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MARIE SKLODOWSKA-CURIE ACTIONS

INDIVIDUAL FELLOWSHIPS (IF)
Call : H2020-MSCA-IF-2018

PART B

"SoMMutaRaTes"

Somatic and Meiotic Mutation Rates in Trees

This proposal is to be evaluated as:
[EF-ST]

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LIST OF PARTICIPANTS

Participating organisations	Legal Entity Short Name	Acade mic (tick)	Non-acade mic (tick)	Dept./ Division/ Laboratory	Supervisor	Role of partner Organization
<u>Beneficiary</u>						
University of Uppsala, Sweden	UU	X		Ecology and genetics/ Plant Ecology and Evolution	Martin Lascoux	Main host
<u>Partner Organisation</u>						
INRA Bordeaux, France	INRA	X		Forest, Grassland and Freshwater Ecology / UMR BioGeCo / Ecology and functional genomics	Christophe Plomion, Catherine Bodénès	Second host
<u>Collaborators</u>						
University of South Carolina	SC	X		College of Arts and Sciences / Biological Sciences / Earth ocean and Environment	Timothy Mousseau	Collaborator
Australian National University	ANU	X		College of Science / Biology/ Mutation, molecular evolution and phylogenetics	Robert Lanfear	Collaborator

1. Excellence

1.1 Quality and credibility of the research/innovation action (level of novelty, appropriate consideration of inter/multidisciplinary and gender aspects)

State of the art:

Mutation is a central force in evolution since it fuels within-population diversity and thus enables evolutionary change. Reliable estimates of heritable mutation rates are therefore crucial for interpreting patterns of broad scale biodiversity, from patterns of diversity within species to divergence among species[1]. A nonzero mutation rate is essential for species to continuously adapt to environmental changes and perturbations[2]. Considerable effort was put into the identification of the genetic bases of new adaptive mutations, but this sometimes obscures the fact that most new variation in protein-coding genes is deleterious[3-4]. As a consequence, theory predicts that species evolve towards lower per-generation mutation rates to avoid the accumulation of an increasing burden of deleterious variants[5]. Highly radioactive areas are, however, human-disturbed environments, particularly those repeatedly bombarded by nuclear weapons or which experienced a major civil nuclear accident, with specific conditions that species have never experienced during the course of their evolution and for which considerably higher mutation rates and load can be expected. As such they provide a unique opportunity to assess the impact that higher mutation rates would have on the fitness and evolution of organisms. Unfortunately, empirical data remains scarce limiting a broad assessment of the theory about mutation rates in undisturbed or highly radioactive environments, particularly in plants.

In plants, knowledge on the timing of germline segregation –when germline cell lineages become physically isolated from somatic cell lineages – remains fragmentary but the broadly shared view is that it occurs very late in development[6]. Following this view, longer-lived plants are expected to accumulate more somatic and heritable mutations per generation than shorter-lived plants. However, since growth slows down as plants increase in size, notably because there are physical limits to the delivery of water and nutrients to apical meristems with height, taller species are also expected to evolve more slowly than shorter ones due to lower rates of mitotic cell division in the apical meristem per unit time, and thus inducing lower mutation rates on a per-year basis[8]. Comparative studies have provided some empirical support for this hypothesis[9]. More surprisingly, the expected relationship between plant age and number of de novo mutations (DNMs) was neither recovered in *Arabidopsis*[10] nor in the domesticated peach[11]. More broadly, the timing of the somatic-to-germinal switch is still unknown for the vast majority of plants species[12]. In other words, there is increasing evidence that the relationship between plant growth, aging and heritable mutation rate is much more complex than previously thought. Our proposal aims to tackle this issue in two tree species.

Research objectives:

The central objective of the project is to obtain reliable estimates of mutation rates in plants by gathering new direct and indirect estimates of mutation rates.

Q1 : Do tree species have lower or higher intergenerational mutation rates than annual plant species? The project should provide germline and somatic mutation rates estimates for a European white oak species and a birch species and will compare these estimates of the mutation rate to at least three estimates for annual plant species.

Q2 : **Does radiation exposure generate temporal bursts or stable high levels of somatic mutations in trees living in Chernobyl surrounding forests?** Our objective is to quantify the spatial and temporal dynamics of DNMs accumulation along growths of several old oak and birch trees upon chronic exposure to radiation. After identifying DNMs that have arisen before and after the Chernobyl

accident (Fig. 1), the project should provide information about a rapid decay or potential chronic consequences of the disaster on the DNA repair machinery, even after a substantial decay of the radioactivity over last 30 years.

Q3: What characterizes radiation-induced mutations? The project will provide data to compare the spectrums of DNMs of the two previous sections of the project in order to identify the specificities of the radiation-induced mutations (WP2), as compared to the spectrum of mutations observed in the undisturbed environment (WP1).
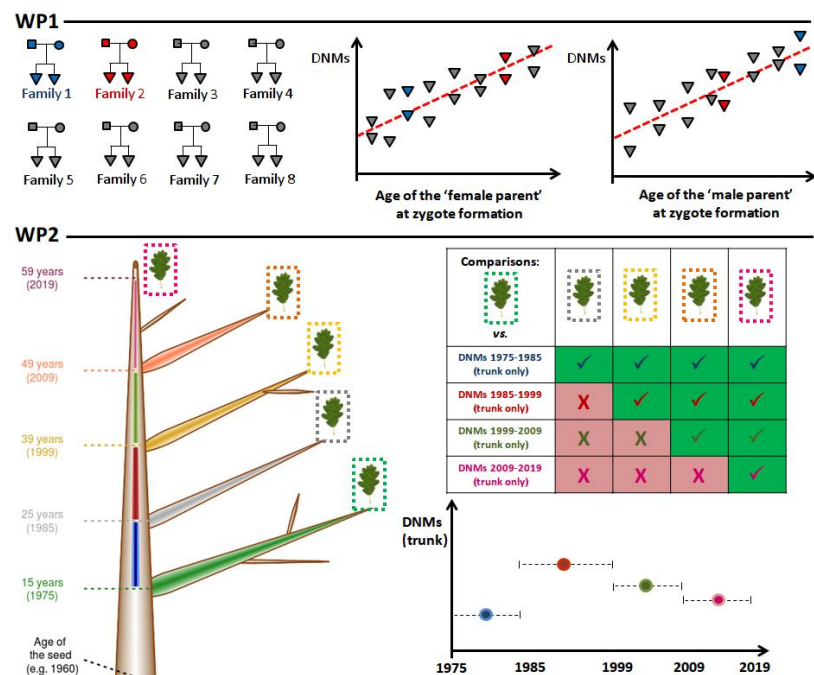

Fig. 1: Graphical abstract of the proposal. WP1) Detection of DNMs in different pedigrees for a given species and linear regressions between DNMs and parental age at zygote formation. WP2) Sampling and sequencing leaves along branches initiated at different time points to identify DNMs and quantify the effects of radioactivity.

Research methodology & approach:

The first part of the project will rely in part on currently available progenies, but also on the development of new F1 crosses, with most efforts devoted to the breeding of pairs of young and old parents. Some full-sib families of *Betula pendula* families are already available within the Swedish and Finnish birch breeding programs, Sweden. Similarly, full-sib families are available for *Quercus robur*[13], the pedunculate oak, through a collaboration with Catherine Bodénès at INRA Bordeaux, France. Indeed, our objective is not only to identify DNMs and estimate an overall intergenerational mutation rate in silver birch and pedunculate oak but rather to separate the contribution of meiotic and mitotic mutations rates. By considering the greatest number of crosses and the largest range of male and female ages at zygote formation, we can expect to observe an increase of the number of mutations along an age gradient, similarly to what was found in humans[14,15] and in two monkey species[16-17]. Consequently, by regressing the number of observed mutations along the age gradient at zygote formation, we will obtain estimates of both meiotic (intercept) and mitotic (slope) mutation rates (Fig. 1). Overall birch and oak per-generation mutation rates will be compared to current estimates for *Arabidopsis*[18-19], rice[19]and peach[11] and some upcoming estimates for additional annual and perennial plant species also obtained from parent-progeny sequencing projects (*Capsella* grandiflora and *Vitis vinifera*, personal communications of S. Wright & T. Kent (Univ. Toronto) and H. Badouin (Univ. Lyon), respectively).

The second part of the project will rely on the availability of tree samples from the Chernobyl Exclusion Zone, through a collaboration with Tim Mousseau at the university of South Carolina, who has worked in the Chernobyl area since 2000. After performing whole genome sequencing using Illumina HiSeq from leaves collected at the branch tips initiated before and after the accident (Fig. 1), following a similar strategy than in Plomion and collaborators[20], we will estimate the temporal dynamics of DNMs accumulation in trees surrounding Chernobyl (at least 3 per species, with up to 8 samples per tree). It must be noted, however, that the identification of DNMs within the same individual remains challenging because DNMs are expected to be at low frequency. Consequently, the sequencing of libraries will be performed at high depth of coverage and the identification of DNMs will be performed using frequency-dependent methods initially developed for cancer research, with additional stringent criteria[20].

<u>Originality and innovative aspects of the research program:</u>

The project tackles fundamental questions and topics relative to mutation.

First, the project proposes to identify DNMs at two different levels; intra- and inter-generational. Robust identification of DNMs – the core of our project – is a major topic in the field. Over the last decade, considerable efforts have been made in order to fine-tune methods to yield accurate estimates of germline mutation rates. But applications of these methods were unequally distributed over clades, with a particular focus on primates[14-17] and a deficit of estimates for plant species. Furthermore, the detection of within-individual DNMs has long been seen as crucial in cancer research, but these methods have only started to be applied to plants[20]. Some refinements of the state-of-the-art methods in cancer research are still needed to fully adapt them to plant research (e.g. performing analyses accounting for the specificities of tree architecture). More broadly, this project will benefit from current advances in both primate genomics and human cancer research, including the recent development of mutation spectrum analyses[e.g.21-23].

Second, our project will include plant mutational specificities into these methods. In contrast to animals, gametogenesis occurs late in plant development and therefore somatic mutations can be transmitted to the next generation. As a consequence, plants are an original system where species with a long life span are expected to accumulate and transmit more mutations per generation than plants with a short life span[20]. As a consequence, we will also take advantage of the different life spans of oaks and birch. Indeed, birch is a pioneer species and has among the shortest life spans for a European tree species while oak are among the longest ones.

Third, the use of DNA material from chronically irradiated trees near Chernobyl is also an original plant material that allows for an important comparison with non-irradiated material. Indeed, even if mutation rates have been estimated in some chronically irradiated animal species[24,25], it remains at an embryonic stage in plants (but see refs. 26-27). A meta-analysis suggested that plants exhibit a larger effect of radiation on mutation rates as compared to animals[28]. One potential explanation is that plants are sessile and therefore cannot flee the most contaminated areas, thus leading to deeper effects on mutation rates. However, molecular data to support these conclusions are extremely sparse (e.g. there is a complete absence of whole genome sequence data for plants) and this effect is probably inflated to some extend by these indirect observations[28].

1.2 Quality and appropriateness of the training and of the two way transfer of knowledge between the researcher and the host

<u>Transfer of knowledge to the experienced researcher (ER):</u>

My previous experience in the field of population genomics of forest tree species and in bioinformatics, especially in the data mining of very large Next Generation Sequencing (NGS) projects, makes me a perfect candidate to carry out this ambitious project. During the past four years, I already started to adapt methods from human cancer to plant genomics. This project will allow me to pursue this line of work and perform more sophisticated population genomic analyses by explicitly taking into account plant specificities, in particular mutational mechanisms (WP2). I will also learn and get feedback through collaborations about the most accurate methods to estimate mutations rates (WP1). More broadly, my objective is to strengthen my current skills. For example, we will benefit from the advances in cancer research. For the past 10 years, one of the top priorities in cancer research has been to identify how mutation spectra vary across cancer types[29]. We have already planned to include a comparison of mutation spectrums between trees growing in undisturbed (WP1) and highly contaminated sites (WP2) in order to be able to identify the characteristics of the radiation-induced mutations (Q3).

The international prestige and expertise of the host institution at Uppsala University will undoubtedly help me to receive training and reinforce my professional skills. During the first year, I will attend

several courses (Graduate school workshops and courses including courses on the genetics of adaptation, on bioinformatics and on leadership). During the second year, I will be associated to courses given at the graduate school level. I will closely interact with Martin Lascoux on the preparation on these courses. The Evolutionary Biology Centre is a very dynamic place where I will also greatly benefit from attending the bi-weekly seminars hosting prestigious scientific guests and the numerous journal clubs. Second, this project will be done in English, within an English-speaking community and therefore will offer me the opportunity to strengthen my English communication skills. Finally, I also want to acquire expertise to be able to supervise and manage scientific projects. More broadly, this project will allow me to collaborate more easily with other specialists and to coordinate new projects concerning mutation. For example, I will also meet Prof. Jarkko Salojärvi (Nanyang Technological University, Singapore, and University of Helsinki, Finland) at the beginning of the project and we will continue to regularly interact for sharing data, resources and discussion on the project.

Transfer of knowledge to the host institutions:

Thibault Leroy's experience will be of particular interest for the Department of Ecology and Genetics at Uppsala University. In the short term, he will provide accurate estimates of mutation rates, which represents a key parameter to calibrate neutral models and gain insights about the evolutionary history of *B. pendula*[30]. This proposal will also contribute to sustain and increase the interactions that have recently emerged on this topic[20,31] between this research department and collaborators at INRA Bordeaux. European birch and white oak species are two important groups of tree species in our European temperate forests. Recent advances in the inferences of the evolutionary history of these species suggested that have common elements in their evolutionary trajectories, particularly regarding the possibility for interspecific postglacial gene flow[32,33].

1.3 Quality of the supervision and of the integration in the team/institution

Main supervisor: Martin Lascoux is a population geneticist who has been working extensively on demographic and evolutionary inferences from DNA sequence data in plants. He has a strong expertise in statistical population genetics. He has published 125 articles, some in leading scientific journals (*Science, PNAS, Nature Communications, Nature Reviews in Genetics*) and many in high ranking journals in population genetics and molecular evolution (*MBE, Genetics, Molecular Ecology, Evolution, Heredity, New Phytologist, Plant Physiology*). He has many collaborators at the European level and has been a member of eight EU projects, including one network of excellence (Evoltree). He was a visiting professor at the Chinese Academy of Sciences in 2010-2011 and at Fudan University in 2012 and 2013. Two of his main current interests is the way selection and demography have interacted in shaping genetic polymorphism linked to phenotypic variation and the evolution of polyploid species, in particular the divergence of the subgenomes. He has established solid cooperation links with other groups working on plant evolutionary biology: Prof. Stephen Wright (University of Toronto, Canada) with whom they have been sharing some of the genomic work in Capsella. He have also been cooperating with Prof Detlef Weigel (Max Planck Institute, Germany), with Prof. Mikkel Schierup (University of Aarhus, Denmark). On forest tree species, Martin Lascoux has established long-term cooperation with Dr. Giuseppe Vendramin (National Research Council of Italy), Prof. Michele Morgante (Uiversity of Udine, Italy), Dr. Christophe Plomion (INRA, France), Prof. Outi Savolainen (University of Oulu, Finland). Finally, the diversity of biological systems on which Martin Lascoux and his co-workers have been focusing over the last 10 years also offer a unique opportunity to compare mutation rates across a series of plants with contrasted life-histories.

Second supervisior: Christophe Plomion is a scientist director at INRA Bordeaux. In 2008, he was appointed as deputy head of the "Forest, Grassland and Fresh Water Ecology" Division of INRA. His current research focuses on the analysis of individual's and species' responses to environmental variations at the phenotypic and genomic levels by integrating functional and evolutionary ecology. He

recently coordinated an international consortium that led to the sequencing, assembly and annotation of the oak genome[20] and now uses this resource as a tool to study demography, local adaptation and speciation in European white oaks. He has published over 170 articles in a wide range of scientific peer-reviewed journals (e.g. Nature Plants, MBE, New Phytologist, Molecular Ecology, Heredity, Genetics, Theoretical and Applied Genetics).

Hosting arrangements: Efficient management of this project will be achieved through a well-established internal organization at Uppsala University, including an administrative staff focused specifically on dealing with European Union contracts, including Marie Curie grants. The host department has also a highly efficient administrative core unit, including administrative officers, personnel officers, systems administrators and a manager. This includes fulltime administrative support to handle all purchasing, accounting and to assist with administrative matters. Staff of this unit will help with insurance and tax issues, health care and social security, permits and accommodation. Most Swedes speak English which will facilitate my integration. In addition, Swedish courses are organized at Uppsala University for foreign students and researchers, for instance a basic Swedish course is offered in August each year. Under the working contract provided by Uppsala University, I will benefit from top research infrastructures (e.g. computers, labs, library) and access to general services provided to Swedish citizens (e.g. gymnasium, childcare).

1.4 Capacity of the researcher to reach or re-enforce a position of professional maturity/independence

Although I am at an early stage of my career (PhD obtained in December 2012), I have already conduced several population genomics studies related to speciation and local adaptation of plant pathogens and forest plant species, with promising upward trajectories in both the number and the quality of my dissemination (4 papers accepted over the last 12 months). My current unpublished work still enlarges this range of species (domesticated plant species, fish and birds) and includes many additional research questions (*e.g.* impacts of deleterious mutations, signatures of past domestication and breeding, evolution of sex chromosomes architecture). My professional independence can also be viewed by my interest in offering some critical perspectives. After a talk in an international congress (Plant Resistance Sustainability International Conference, 2012), I was invited to write a review[34] in which I evaluate the advances and promises of population genomics for geneticists working on plant pathogen species. More recently, I was invited to contribute to a review on the genomics of hardwood species, a decade after the release of the first hardwood genome[35]. I am currently writing another review for a broader readership, a 'Tansley insight' upon the invitation of the board of New Phytologist[36]. Similarly, I was also recently invited to write a public outreach of our recent work in oaks[32,37] in "Espèces", a French nature and ecology magazine, printing up to 15,000 copies. I am also regularly invited to review papers for various journals on ecology and evolutionary biology (5 over last 12 months) and as speaker in seminars. I had also the chance to mentor 7 MSc students and to give advice to 3 PhD students in the field of population genomics and bioinformatics, particularly for demographic inferences of species using Approximate Bayesian Computations (e.g. ref. 38). Given that I have a solid background in both bioinformatics and high-performance computing, I also offered training in programming (bash, python, R) and bioinformatics (uses of computing clusters and command line tools) to several of my former permanent and nonpermanent colleagues at INRA Bordeaux. This project will be a perfect opportunity to gain a valuable international experience, with positive impacts on my English level and the breadth of my research skills and interests. In the near future, I aim to establish myself as an independent scientist through both project proposals, including an ERC Starting Grant, and to different programs for tenure-tracks in France or in some other European countries.

2. Impact

2.1 Enhancing the potential and future career prospects of the researcher

My long-term objective is to gain valuable experience, knowledge and skills to obtain a permanent

academic research position in France or elsewhere in Europe. I have so far spent my whole research career in France. This constitutes a hindrance to the development of my career because it has limited my international collaborations and it could also limit the opportunities to get a senior scientist position, as international experience is usually mandatory to get such a position, especially at CNRS. The fellowship will thus allow me to fill this gap. By spending two years at the EBC, I will move to and benefit from a world-class infrastructure and I will work in an excellent research institution. EBC will provide a significant change in my working environment by allowing interactions with researchers involved in sophisticated analysis of population genomics data geared towards identifying genes involved in adaptive traits in natural plant populations, and in functional approaches (gene expression, genotype-phenotype relationships). This will complement the competencies and research topics of the current research team I belong to, which are oriented towards phylogenetic approaches and global analysis of genome evolution. In addition, I will work in a sub-department dedicated to the study of plant ecology and evolution. This will also provide a substantial change compared to my current research team in which animal models (including mammals, birds and tunicates) largely predominate. Finally, in the host program, I will have the opportunity to interact with plant ecologists (from evolutionary to community ecology), working both on basic and applied research, for instance to understand the consequences of change in land use and other human-induced changes. This will provide me with a very new working environment that will help me broadening my views on plant evolution. I will also have the opportunity to (co-)supervise students, including those of the European Erasmus Mundus Master's programme in Evolutionary Biology (MEME). MEME involves four European universities, including Uppsala, Gröningen, Munich and Montpellier Universities, and Harvard University (USA), and is dedicated to train talented students in evolutionary biology. In summary, this fellowship will thus clearly contribute to objectives of the European Research Area through the transfer of knowledge and improved collaboration between European researchers and institutions.

2.2 Quality of the proposed measures to exploit and disseminate the action results

Dissemination of the results: I plan to publish the results of these two work packages in two high-impact journals. Peer-reviewed academic journals with large audience such as *Nature*, *Nature Communications, Nature Genetics*, *Nature plants*, *PLoS Biology, Science* or *Science Advances* will be targeted. I will also write an opinion paper about the need for more studies on plant genetics and phenotypes of trees surrounding Chernobyl for *Plants, People, Planet*, a new journal of the New Phytologist Trust. I will also present advances on the project to the scientific community through seminars and international conferences, such as the 2021 congress of the *European Society for Evolutionary Biology* (ESEB 2021, Prague, Czech Republic). If possible, I will also try to join a summer school in cancer genomics in order to get training on analyzing large cancer data, to present the goal of our project and to get some feedbacks. As an alternative, I will join an international congress on cancer genomics, such as the 2021 *Cancer Genetics and Epigenetics* conference.

Data Availability: All preprints, scripts and data will be made available publicly on long-term repositories, through bioRxiv, Git repositories and Sequence Read Archive (SRA) respectively. Particular interest will be given to make our data and results easy to find, freely available and reusable by the scientific community, regardless of any country or affiliation.

2.3 Quality of the proposed measures to communicate the action activities to different target audiences

Individually, we are all supporters of the ongoing science-popularizing movement with the underlying objective of an increased communication between the scientific community and society. We are fully convinced that the two parts of the projects will be of interest to many European citizens, particularly in a context of the increased awareness about the importance of biodiversity, and the intrinsic risks of nuclear energy. We have planned to do several other actions to increase this communication. First, we

will provide our own scientific press release after each publication, in collaboration with the communication departments of Uppsala University and INRA. This strategy will be put in place in order to ensure a wide dissemination to the general public of our research, especially in newspapers and non-specialized journals. Second, we will create a website for the project and a twitter account to directly proceed to informing both scientists and the general public throughout the project. Both Martin and I will like also to participate to the "*European Researchers' Night*" in Sweden, a main social event coordinated there by the non-profit organisation Vetenskap & Allmänhet.

3. Quality and Efficiency of the Implementation

3.1 Coherence and effectiveness of the work plan

The project duration is 24 months which has been divided into two main work packages. I will spend most of the fellowship time at Uppsala University (at least 10 months/year) with only few stays at INRA Bordeaux Pierroton (up to 2 months/year).

Months	A	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Main location		S	S	S	S	S	S	F	S	S	S	S	S	S	S	F	S	S	S	F	S	S	S	S	S
> Field work																									
- WP1	░																								
- WP2	░	▓	░																						
> DNA Extraction & Sequencing																									
- WP1								▓	░	░	░														
- WP2			░	▓																					
> Data Processing & Informatics																									
- WP1												░	░	▓	▓	▓	▓								
- WP2																									
Mutation spectrums																				░	░				
> Deliverables																									
- Opinion			▓	░																					
- Article WP1																					░	░	▓	▓	▓
- Article WP2									▓	▓	▓	░													
- Conferences																		▓							░
> Public engagements*																									
> Training		░	░	░	▓	░	░																		

▓ Main activity ░ Secondary

A *Plant material already available or expected to be sampled before the start of the project.*
* *Weekly routine actions for public engagements (e.g. Twitter posts) are not included in this timeline.*
Main location: S = Uppsala, Sweden, F= Bordeaux, France

3.2. Appropriateness of the allocation of tasks and resources

Before the start of the project, a first sampling trip - funded by Christophe Plomion (INRA Bordeaux) - will be done in the Chernobyl area (from 24th to 28th of September 2018, WP2), to bore several old trees in order to date the age of the tree after counting tree rings. The project also partially relies on the annual production of seeds from different oak and birch crosses at INRA Bordeaux and in Sweden, respectively (WP1). Indeed, for both species, such breeding effort had been continuously and continues to be done for different umbrella projects. Some acorns and seedlings from different progenies are already available. Additional field work at Chernobyl (WP2, 5-10 days) and in both partner research stations (WP1, 2*5 days) will be needed at the beginning of the project in order to complete the sampling. We do not anticipate any difficulties or obstacles regarding the isolation of genomic DNA for sequencing since routine procedures are available for oaks[20] and birches[30]. I expect to spend no more than 1.5 months in the laboratory. The remaining laboratory work (library constructions and sequencing) will be outsourced. The vast majority of my time will be devoted to the scripting, processing of raw data, the post-processing of the analyses and writing the articles. Even if the required genome-sequencing effort may seem massive, rapid decrease in DNA sequencing costs will allow us to cover these research costs with both the Marie Curie funds and some ongoing projects of Martin Lascoux, Christophe Plomion and Robert Lanfear.

3.3 Appropriateness of the management structure and procedures, including risk management

Quality management:

I will hold regular meeting in person or via Skype with both Martin and Christophe, depending on my location. In addition, we will meet at the most important moments, such as the launching of the project or the transitions between WPs and regularly during the drafting of manuscripts. I will also regularly share methodological improvements and new results in lab meetings at the two research institutions to benefit from the feedback of team members. At the EBC, I will be provided with a fully equipped office, including a high performance computer with high speed Internet connection, all required software, and electronic access to all required journals. I will have access to the high performance computer cluster for management and analyses of NGS data. All members of the team have an office in the same corridor and other researchers that will interact with the fellow are closely located one stairway above, which will facilitate daily interactions. The grant will be managed by Uppsala University. This university has vast experience in setting up and managing European projects. I will manage my own budget with the mentoring of Martin Lascoux.

Risk management:

We identified the following potential risks and the strategies to limit them.

Time and Resources: the previous Gantt chart was estimated in a conservative manner and we can expect deliverables to be ready before. Some periods labeled as "secondary" in the diagram were included in order to make a provision for delays. *Improvements of methodologies*: the most challenging part is the fine-tuning of variant frequency-dependent methods initially developed for cancer research to take into account plant specificities. Performing analyses under an explicit phylogenetic context, where the phylogeny would be the architecture of the tree, is for example a promising avenue for detecting DNMs in plants. This will require some programming and simulation work. We will co-operate with Robert Lanfear (Australian National University at Canberra) on this issue. Furthermore, while this is expected to be helpful, this refinement will not be mandatory for the project and need to be considered as a plus.

3.4 Appropriateness of the institutional environment (infrastructure)

The main supervisor: Prof. M. Lascoux is a highly experienced researcher in the field of population genetics and genomics at the interface between theory, sequence data analyses and functional analyses. He has strong experience in training and mentoring researchers: eleven PhD students have completed their theses under his supervision and he has hosted more than 15 postdoctoral fellows. His group currently includes three PhD students, three postdocs and one technician. He is currently leading or participating to 5 research projects, including two EU-supported projects. He is also an experienced teacher in population genetics and genomics.

The main institution: the EBC, is one of the top European institutions devoted to Evolutionary Biology, and the Ecology and Genetics subdepartment covers a broad range of issues related to the present project. The university is ranks among the world's 100 best universities and is at the forefront of ambitious policies, including gender mainstreaming and an Equal Opportunities Programme to struggle against any kind of discrimination (gender, transgender identity or expression, ethnicity, religion or other belief, disability, sexual orientation or age).

Main collaborators at the host institution: Martin Lascoux and Arild Husby will provide expertise in population and quantitative genetics analysis. Martin Lascoux and Ulf Lagercrantz will provide expertise in plant genomics. Hans Ellegren is one of the leading European researchers in molecular evolution and has already worked on the effects of the Chernobyl accident on birds.

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