École doctorale 304
Sciences et environnements (EDSE)

Thématique : Écologie évolutive, fonctionnelle et des communautés
Année universitaire 2016-2017

➢ TITRE DU SUJET DE THÈSE :

Génomique écologique de l’adaptation locale chez le pin maritime (Ecological genomics of local adaptation in maritime pine)

➢ DIRECTEUR DE THÈSE :

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➢ CODIRECTEUR DE THÈSE :

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➢ DESCRIPTION DU SUJET DE THÈSE :

Climate change has profound impacts on ecosystems and there is an increasing concern on the effects of climate change on natural and plantation forests, with 21-50% of economic value loss expected for European forests by 2071-2100 (Hanewinkel et al. 2012). The main goal of the PhD thesis would be to study the processes involved in genetic adaptation of maritime pine (*Pinus pinaster* Aiton), an iconic conifer of great ecological and economic importance, at different spatial and temporal scales, and to identify valuable genetic variation for adaptation to new environments. Frontier research across ecology, ecophysiology, quantitative and population genetics, bioinformatics, and genomics will be developed to shed light on this fundamental ecological problem, as well as to foster the maritime pine breeding program in south-western France.

Background & Objectives

A relatively new discipline, ecological genomics, is expected to provide answers to questions related to adaptation to new environments, in space and time. Ecological genomics relies on the integration of large scale genomic data with phenotypic and environmental information (Barrett & Hoekstra 2011). Most ecological genomics research so far has, however, failed to integrate these sources of information, as well as to consider the polygenic nature of adaptive traits. We are currently experiencing a shift from views centered on single genes to others that consider epistatic interactions and gene networks as the base for adaptive divergence and phenotypic innovation (Olson-Manning et al. 2012). Increased allelic covariance rather than sharp allele frequency changes may indeed underlie genetic divergence at loci underlying quantitative traits (Kremer & Le Corre 2012). Recent research in humans suggests polygenic adaptation that is reflected in small differences in allele frequencies with weak selection coefficients (e.g. ~10^{-3}-10^{-5} for human height, Turchin et al. 2011) and epistatic interactions. Evidence from QTL mapping and genetic association studies suggest that most adaptive traits are also polygenic in forest trees, highlighting the importance of soft sweeps acting on standing genetic variation (in contrast with hard sweeps driving new mutations to fixation). In recent years, analytical approaches have been developed to test for polygenic adaptation using genomic data (e.g. Berg & Coop 2014). But such examples are still scarce, and there is an urgent need for further development and application, in particular in species such as forest trees, for which adaptation to new environments is fundamental for provision of ecosystem services. In addition, recent evidence suggests that most genetic polymorphisms responding to climate could be lineage-specific, following a conditional neutrality model (e.g. Tiffin & Ross-Ibarra 2014), which claims for multi-population approaches and the exploration of geographical variation in adaptive responses. The temporal scale of genetic adaptation is also important for predicting the consequences of ongoing climate change (Hoffmann & Sgrò 2011). Annual plants are able to adapt gradually, year by year, but long-lived species such as forest trees are experiencing abrupt shifts of environmental conditions, corresponding to accumulated annual changes. Whether evolutionary rates in these species are fast enough to mitigate the effects of rapid climate change is currently unknown.

The main objective of this PhD thesis is then to investigate ***the geographical and temporal scales of genetic adaptation***, in particular whether ***rapid genetic change*** can take place in long-lived trees in response to environmental changes and with a focus on ***polygenic adaptation***.

Implementation

The PhD student will use two large common garden experiments. The first one is a collection of 512 clonally-propagated genotypes from 35 populations representing the six distinct gene pools known in maritime pine (CLONAPIN, see details in this link). This collection is planted in five sites in France, Spain and Portugal, and provides a complete picture of maritime pine genetic variation. The second common garden consists of over 900 families from 30 Corsican populations (PINCORSE, see details in this link) and complements CLONAPIN by providing a detailed sampling of a region with high environmental heterogeneity and that is of great interest for the maritime pine breeding program (as it shows higher tolerance to drought and better straightness than the local Landes provenance). Finally, natural selection (fitness) experiments will be established in Hourtin and Mimizan, Aquitaine; both sites being part of the maritime pine Network of Conservation Units and considered important reserves of local genetic variation.

The PhD student will develop the following tasks:

Task 1. Identification of genes and polymorphisms underlying ecologically-relevant adaptive traits.

The PhD student will complete the measurements of adaptive traits related to growth (including annual growth), bud phenology, and resistance to water deficit (e.g. isotope discrimination) in the two large common garden experiments, CLONAPIN and PINCORSE, described above. In close collaboration with the rest of the research team he/she will develop association studies to identify genes and polymorphisms underlying ecologically-relevant adaptive traits, using both already available molecular data (8,949 SNPs, using Illumina Infinium technology, Plomion et al. 2015) and a second-generation SNP genotyping assay focused on gene networks underlying adaptive traits (currently under construction in the framework of EU H2020 GenTree project).

Task 2. Study of polygenic adaptation to heterogeneous environmental conditions.

Allelic effects on adaptive phenotypes obtained in Task 1 will be used to apply different methods to study polygenic adaptation. A first approach is based on pairwise population comparison of allele frequencies, while controlling for genetic drift (Turchin et al. 2011). The second approach, also relying on previous computation of allelic effects, is based on the construction of a compound statistic, Q_X, which is then compared with the expected values under neutral evolution, and correlated with environmental variables (Berg & Coop 2014). By working in parallel with both CLONAPIN and PINCORSE maritime pine collections, the PhD student will obtain unprecedented complete views on polygenic adaptation under contrasted environmental conditions at different spatial scales.

Task 3. Short-term evolutionary responses in maritime pine.

To study the temporal scale of genetic adaptation and expected short-term evolutionary responses in maritime pine (i.e. contemporaneous adaptation), the PhD student will establish natural selection (fitness) experiments in contrasted environmental sites (see Vizcaíno-Palomar et al. 2014, for a similar experimental setting). The experiments will use seeds directly sown in the local environment (25 families from each of the three main maritime pine European lineages, plus 25 families from the breeding program), so that natural selection during germination and early establishment is not avoided, and they will follow a replicated experimental design (6 blocks). Saplings will be phenotyped for growth and resistance to water deficit to compute genetic selection gradients using survival as fitness proxy. They will also be sequenced and compared to control samples following a 'targeted resequencing' strategy on pooled samples to reduce costs. Natural selection (fitness) experiments will be located in maritime pine Conservation Units, which are naturally regenerated, and the main future source of genetic variation for the breeding program.

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Publications du directeur de thèse depuis 2011 (cinq dernières années) :

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➢ COLLABORATIONS SCIENTIFIQUES :

The team at the host UMR Biogeco supporting this research is highly multidisciplinary providing expertise in evolutionary genetics (Antoine Kremer, Myriam Heuertz), genomics (Christophe Plomion), ecophysiology (Annabel Porté, Sylvain Delzon), tree breeding and quantitative genetics (Annie Raffin, Laurent Bouffier), ecological modelling (Marta Benito-Garzón), and networks (Jean-Charles Leplé, Corinne Vacher). Thus, it constitutes an ideal environment for the development of a PhD thesis, fostering multiple stimulating interactions for the student. Collaboration with researchers from other UMRs will connect the research to other on-going initiatives on tree genetic adaptation (e.g. Oliver Brendel for ANR H2Oak project and Ivan Scotti for ANR FLAG project).

Main international collaborators include researchers from Italy (Giovanni G. Vendramin, IBBR, Firenze), Spain (Ricardo Alía, Juan José Robledo-Arnuncio and Delphine Grivet, INIA, Madrid), UK (Stephen Cavers, CEH, Edinburg), Canada (Sam Yeaman, University of Calgary) and the USA (Andrew Eckert, VCU, Richmond), which are developing similar projects on conifer genetic adaptation. This rich network of collaborators will facilitate the PhD student research stays abroad and his/her contact with leading international scientists. Colleagues in Spain and Italy will establish replicates of the maritime pine natural selection (fitness) experiments in their countries in the framework of GenTree EU H2020 project, providing excellent additional opportunities for the internationalization of the PhD research.

- **RELATIONS INDUSTRIELLES** :

Two types of industrial partners would be involved in the PhD project. On the one side, the research to be conducted is highly relevant for the identification of plant material adapted to new environmental conditions in South-Western France and it will closely interact with the maritime pine breeding program (developed, among others, by INRA). This has attracted the attention of the ‘Centre Régional de la Propriété Forestière d’Aquitaine’ (CRPF AQUITAINE), which stands up as the main liaison with industrial partners. On the other side, the work is also relevant for conservation of semi-natural populations of maritime pine in public lands. These forests are rich reservoirs of genetic diversity and the origin of the materials used for commercial plantations in the Landes region. Thus, they have a very important strategic interest. Moreover, the PhD student will conduct its fitness experiments within some of these forests, providing valuable information on their expected short-term evolutionary responses. This work will involve the ‘Office National des Forêts’ (ONF), both as facilitators and final destination of translational efforts.

- **FINANCEMENT** :

Funding to support the PhD thesis will come from a new European H2020 project that will start in May 2016 (*GenTree*: Optimising the management and sustainable use of forest genetic resources in Europe, 2016-2020). The student will be expected to develop (partially) the activities related to maritime pine in WP3 and WP4. Additional funding may come from a proposal for a ‘Chaire d’Installation Senior’ of the IdEx, University of Bordeaux (*EcoGenPin*: Ecological genomics of local adaptation in maritime pine, an iconic conifer with large ecological and economic value in SW Europe, 2016-2019). This IdEx proposal was submitted in November 2015 and includes funding for further genotyping/sequencing and phenotyping in maritime pine.

Speciality: Evolutionary, functional and community ecology
Year 2016-2017

➢ **SUBJECT**:

Ecological genomics of local adaptation in maritime pine (Génomique écologique de l'adaptation locale chez le pin maritime)

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➢ **PRESENTATION**:

Climate change has profound impacts on ecosystems and there is an increasing concern on the effects of climate change on natural and plantation forests, with 21-50% of economic value loss expected for European forests by 2071-2100 (Hanewinkel et al. 2012). The main goal of the PhD thesis would be to study the processes involved in genetic adaptation of maritime pine (*Pinus pinaster* Aiton), an iconic conifer of great ecological and economic importance, at different spatial and temporal scales, and to identify valuable genetic variation for adaptation to new environments. Frontier research across ecology, ecophysiology, quantitative and population genetics, bioinformatics, and genomics will be developed to shed light on this fundamental ecological problem, as well as to foster the maritime pine breeding program in south-western France.

Background & Objectives

A relatively new discipline, ecological genomics, is expected to provide answers to questions related to adaptation to new environments, in space and time. Ecological genomics relies on the integration of large scale genomic data with phenotypic and environmental information (Barrett & Hoekstra 2011). Most ecological genomics research so far has, however, failed to integrate these sources of information, as well as to consider the polygenic nature of adaptive traits. We are currently experiencing a shift from views centered on single genes to others that consider epistatic interactions and gene networks as the base for adaptive divergence and phenotypic innovation (Olson-Manning et al. 2012). Increased allelic covariance rather than sharp allele frequency changes may indeed underlie genetic divergence at loci underlying quantitative traits (Kremer & Le Corre 2012). Recent research in humans suggests polygenic adaptation that is reflected in small differences in allele frequencies with weak selection coefficients (e.g. ~10^{-3}-10^{-5} for human height, Turchin et al. 2011) and epistatic interactions. Evidence from QTL mapping and genetic association studies suggest that most adaptive traits are also polygenic in forest trees, highlighting the importance of soft sweeps acting on standing genetic variation (in contrast with hard sweeps driving new mutations to fixation). In recent years, analytical approaches have been developed to test for polygenic adaptation using genomic data (e.g. Berg & Coop 2014). But such examples are still scarce, and there is an urgent need for further development and application, in particular in species such as forest trees, for which adaptation to new environments is fundamental for provision of ecosystem services. In addition, recent evidence suggests that most genetic polymorphisms responding to climate could be lineage-specific, following a conditional neutrality model (e.g. Tiffin & Ross-Ibarra 2014), which claims for multi-population approaches and the exploration of geographical variation in adaptive responses. The temporal scale of genetic adaptation is also important for predicting the consequences of ongoing climate change (Hoffmann & Sgrò 2011). Annual plants are able to adapt gradually, year by year, but long-lived species such as forest trees are experiencing abrupt shifts of environmental conditions, corresponding to accumulated annual changes. Whether evolutionary rates in these species are fast enough to mitigate the effects of rapid climate change is currently unknown.

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Task 2. Study of polygenic adaptation to heterogeneous environmental conditions.

Allelic effects on adaptive phenotypes obtained in Task 1 will be used to apply different methods to study polygenic adaptation. A first approach is based on pairwise population comparison of allele frequencies, while controlling for genetic drift (Turchin et al. 2011). The second approach, also relying on previous computation of allelic effects, is based on the construction of a compound statistic, Q_X, which is then compared with the expected values under neutral evolution, and correlated with environmental variables (Berg & Coop 2014). By working in parallel with both CLONAPIN and PINCORSE maritime pine collections, the PhD student will obtain unprecedented complete views on polygenic adaptation under contrasted environmental conditions at different spatial scales.

Task 3. Short-term evolutionary responses in maritime pine.

To study the temporal scale of genetic adaptation and expected short-term evolutionary responses in maritime pine (i.e. contemporaneous adaptation), the PhD student will establish natural selection (fitness) experiments in contrasted environmental sites (see Vizcaíno-Palomar et al. 2014, for a similar experimental setting). The experiments will use seeds directly sown in the local environment (25 families from each of the three main maritime pine European lineages, plus 25 families from the breeding program), so that natural selection during germination and early establishment is not avoided, and they will follow a replicated experimental design (6 blocks). Saplings will be phenotyped for growth and resistance to water deficit to compute genetic selection gradients using survival as fitness proxy. They will also be sequenced and compared to control samples following a ‘targeted resequencing’ strategy on pooled samples to reduce costs. Natural selection (fitness) experiments will be located in maritime pine Conservation Units, which are naturally regenerated, and the main future source of genetic variation for the breeding program.

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➢ SCIENTIFIC PARTNERS:

The team at the host UMR Biogeco supporting this research is highly multidisciplinary providing expertise in evolutionary genetics (Antoine Kremer, Myriam Heuertz), genomics (Christophe Plomion), ecophysiology (Annabel Porté, Sylvain Delzon), tree breeding and quantitative genetics (Annie Raffin, Laurent Bouffier), ecological modelling (Marta Benito-Garzón), and networks (Jean-Charles Leplé, Corinne Vacher). Thus, it constitutes an ideal environment for the development of a PhD thesis, fostering multiple stimulating interactions for the student. Collaboration with researchers from other UMRs will connect the research to other on-going initiatives on tree genetic adaptation (e.g. Oliver Brendel for ANR H2Oak project and Ivan Scotti for ANR FLAG project). Main international collaborators include researchers from Italy (Giovanni G. Vendramin, IBBR, Firenze), Spain (Ricardo Alía, Juan José Robledo-Arnuncio and Delphine Grivet, INIA, Madrid), UK (Stephen Cavers, CEH, Edinburg), Canada (Sam Yeaman, University of Calgary) and the USA (Andrew Eckert, VCU, Richmond), which are developing similar projects on conifer genetic adaptation. This rich network of collaborators will facilitate the PhD student research stays abroad and his/her contact with leading international scientists. Colleagues in Spain and Italy will establish replicates of the maritime pine natural selection (fitness) experiments in their countries in the framework of GenTree EU H2020 project, providing excellent additional opportunities for the internationalization of the PhD research.

➢ INDUSTRIAL PARTNERS:

Two types of industrial partners would be involved in the PhD project. On the one side, the research to be conducted is highly relevant for the identification of plant material adapted to new environmental conditions in South-Western France and it will closely interact with the maritime pine breeding program (developed, among others, by INRA). This has attracted the attention of the ‘Centre Régional de la Propriété Forestière d’Aquitaine’ (CRPF AQUITAINE), which stands up as the main liaison with industrial partners. On the other side, the work is also relevant for conservation of semi-natural populations of maritime pine in public lands. These forests are rich reservoirs of genetic diversity and the origin of the materials used for commercial plantations in the Landes region. Thus, they have a very important strategic interest. Moreover, the PhD student will conduct its fitness experiments within some of these forests, providing valuable information on their expected short-term evolutionary responses. This work will involve the ‘Office National des Forêts’ (ONF), both as facilitators and final destination of translational efforts.

➢ FUNDING:

Funding to support the PhD thesis will come from a new European H2020 project that will start in May 2016 (*GenTree*: Optimising the management and sustainable use of forest genetic resources in Europe, 2016-2020). The student will be expected to develop (partially) the activities related to maritime pine in WP3 and WP4. Additional funding may come from a proposal for a ‘Chaire d’Installation Senior’ of the IdEx, University of Bordeaux (*EcoGenPin*: Ecological genomics of local adaptation in maritime pine, an iconic conifer with large ecological and economic value in SW Europe, 2016-2019). This IdEx proposal was submitted in November 2015 and includes funding for further genotyping/sequencing and phenotyping in maritime pine.