EUROPEAN SCIENCE FOUNDATION

SETTING SCIENCE AGENDAS FOR EUROPE

RESEARCH NETWORKING PROGRAMME

FRONTIERS OF SPECIATION RESEARCH (FroSpects)

Standing Committee for Life, Earth and Environmental Sciences (LESC)

FROSpects

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Cover images:
Top left: *Ephemera danica*

Top right: *Phyllomyias zeledoni viridiceps*

Bottom: *Perca flavescens*

Summary

With millions of species currently existing on earth, understanding how all this magnificent variety arose is no small task. Biologists have long accepted Darwinian selection as the central explanation of gradual adaptation and long-term evolutionary change; yet, to date, no similar agreement has emerged about how genetic, geographical, ecological, evolutionary, and environmental factors interact to create two species out of one.

Classical theories of speciation emphasise geographic isolation and often relegate ecological factors to the background, whereas modern theories tend to emphasise, in addition, ecological and sexual interactions. Many other issues, concerning the roles of spatial structure, reproductive isolation, genetic drift, pleiotropic correlation, mate choice, and environmental change, also remain contested.

The aim of the Research Networking Programme Frontiers of Speciation Research (FroSpects) is to facilitate bridge-building between disparate approaches to speciation research, by bringing together young and senior European speciation scientists around a number of conferences, workshops, symposia, and schools. A major promise of the Programme is to strengthen Europe's position in speciation research through the cross-fertilisation and integration of empirical and theoretical approaches.

The running period of the ESF FroSpects Research Networking Programme is five years from May 2008 to April 2013.

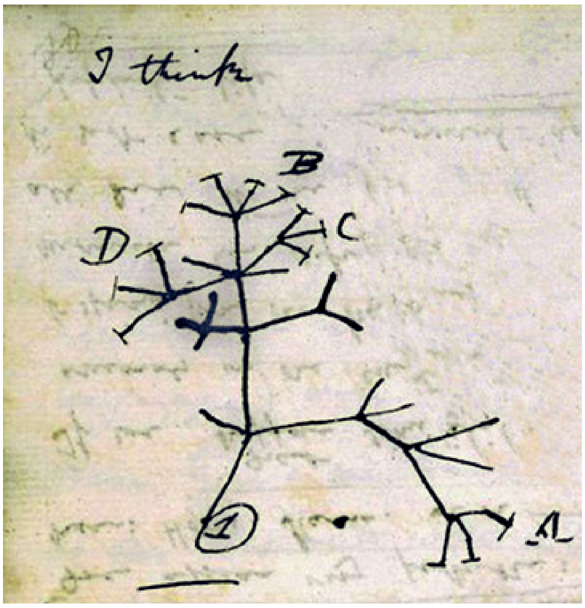
Summary of key objectives

- Facilitate bridge-building between different approaches to speciation research
- Strengthen Europe's position in speciation research
- Promote integration of speciation research into the management of biodiversity
- Foster development of a new generation of speciation scientists in Europe

Summary of major activities

- Conferences, workshops, and symposia
- Advanced training schools
- Travel grants for scientific exchange

A portrait of 31-year-old Charles Darwin.



In his notebooks, Charles Darwin sketched out the fundamentals of his theory of evolution in simple drawings.

Introduction

Frontiers of speciation research

The grand challenge in speciation research is to understand the conditions that promote alternative modes of speciation. To meet this challenge, an integrative approach will be required, combining empirical insight with theoretical advances and bringing together developments in ecology, systematics, and genetics. On this basis, methods for interpreting and classifying the early phases of speciation need to be developed and, for each of the alternative speciation modes, the importance of spatial structure, genetic architecture, reproductive isolation, mating traits, and ecological characteristics need to be elucidated.

The traditional view of speciation, proposed as part of the Modern Synthesis, rests on the assumption of geographical isolation. After a population has become subdivided by external causes – like fragmentation due to environmental change or colonisation of a new, disconnected habitat – and after the resulting sub-populations have remained separated for sufficiently long, genetic drift and pleiotropic effects of local adaptation are supposed to lead to partial reproductive incompatibility. When the two incipient species get into secondary contact, individuals from one species cannot mate with those of the other or, if mating is still possible, their hybrid offspring are inferior. Further evolution of pre-mating isolation (like assortative mate choice or seasonal isolation) and/or post-mating isolation (like gametic incompatibility) eventually ensures that the two species continue to steer separate evolutionary courses. The trigger for speciation in this process is geographical isolation. It is for this reason that the distinction between allopatric speciation (dependent upon geographical isolation) and sympatric speciation (without geographical isolation) has taken centre stage in the speciation debate. Various other notions of speciation have been suggested in the literature including competitive speciation, ecological speciation, and adaptive speciation. Assessing the relative importance of these alternative modes of speciation remains an open question of tremendous interest. This problem lies right at the heart of biodiversity science, as the various types of speciation process outlined above differ in many critical assumptions and predictions, often providing different answers to questions such as the following:

- *What timescales are expected for speciation?* Which empirically observable phases can be distinguished? What is the likelihood of finding species pairs in any of these phases?
- *What are the biogeographical premises and implications of speciation?* When is spatial segregation between newly formed species expected as cause or consequence of the speciation process? What is the evolutionary origin and significance of hybrid zones?
- *Is speciation a one-way road or is its reversal also a common evolutionary phenomenon?* What consequences does it have for genome evolution?
- *Which types of interactions are involved in speciation processes?* Are ecological interactions between conspecifics more important than sexual interactions between mating partners, or vice versa? In addition to intraspecific competition, what are the roles played by interspecific interactions like mutualism and exploitation?
- *Is prezygotic isolation preceded by postzygotic isolation, or vice versa?* What are the roles of hybridisation and reinforcement in speciation processes?
- *What are the ecological, genetic, and geographical signatures of speciation?* What information needs to be collected empirically before past process can be inferred from present pattern?
- *What is the interplay between speciation processes and environmental stressors?* Must trends in the environment be expected to help or hinder speciation?

Commitment to scientific pluralism

To reinvigorate the scientific debate, and to progress with answering the questions above in a comprehensive manner, the Research Networking Programme FroSpects will strengthen the dialogue between at least five groups of researchers: evolutionary ecologists, molecular biologists, systematists, biogeographers, population geneticists, and ecological theorists.

All too often, discussions about speciation get bogged down by tendencies to overemphasise, in the empirical domain, the need for unambiguously proving good cases of (sympatric) speciation or, in the theoretical domain, the mutual exclusiveness of alternative speciation models. The Research Networking Programme FroSpects is built, instead, on the recognition that speciation is a complex and dynamic process that needs to be understood, throughout its potentially intricate phases and alternative pathways, from start to finish. It is believed that this commitment to scientific pluralism will be a key factor in encouraging the open dialogue this Research Networking Programme is meant to bring about.

Topic Areas

Diversity of diversification

The entire range of evolutionary diversification mechanisms needs to be explored to understand the ecological, evolutionary, and environmental factors that favour, alternatively, the evolution of phenotypic plasticity in ecological traits, ecologically neutral differentiation in mating traits, the broadening of intraspecific polymorphisms by rearrangement of a population's genetic architecture, the emergence of sexual dimorphisms, and – as just one among these several options – speciation. This begs questions about the mechanisms preventing speciation in the first four processes, and whether the fifth process, successful speciation, may entail the loss of diversity.

Signatures of speciation

The generation of differential testable hypotheses is urgently needed for empirically identifying alternative speciation modes and for moving towards the quantitative and standardised assessment – based on the joint utilisation of phylogenetic, genetic, ecological, and spatial data – of the relative frequencies with which these modes occur in nature.

Species cohesion

The flipside of speciation is species cohesion. It remains to be understood how genetic, ecological, and spatial factors interact in preventing species from splitting. This question is particularly relevant for asexual species, and indeed for their definition, since traditional species concepts based on interbreeding can only be applicable to asexual species.

Speciation models for specific systems

There currently exists a gap between general speciation models and the features of specific natural systems. General models play an important role in the speciation debate by addressing the complexities of speciation dynamics that cannot be captured by verbal models. However, an intermediate approach will have to be established in the medium term, so that the specifics of individual systems can be integrated and explored with the same flexibility and thoroughness. Devising and calibrating such system-specific speciation models will only be successful if based on an open and intensive dialogue between empirical and theoretical experts.

The role of interspecific interactions

While the dominant selection pressures involved in speciation processes may often be intraspecific, many such processes will be strongly influenced by interspecific interactions. Both types of interactions may drive competitive, ecological, and adaptive speciation, and may also be responsible for the reinforcement of reproductive isolation in allopatrically-initiated speciation. Ultimately, large-scale phylogenetic and biogeographical patterns can only be understood from a perspective sufficiently informed by, and embedded in, community ecology. Models of evolving communities and food webs have recently emerged to address the community dimension of speciation patterns and processes. Starting from only fundamental assumptions on the number of different resources, and possible types of ecological interactions, these models can be used to study the conditions under which different modes of speciation can be expected. Systematic comparisons of predictions based on ecologically detailed speciation models with those obtained from the neutral theory of biodiversity and biogeography will prove particularly important in this context. In the long-term, these seemingly disparate approaches will need to be integrated into a more encompassing, overarching framework.

Speciation and bioinvasions

With the transport of alien species into new environments now being accelerated on a global scale – resulting in invading pioneers that occur in small numbers, are geographically isolated, and experience strong local selection pressures – the impacts of bioinvasions on speciation rates deserve to become better understood.

Hybridisation and adaptive radiations

Since it is not uncommon for hybridisation and adaptive radiations to occur together, their interplay needs to be better understood. Both processes are associated with, and promoted by, colonisation, but might also promote each other. Moreover, hybridisation and gene flow between radiating populations may be critical for generating and maintaining genetic variation required for selection-driven speciation.

Genetics and genomics of speciation

Reproductive isolation is, in many modes of speciation, initially concentrated around a few genes and then spreads to encompass the whole genome. The technology is now available to describe genome-wide patterns of genetic differentiation, to identify key genes, and to ask about the relative importance of different types of genetic change in the build-up of reproductive isolation. New analytical techniques will be needed to make the most of the growing amounts of data available.

Biodiversity losses through reverse speciation

Since a large fraction of the world's species diversity is of recent evolutionary origin, the ecological and evolutionary processes underlying biodiversity formation and loss deserve to be analysed within a common framework. In particular, as much as environmental heterogeneity may foster the emergence of species, anthropogenic environmental homogenisation may cause their demise.

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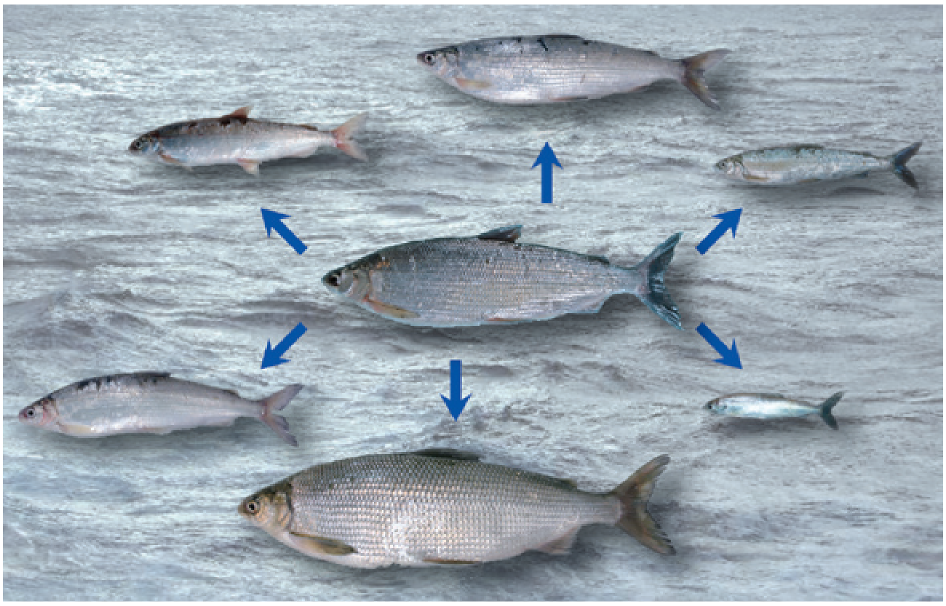


A European model system in adaptive-radiation research: the whitefish in large Swiss pre-Alpine lakes. The central phenotype is widespread in rivers and along the shallow shores of lakes. The others are derived species, many of which are endemic to one or a few lakes. All species shown, except the one at the bottom, are sympatric in Lake Thun.

Speciation in ecosystems

Currently-available empirical *and* theoretical insights will have to be extended to understand the embedding of gradual evolution and speciation into multi-species communities and food webs, thus contributing to the prediction of evolutionarily-robust patterns of ecosystem structure and functioning.

Evolutionary biogeography

Eco-genetic models of speciation dynamics are to be studied on increasingly realistic spatial landscapes, with the ultimate aim of devising the fundamentals of a new process-based approach to evolutionary biogeography, including an improved understanding of the evolutionary ecology of hybrid zones.

Macro-ecological explanations of biodiversity

The neutral theory of biodiversity and biogeography on the one hand, and speciation theories based on niche differentiation on the other, offer radically different views on how biodiversity arises and is maintained, highlighting a rift in the scientific understanding of biological diversity that needs to be reconciled.

Applied Dimensions

The Research Networking Programme FroSpects will promote research of applied interest. Several such dimensions are described below.

Biodiversity crisis and speciation

A region's biodiversity is determined by the balance between the rate of species extinction through extirpation or speciation reversal compared with the rate at which new species arise through speciation and immigration. The role of speciation in this balance is generally ignored in biodiversity conservation efforts, based on the assumption that speciation rates are always too slow to contribute substantially. However, several empirical examples of fast speciation have now been documented, challenging this assumption. As data on species ages become progressively more available, we can begin to consider the biodiversity consequences of altered rates of speciation and speciation reversal.

Understanding biodiversity hotspots

It has often been argued that it is impossible to protect all global biodiversity, and that protective measures thus ought to be concentrated on biodiversity hotspots. Such hotspots are often identified by descriptive criteria, e.g., as areas with the highest species numbers in a particular taxonomic group. However, to protect future biodiversity it will be important to characterise hotspots in terms of the processes that generate new species in a hotspot and to understand what makes a particular environment conducive to the formation of new species.

Climate change and speciation

Paleontological and molecular studies suggest that periods of speciation alternate with periods of stasis. Rapid changes in the environment, for example climate, could be at the basis of punctuations in speciation rates. Understanding the consequences of large-scale environmental changes induced by humans is important, not only in terms of increased rates of extinction, but also in terms of the risks associated with the, often remarkably rapid, evolution of new ecotypes.

Speciation in agriculture and medicine

Theory on the evolution of resistance and virulence suggests that pathogens, parasites, and pests often specialise on a particular host species, because the costs associated with the development of virulence do not allow the simultaneous evolution of virulence on different host species. Coevolutionary arms races are thus likely to affect parasite diversity. Shifts in distribution caused by climate change may expose hosts to new parasites, and vice versa. Understanding speciation in pathogens, parasites, and pests is therefore of considerable relevance for medicine and agriculture.

Tropical forest as biodiversity hotspot.

Speciation in Europe

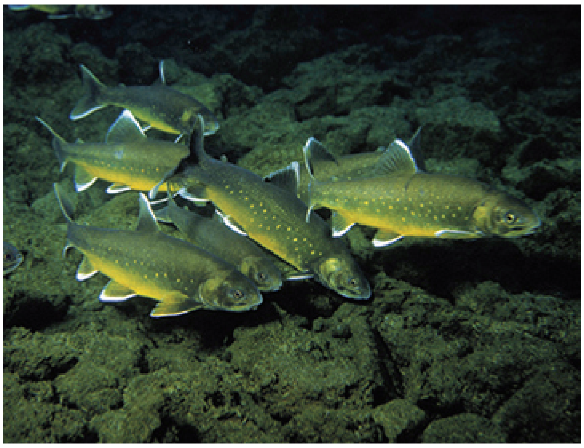
Europe hosts a fascinating variety of examples of speciation at work. The examples below demonstrate the recent achievements and excellent potential of empirical speciation research in Europe.

Speciation in plants

- The European *Populus* tree (*P. alba* or White poplar, and *P. tremula* or European aspen) is becoming established as a model for research on the genetics of species barriers. Work on this genus benefits from a near-complete genome sequence and high applied interest with regard to carbon mitigation. Instead of directly dealing with the process of speciation, European *Populus* offers a case of "porous" species boundaries resulting from secondary contact and thus allows the maintenance of species barriers to be studied.
- The salt marsh grass species *Spartina anglica (Poaceae)* is a nascent allopoly-ploid formed in England during the end of the 19th century by hybridisation between an indigenous and an invasive species. It has rapidly expanded in range, and has now invaded several continents. This species has larger ecological amplitude than its parental species and illustrates particularly well the short-term success of a new species following hybridisation and genome duplication.
- Orchids in the genus *Ophrys* attract male hymenopterans by mimicking sex pheromones and are pollinated by pseudocopulation. Coevolution between pollinaters and orchids underlies sympatric diversification in this genus, and a role for selection on floral odour in promoting differentiation has been suggested.

Speciation in fish

- Arctic charr (*Salvelinus alpinus*) often form ecomorphs in lakes. In many cases, these morphs are genetically distinct. Lake Galtaból in Iceland harbours eco-morphs for which the analysis of microsatellite variation strongly indicates complete reproductive isolation. This example has been referred to as one of three studies (of many candidates) *strongly* suggestive of sympatric speciation. In addition, some dwarf forms of Icelandic Arctic charr, living in confined cold spring habitats, may be on the road to allopatric speciation. Also two morphs of Arctic charr – one littoral, the other profundal – in the Norwegian Lake Fjellfrøsvatn have been documented to exhibit reproductive isolation in space and time, segregation of their ecological niches, genetic differentiation, as well as genetically-based differences in morphology and behaviour. Coexisting ecomorphs of Arctic charr are known also from several Swiss lakes.
- Three-spined stickleback (*Gasterosteus aculeatus*) often form morphs within lakes that show clear signs of genetic, ecological, and morphological divergence. In Iceland, such divergence has occurred at a timescale of no more than 2000 generations (about 10000 years). Stickleback is already an important model species for speciation studies in North America and has recently become a genome species, with a full genome sequence only just published (http://www.ensembl.org/Gasterosteus_aculeatus/index.html). Parallel cases of speciation in different European settings are studied by several labs.



Arctic charr in Lake Thingvallavatn, Iceland.

- Whitefish (*Coregonus* spp) are becoming one of the major vertebrate model systems for studying rapid speciation and adaptive diversification. European centres of diversification are the pre-Alpine lake system with up to 20 parallel adaptive radiations, ranging from 2 to 7 incipient species per lake, and the Fenno-Scandian lake systems from Lake Onega in the East to Norway in the West. Smaller radiations exist in other parts of Europe, like the United Kingdom, northern Germany, and Poland. Using this system across the European distribution of the genus *Coregonus* thus offers unique opportunities for developing a comparative adaptive radiation research programme.
- The trout, *Salmo trutta*, is a species complex covering all Europe. Five main geographic lineages have been described and all are interfertile, with interbreeding occurring through natural secondary contacts or human translocations. In total eight deeply differentiated forms of trout have been identified, creating examples at the frontier between species and differentiated populations.
- Recently, it has been established that the species of bullheads (*Cottus gobio*) in fact constitutes a species complex, with derived species of recent hybrid origin in the lower reaches of the River Rhine.
- Genesis and maintenance of the species complex of Iberian minnows, *Squalius alburnoides*, involves polyploidy, hybridisation, and variation in mating systems. While *S. alburnoides* populations are mainly composed of triploid and diploid hybrid forms, two symmetric

allotetraploid populations were found to resume normal meiosis after undergoing intermediate processes of non-sexual reproduction. The resultant new sexually reproducing polyploid species in the Iberian Douro river illustrate how hybrid polyploid complexes may lead to speciation.

Speciation in birds

- Recent analyses of natural hybridisation between pied flycatchers (*Ficedula hypoleuca*) and collared flycatchers (*F. albicollis*) have shown that both phenotypically plastic sexual signals (e.g., song) and genetically determined sexual signals (e.g., plumage) cause reproductive isolation between the two species.
- The crossbill (*Loxia curvirostra*) in North America features cryptic species feeding on different species of conifers, recognisable by vocalisations and bill morphology. In Europe, assortative mating between different vocal types has been found, and also morphological differentiation between vocal types has been documented.
- The nightingale (*Luscinia megarhynchos*) and the thrush nightingale (*Luscinia luscinia*) are morphologically and ecologically very similar species that hybridise in a narrow region of sympatry. According to Haldane's rule, hybrid females are sterile, while hybrid males are fertile. Preliminary results show that the Z chromosome contributes disproportionately to reproductive isolation, highlighting similarities in the genetic basis of reproductive isolation in organisms with heterogametic males and females.

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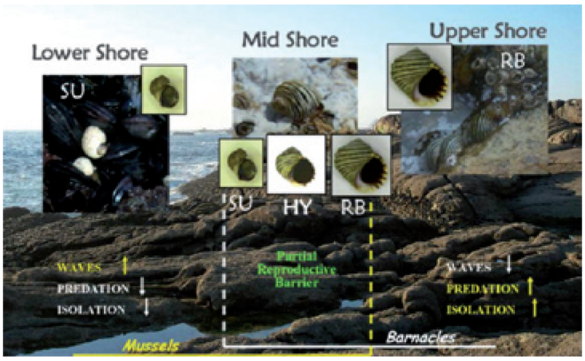
Nightingale near village Wielowies, Poland.



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Periwinkle ecotypes along rocky marine shores in Spain.

Speciation in snails

- Morphologically distinct forms of the periwinkle (*Littorina saxatilis*) have evolved independently on steep environmental gradients on the coasts of Spain, Sweden and England, and even in geographically-distant localities from Spain. These populations show varying degrees of reproductive isolation through local adaptation, habitat choice, assortative mating, and genetic incompatibility. These ecotypes show differences in morphometric, biochemical, behavioural, ecological and genetic traits being a consequence of their adaptation to distinct micro-habitats.
- Morphologically and genetically distinct forms of the speciose door-snail *Albinaria* show varying degrees of (mostly pre-mating) reproductive isolation. A weak association with genetic divergence and environmental conditions may indicate non-adaptive radiation and a profound role for sexual selection as a driver of differentiation.

Speciation in insects

- Damselflies of the genus *Calopteryx* have diverged in their degree of melanistic wing colouration, a trait subject to both natural and sexual selection that also contributes to sexual isolation between species. While previous work on this genus has focused on North American species, recent years have witnessed increased contributions by European research groups. In parti-cular, sexual isolation between parapatric populations of *C. splendens* has recently been demonstrated.
- A European example of host race formation in phytophagous insects is that of *Ostrinia nubilalis*, the European corn borer. This species is a pest of corn in both North America and Europe. However, in Europe there exists a genetically distinct population on *Artemisia vulgaris*, with mating preference for its own kind, likely representing a recent host shift
- Grasshoppers in the genus *Chorthippus* provided a classical example of the role of mating-signal diver-

gence in reproductive isolation and were the subject of one of the first phylogeographic analyses of post-glacial colonisation involving parapatric speciation. Investigations of a hybrid zone in the Pyrenees have shown that selection following secondary contact can break down gene combinations responsible for hybrid male sterility and have yielded much information about the morphometric, biochemical, behavioural, ecological, chromosomal, genetic, and molecular genetic aspects of the underlying evolutionary processes.

Speciation in other animals

- Many species of mice (*Mus* spp) are now recognised in Europe. The most recent addition stems from the recent discovery of the new species *Mus cyprianus* on Cyprus. Analyses of hybrid zone between two subspecies of house mouse, *Mus musculus musculus* and *Mus musculus domesticus*, as well as genetic crosses have shown that the X chromosome has a disproportionately large effect in speciation.
- The fire-bellied toads, *Bombina bombina* and *B. variegata*, are highly dissimilar species that hybridise in a long, but narrow, zone that stretches across the European continent. Several detailed analyses along transects show that introgression is limited by selection at multiple loci. The *Bombina* hybrid zone offers a window on some important evolutionary processes underlying speciation, and has been at the forefront of research for the last two decades.

Many more examples exist in the work of European speciation researchers on systems outside of Europe. Better understanding of the ecology and genetics of such examples of speciation will strengthen conservation biology, aid the protection of biodiversity, and contribute to the management of pathogens, parasites, and pests in the context of agriculture and medicine.

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Meadow grasshopper from the Pyrénées.

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Fire-bellied toad from Pińczów, Poland.

Activities

Conferences, Workshops, and Symposia

The programme will organise two large international conferences that will provide a broad overview of contemporary speciation research, bring together leading researchers on speciation, serve as an inroad into the field for young researchers, and enable senior researchers to make connections outside their immediate area of work. In addition to these conferences, the programme will also arrange six smaller, focused meetings devoted to the advancement of specific research fields.

During each year of the programme, one or two workshops on contemporary topics in empirical speciation research, eco-evolutionary modelling, and food web theory will be organised.

Symposia at conferences that focus on speciation research and related topics can be supported.

Schools

To promote the involvement of young scientists in the many facets of European speciation research, the programme will organise a total of four schools. Both summer and winter schools will be planned. These will form a coherent introduction to the frontiers of speciation research, with the two comprehensive modules being accessible to students within the time horizon of a single year.

Two schools on eco-evolutionary modelling will be organised. This will provide young European researchers with a firm grounding in the concepts and tools required to understand, analyse, and model processes of speciation in sexual and asexual populations.

Two schools on empirical methods of speciation research will be organised. One of the schools will provide an introduction to modern methods of molecular biology for identifying the signatures of natural selection and recent speciation from sequence data collected in the field. The other school will focus on a carefully-assembled set of case studies that offer empirical insights into natural processes of speciation.

Travel grants

To help young and senior researchers initiate collaborations by spending up to three months at leading European research institutions, the programme will issue open calls for grants covering all aspects of speciation research, with priority given to applicants and hosts from ESF member states.

Calls for travel grants, including short stays (1-2 weeks) and longer exchange visits (up to 3 months), will be issued during each of the programme's first four years.

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