, A.S., Marvaldi, A.E., Farrell, B.D., 2009. Temporal lags and overlap in the

- diversification of weevils and flowering plants. *Proc. Natl. Acad. Sci. USA* 106, 7083-7088
- Michaloud, G., Michaloud-Pelletier, S., Wiebes, J.T., Berg, C.C., 1985. The co-occurrence of two pollinating species of fig wasp and one species of fig. *Proc. K. Ned. Akad. Wet. C* 88, 93-119.
- Millar, J.G. J.S. Mcelfresh, C. Romero, M. Vila, **N. Mari Mena** & **C. Lopez-Vaamonde** (2010). Identification of the Sex Pheromone of a Protected Species, the Spanish Moon Moth *Graellsia isabellae* (Lepidoptera: Saturniidae). *Journal of Chemical Ecology*, 36 : 923-932
- Molbo, D., Machado, C.A., Sevenster, J.G., Herre, E.A., 2003. Cryptic species of figpollinating wasps: implications for the evolution of the fig-wasp mutualism, sex allocation, and precision of adaptation. *Proc. Natl. Acad. Sci. U.S.A.* 100, 5867-5872.
- Moe, A.M., Rossi, D.R., and Weiblen, G. 2011. Pollinator sharing in dioecious figs *Biological Journal of the Linnean Society*, 103: 546-558.
- Nanork P, Paar J, Chapman NC, Wongsiri S, Oldroyd BP (2005) Asian honeybees parasitize the future dead. *Nature* 437:829
- Nanork P, Chapman NC, Wongsiri S, Lim J, Gloag RS, Oldroyd BP (2007) Social parasitism by workers in queenless and queenright *Apis cerana* colonies. *Mol Ecol* 16:1107-1114
- Nieukerken E.J. Van, Kaila L., Kitching I.J., Kristensen N.P., Lees D.C., Minet J. et al. 2011: Order Lepidoptera Linnaeus, 1758. In Zhang Z.-Q. (ed.): *Animal biodiversity: An outline*. *Zootaxa* 3148 : 212-221.
- Nyman, T., Bokma, F. & Kopelke, J.P. (2007). Reciprocal diversification in a complex plant-herbivore-parasitoid food web. *BMC Biol.*, 5, 49.
- Price, P. W. 2002. Species interactions and the evolution of biodiversity. Pages 3-26. In O. Pellmyr and C. Herrera (eds). *Plant-animal interactions*. Blackwell Science, Oxford.
- Renoult JP, Kjellberg F, Grout C, Santoni S, Khadari B. 2009. Cyto-nuclear discordance in the phylogeny of *Ficus* section *Galoglychia* and host shifts in plant-pollinator associations. *BMC Evolutionary Biology* 9: 248.
- Roques A., Rabitsch W, Rasplus JY, **Lopez-Vaamonde C**, Nentwig W, Kenis M, 2008. Alien terrestrial invertebrates of Europe. In W. Nentwig, P. Hulme, P. Pysek, M. Vila (Eds), *Handbook of Alien Species in Europe*. Springer-Verlag, 63-79.
- Roques A, Kenis M, Lees D, **Lopez-Vaamonde C**, Rabitsch W, Rasplus Jy, Roy D. 2010. Alien terrestrial arthropods of Europe. *BioRisk Volumes I & II*. 1028 pp.
- Rougerie, R., M. A. Smith, J. Fernandez Triana, **C. Lopez-Vaamonde**, S. Ratnasingham, P. D.N. Hebert (2010). Molecular Analysis of Parasitoid Linkages (MAPL): gut-contents of adult parasitoid wasps reveal larval host. *Molecular Ecology*, 20: 179-186
- Segar, S.T., **Lopez Vaamonde, C.**, Rasplus, J-Y and Cook, J.M. submitted. The global phylogeny of the subfamily Sycoryctinae (Pteromalidae): Parasites of an obligate mutualism. *Molecular Phylogenetics and Evolution*.
- Spinoza, J.C., Infante, F., Castillo, A., Perez, J., Nieto, G., Pinson, E., Vega, F. 2009. The biology of *Phymastichus coffea* LaSalle (Hymenoptera: Eulophidae) under field conditions. *Biocontrol*, 49: 227-233.
- Stireman, J.O., Nason, J.D., Heard, S.B. & Seehawer, J.M. 2006. Cascading host-associated genetic differentiation in parasitoids of phytophagous insects. *Proceedings of the Royal Society B: Biological Sciences*, 273, 523-530.
- Su ZH, Iino H, Nakamura K, Serrato A, Oyama K. 2008. Breakdown of the one-to-one rule in Mexican fig-wasp associations inferred by molecular phylogenetic analysis. *Symbiosis* 45: 73-81.
- Takahashi J, Martin SJ, Ono M, Shimizu I (2010) Male production by non-natal workers in the bumblebee, *Bombus deuteronymus* (Hymenoptera: Apidae). *J Ethol* 28:61-66
- Thompson, J. N. 1988. Coevolution and alternative hypotheses on insect plant interactions. *Ecology* 69: 893-895.
- Tzeng, H.-Y., Tseng, L.-J., Ou, C.-H., Lu, K.-C., Lu, F.-Y. & Chou, L.-S. 2008. Confirmation of the parasitoid feeding habit in *Sycoscapter*, and their impact on pollinator abundance in *Ficus formosana*. *Symbiosis*, 45,

- Valade R., Kenis M., Hernandez-Lopez A., Augustin S., Mari Mena N., Magnoux E., Rougerie R, Lakatos F., Roques A., Lopez-Vaamonde C., 2009. Mitochondrial and microsatellite DNA markers reveal a Balkan origin for the highly invasive Horse-Chestnut leaf miner *Cameraria ohridella* (Lep. Gracillariidae). *Molecular Ecology*, 18, 3458-3470.
- Vilà, M., C. Basnou, P; Pys̃ek, M. Josefsson, P; Genovesi, S. Gollasch, W. Nentwig, S. Olenin, A. Roques, D. Roy, P. Hulme, And Daisie Partners Including Augustin S., Lopez-Vaamonde C. & Yart A., (2009) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* 8 (3): 135-144.
- Vila, M., Auger-Rozenberg, M.A., Goussard, F., Lopez-Vaamonde, C. (2009). Effect of non-lethal sampling on life history traits of the protected moth *Graellsia isabelae* (Lepidoptera: Saturniidae). *Ecological Entomology*, 34 : 356-362.
- Vila, M., Mari Mena, N., Yen, S-H. & Lopez-Vaamonde, C. (2010). Characterization of ten polymorphic microsatellite markers for the protected Spanish Moon Moth *Graellsia isabelae* (Lepidoptera: Saturniidae). *Conservation Genetics*, 11 (3): 1151-1154.
- Winkler & Mitter, 2008. The Phylogenetic Dimension of Insect-Plant Interactions: A Review of Recent Evidence. In Timon ed. *The Evolutionary biology of herbivorous insects : specialization, speciation and radiation*. University of California Press. Pp : 240-263.
- Wood, S.L., 2007. *Bark and Ambrosia Beetles of South America (Coleoptera: Scolytidae)* (Monte L. Bean Life Science Museum, Brigham Young University, Provo. 230 plates
- Zanette, L. R. S., S. M. Miller, C. Faria, C. Lopez-Vaamonde & A. F. G. Bourke (submitted). Spatial ecology of drifting bumble bee workers in field conditions. *Oecologia*

Selected Publications