

WHITE PAPER

“LONG DISTANCE GENE FLOW AND ADAPTATION”

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1. Introduction Main questions

While evidence of climate change and its impact on vegetation is steadily increasing, so are the concerns about the inherent or human mediated capacities of species to cope with these changes (Solomon *et al.* 2007). These concerns are even more acute for sedentary and long lived species as trees that are less prone to tracking favourable conditions fast via migration within a short time period. Migration and adaptation are often cast as alternative responses to climate change (Aitken 2008) because adaptation allows populations to adjust to novel conditions without moving, whereas migration lets populations track favourable conditions through space without evolving (Pease *et al.* 1989; Polechova *et al.* 2009). However, gene flow via both seed and pollen also affects adaptation by shaping the distribution of genetic diversity both within and among populations (Lopez *et al.* 2008). Given the extant knowledge of the intensity and directionality of climatic change, have trees inherent resources or mechanisms that would enhance their local adaptation? An immediate clue to this question can be afforded by a retrospective insight of the evolutionary changes that trees underwent during “natural” climate change that operated over longer time periods since the last glaciation (Petit *et al.* 2008). A large body of evidence stemming from common garden experiments installed since decades in the Northern hemisphere suggest that a balance between divergent selection across contrasted ecological sites and reproductive contact via pollen flow has maintained enough diversity to trigger adaptability to changing environments in the past (Kremer *et al.* 2010). Whether interactions between selection and gene flow will be efficient to cope with future changes remains an open question, as future predicted rates of environmental changes and strength of selection are quite different from historical records. As environments are continuously changing, so are the local optima for populations and the evolutionary response of populations can be pictured as a race where populations are tracking the moving optima (Pease *et al.*, 1989; Bürger & Krall, 2004). The race is unidirectional, as suggested by shifts of climatic envelopes (Iverson *et al.* 2008). However genes are moving as well and the race can be either restrained or accelerated depending on the direction and extent of gene flow in comparison to the velocity and direction of the moving optima. Hence the adaptive responses can be very differently mediated by gene flow (Bridle & Vines 2007). Predictions of the possible outcomes are dependent on a number of questions that need to be addressed by theoretical and experimental approaches.

- (1) What is the relative contribution of long-distance gene flow to standing variation and under what circumstances does it enable rapid adaptive responses of tree populations?

- (2) What are the actual dispersal distances and potential migration rates of pollen and seed in trees in comparison to predicted shifts of climate changes?
- (3) Will pollen and seed flow – directions, distances, rates – be affected by climate change?

This contribution is a review of the state of knowledge on selection /gene-flow interactions in the context of environmental changes in forest tree populations, and offers different avenues for future research.

2. What do we know?

2.1. Predicted direction and range of environmental change based on niche modelling.

Retrospective monitoring of vegetation distribution during the past century demonstrated that tree species have migrated along altitude (Lenoir *et al.* 2008) and latitude (Walther *et al.* 2005) as a result of ongoing environmental changes. Niche modelling under various climatic and greenhouse emission predictions suggest that these trends will continue over the next decades and that bioclimatic envelopes will be shifted Northwards in North America (Iverson *et al.* 2008) and Northeastwards in Europe (Thuillier 2003). The estimated shift distance varies from 300 to 800 km depending on the climate or greenhouse gas emission scenario within one century (Mc Kenney *et al.* 2007) and considerable variations were reported according to models, species and methods (Thuiller 2004). However, despite their uncertainties these figures show that spatial shifts of selection pressures under environmental change are directional. Furthermore while the shift distances are much larger than the seed dispersal in trees (Iverson *et al.* 2004), they encompass the range of long distance pollen flow, suggesting therefore that climate change velocities (Loarie *et al.* 2009) can actually be met by gene propagation velocities due to pollen flow.

2.2. Distribution of genetic variation for fitness related traits: within vs between pop distribution of diversity.

The adaptive impact of long-distance gene flow will largely depend on the genetic architecture of fitness related traits and the spatial distribution of the associated genetic variation across populations. Isozyme studies have framed much of the classical view that woody species with large geographic ranges, outcrossing breeding systems, and wind or animal seed dispersal have more genetic diversity within species and populations, but less variation among populations (Hamrick *et al.* 1992). This review was based entirely upon isozyme studies and others based neutral genetic markers (Petit *et al.* 2010) may not be indicative of adaptive variation. In fact, neutral markers can be used as a yardstick to detect quantitative traits subject to diversifying selection (Whitlock 2008). Indeed the subdivision of genetic variation for adaptive related traits contrasts markedly with the review based on molecular markers. Phenotypic traits exhibit very large population differentiation in spite of extensive gene flow (Savolainen *et al.* 2007), that is mostly generated by intergenic disequilibria among genes contributing to the traits (Le Corre & Kremer, 2003; Latta, 2004). Furthermore phenological traits follow sharp clinal variation under common garden conditions suggesting directional selection fostered by climatic gradients (Morgenstern, 1996).

QTL experiments conducted in breeding programs indicate that growth and developmental related traits (which are economically important traits but also related to viability) are polygenic, as most QTLs contribute to less than 10% of the phenotypic variation in segregating populations (White *et al.* 2007; Kole 2007). This picture is reinforced by recent emerging pangenomic association studies in natural populations of trees, showing that single SNPs contribute to less than 5% of observed variation (Grattapaglia *et al.* 2009; Eckert *et al.* 2009). Given the limited statistical power of QTL and SNP detection due to sampling limitation, the genetic architecture of complex traits is likely to be composed of a large number of genes with moderate to small effects.

2.3. Theoretical expectations of positive and negative effects of gene flow on adaptation.

Because migration homogenizes gene frequencies across space, high gene flow could severely constrain adaptive divergence in heterogeneous habitats (Hendry *et al.* 2001; Bohrer *et al.* 2005; but see Yeaman & Guillaume 2009 for a revised appreciation of the strength of such constraints). Theoretical models predict in particular that asymmetric gene flow from large central populations to small peripheral ones may swamp local adaptation in marginal areas, and increase standing genetic load within populations, so preventing range spread beyond some critical environmental limit (Kirkpatrick & Barton 1997; see a review in Bridle & Vines 2007). Empirical evidence for constraining effects of gene flow on divergence and demography is, however, limited (Bridle *et al.* 2009a and b; Moore & Hendry 2009).

Conversely, other theoretical studies suggest that migration can facilitate adaptation to new environmental conditions by replenishing genetic variance within populations (Barton 2001; Holt *et al.* 2003; Polechova *et al.* 2009; Bridle *et al.* 2010) and by attenuating drift load in small populations (Alleaume-Benharira *et al.* 2006; Lopez *et al.* 2009). Experimental evidence that migration enhances fitness in marginal habitats (Tallmon *et al.* 2004; Kawecki 2008; Emery 2009) or facilitates local adaptation in microcosms (Venail *et al.* 2008; Perron *et al.* 2008) supports such predictions. The impacts of gene flow on adaptation are particularly critical when selection varies over space and time (Gandon *et al.* 1996), which has strong relevance in the context of climate change.

A key issue, however, is the scale at which these costs and benefits of migration operate, and how it is affected by the genetics of traits involved in fitness. The net effect of migration on adaptation depends strongly on the extent of gene flow, such that the greatest potential for adaptation is predicted to occur with between one and ten immigrants per generation (Lopez *et al.* 2009). The constraining effects of migration on divergence are more severe when divergence must be achieved at many loci of small effects rather than few major genes with large effects on the phenotype (Yeaman & Guillaume 2009). Migration can have contrasting consequences for populations at trailing and leading edges of a shifting range (Hampe & Petit 2005): migration from southern populations may indeed help northern populations adapt to warming climates but gene flow from central populations may be mostly constraining at the southern margins (Polechova *et al.* 2009).

2.4. Extent and determinants of pollen and seed flow: short vs long distance

The spatial scale of propagule (e.g. pollen or seed) dispersal and gene flow in plants depends on the physical and biological processes that determine the amount and availability of propagules, the spatial extent of their passive transport by an external vector, and the survival of the propagule before, during and after the movement phase. Different combinations of these components yield effective dispersal distances spanning from a few centimeters to thousands of kilometers (Nathan *et al.* 2008). Effective dispersal kernels of pollen and seeds are strongly leptokurtic, exhibiting excessive proportions of both short- and long-distance dispersal events compared to an equivalent normal distribution of the same mean. The spatial extent of pollen dispersal, especially by wind, is considered to be much larger than that of seed dispersal (e.g., Liepelt *et al.* 2002); yet, this generalization should be examined for particular applications given the growing evidence for cases of larger spatial extent of seed- versus pollen-mediated gene flow (e.g., Bacles *et al.* 2006).

Phenomenological approaches for assessing the spatial extent of effective dispersal calibrate pollen/seed dispersal kernels from propagule sampling data (Clark *et al.* 1998) or effective dispersal kernels from the genetic profiles of potential parents and juveniles (Broquet & Petit 2009). These models can accurately quantify the spatial extent of gene flow of a species in a particular site, but inference beyond the often limited scale of sampling is questionable. Mechanistic approaches incorporate the effects of the key underlying mechanisms, such as windspeed and propagule terminal velocity, in wind dispersal models (Kuparinen 2006). More generally, mechanistic assessment of effective propagule dispersal by any vector (e.g., wind, water, animals) requires quantifying the number, the dispersal kernel and the post-dispersal survival of viable propagules. The dispersal kernel can be derived mechanistically as the product of two probability density functions: that of the vector displacement velocity (i.e., how fast the vector moves away from the propagule source?) and the one of the propagule passage time (i.e., how long after loading by the vector the propagule deposits?) (Nathan *et al.* 2008). The broad array of existing mechanistic models based on these measurable parameters provides the means to assess the extent of gene flow of plants in many dispersal systems, including complex ones involving multiple vectors (e.g., Spiegel and Nathan 2007).

3. What don't we know?

3.1. What is the relationship between phenotypes and fitness and how does it vary through time and space?

Population fitness depends on how well a population is adapted to its local ecological conditions, i.e., how the population's phenotypic mean matches its optimum. In principle, there are three main ways that a population's mean fitness is reduced in a population subject to stabilizing selection for a given optimum: (1) *Standing load*: caused by standing genetic variation for the phenotypes and the ensuing phenotypic variation around the population mean; (2) *Lag load*: due to the departure from optimum of population's mean phenotype when it lags behind the optimum and the optimum changes through time; (3) *Migration load*: caused by the departure from optimum of population's mean phenotype due to introgression of maladapted alleles by gene flow from phenotypically divergent populations (see Bridle *et al.* 2009b for a review).

Variation in (1) arises from mutation, migration, recombination, and fluctuating or balancing selection. Balancing selection will maintain higher levels of standing variation than mutation, which increases (1), but should reduce (2) and (3).

Increased genetic variation caused by mutations has a similar dual effect by increasing (1) but reducing (2) and (3) through increased rates of adaptation. Also, although the size of loads (1), (2), and (3) is increased by higher stabilising selection, stronger selection increases the rate of adaptation, meaning that the population remains distant from the optimum for fewer generations. This nevertheless depends on how independent are phenotypic traits to respond to selection pressures and thus depends on genetic correlations among multiple traits.

Variation through space and time of the ecological factors driving local adaptation in tree populations will affect the magnitude of the three fitness loads. Key parameters that need estimation are: the strength of within population (or habitat) selection, the strength of spatial (and time) gradients of key ecological factors (among habitats selection), and the strength of the genetic constraints arising from among-traits genetic correlations. An integrated approach would be to estimate how the multivariate pattern of genetic variation among phenotypic traits matches the direction of selection in multidimensional ecological habitats in the presence of gene-flow to understand how genetic constraints jointly evolve with migration and selection (e.g. Guillaume & Whitlock 2007, Guillaume *submitted*) and affect local adaptation. Finally, a key issue is whether the costs and benefits of migration operate on similar spatial scales. For example, a small amount of long distance gene flow (or translocation of seed) may increase (1) (improving the response to ecological change), without shifting the mean substantially from the local optimum (3). Predicting the evolutionary responses in real populations is unfortunately hampered by too few empirical estimates of these parameters.

3.2. What is fitness in trees?

Fitness describes the contribution of an individual to the gene pool of the next generation (Fairbairn 2006). Therefore, fitness is intimately related to the survival and reproductive success of an individual at each age and stage of its life (Caswell 2001). In trees, the reproductive capacity of an individual firstly depends on the amounts of seed and pollen it produces, both of which depend on the size of the tree (basic allometric theories) and on environmental resources and triggers, which also often reflect tree size. Therefore, not surprisingly, a tree's height has been considered to provide a good proxy of its fitness (Savolainen *et al.* 2007).

The capacity of a tree to contribute to the gene pool of the next generation via pollen depends exclusively on the ability of the pollen to fertilize flowers. Two key determinants of this ability are the viability and dispersiveness of pollen, both of which enhance the rate of gene flow (e.g. Bohrerova *et al.* 2009). In the case of seeds, survival and germination determine whether an offspring will successfully establish. As in the case of pollen, dispersal plays a key role by increasing the odds that at least some seeds land in suitable habitats and avoid competition and/or predation in the near vicinity of the parental tree (Janzen 1970). However, local adaptation is likely to set some limits to the distances at which a seed can successfully establish (Savolainen *et al.* 2007).

3.3. How much maladaptation is too much?

Long-range gene flow will often introduce genes to a population that are selectively favoured in other, often distant, parts of the species' range but suboptimal in the local environment (e.g. Savolainen *et al.* 2004). Because

relative maladaptation is an inevitable product of genetic variation in fitness, it is unavoidable for allowing adaptive evolution of the local population. However, in extreme cases maladaptation can be manifest as lower survival and reproductive success to such an extent that the viability of population can itself be put at risk. There is no general relationship between the relative maladaptation required of adaptive evolution and the "absolute" level of maladaptation that can lead to extinction. However, quantitative estimates for this issue, specifically for trees, are critical for assessing both the evolutionary and population dynamic consequences of long-distance gene flow. To this end, provenance trials can provide valuable information (Savolainen *et al.* 2004; Reich and Oleksyn 2008).

3.4. Extent of long distance gene flow

The effective range of long distance gene flow is the combination of all physical and biological processes that affect the amount and availability of pollen and seeds, their movement, their viability and the effective pollination and seedling establishment rates. Particularly unknown are the interactions of the different processes and the way these will be affected in a changed climate. For example the interaction between relative flowering intensity and overlap between source and recipient populations (with a direct effect on pollination rates) with the wind patterns or insect movement that drive long distance dispersal of pollen from remote sources (Schueler & Schlünzen, 2006). Another important interaction is between weather patterns that drive very long distance dispersal, with the conditions that affect pollen survival during the dispersal event (e.g., Aylor, 2003, 2004; Schueler *et al.*, 2005; Bohrerova *et al.* 2009). The local environment around the release point of the propagule and the conditions at which the propagule was selected to be released can also have strong effects on the rate and extent of long distance dispersal (Bohrer *et al.* 2008; Wright *et al.* 2008)

In addition to resolving the physical dispersal kernel, study of pollen dispersal should be accompanied with controlled study of the viability parameters of pollen during the dispersal event. For wind dispersing pollen, this could be done following the methods in Bohrerova *et al.* (2009), testing for the independent and combined effects of temperature, humidity and UV radiation. For animal dispersed seeds or pollen, stomach retention time, and viability during extended stay on/in the host should be conducted. Experimental and theoretical studies on the relationship between pollen deposition, female flowers and seed set are strongly needed for interpretations of pollen dispersal towards gene flow. Furthermore, typical gene flow estimates from single year studies need to be translated into gene flow rates per generation using multiyear studies and models of life time reproductive / gene flow success. Traits controlling pollen production rates, the amount of female flowers, and timing of receptiveness should be identified and their weather dependencies should be measured. This also includes the understanding of the variability of pollen and seed production (e.g. masting) which is potentially an important driver for long-range gene flow events (Koenig & Ashley 2003). Genetic assignment methods linking established seedlings to potential parental populations could be used to evaluate in situ the effective rates and range of gene migration (e.g. Manel *et al.* 2005; Robledo-Arnuncio in press), though this inference will be problematic for abundant and continuously distributed species, for which we lack efficient statistical tools.

3.5. Effect of climate change (short and long term) on long distance gene flow

Despite ample research, understanding how gene flow patterns of plants will be affected by climate changes remains a formidable challenge to be confronted. Extrapolations from the past, inferring, for example, future trends from post-glacial range expansions, are of limited utility due to high uncertainty about these historical reconstructions and the low similarity between post-glacial conditions during the Holocene and the ongoing and projected global changes in climate, land use and other environmental features. Multiple levels of uncertainty also limit mechanistically derived predictions of gene flow in future environments (Higgins *et al.* 2003). One potential approach to address this challenge implements projected changes such as warmer atmosphere (Kuparinen *et al.* 2009), or higher fecundity, earlier maturation and changes (reduction or increase) in surface windspeed (Nathan *et al.*, 2011), into mechanistic models of plant spread in future environments. Although this approach facilitates assessing the upper and lower bounds of future gene flow and population spread more specifically, it is unlikely to provide accurate predictions for a particular species and system, due to the large uncertainty about key hard-to-measure parameters, such as the spatial patterns of phenological schedules for pollen and of post-dispersal survival of seeds.

3.6. Impact of the dispersal kernel on adaptation

More modelling and experimental work is needed to understand how long-distance dispersal and the shape of the dispersal kernel contribute to adaptation. The lever effect of LDD and fat-tailed dispersal kernels on the ability and time to invade new areas (e.g. that recently became favourable) was clearly demonstrated these last years (e.g. Clark *et al.* 2001, Thompson and Katul 2008). From a population genetics point of view, it is obvious that the longer dispersal range is, the more genetically divergent migrants will tend to be, provided the species is distributed across heterogeneous environments and particularly, along a clinal environmental gradient. For example, if dispersal is sufficiently long ranged it may, supply populations in colder regions with genotypes adapted to substantially warmer conditions, potentially enhancing the response of the former to climate warming (Davis & Shaw 2001). How the precise shape of the dispersal kernel, independently from the mean dispersal distance, affects adaptation however is not known; More generally, the ultimate adaptive effect of dispersal will certainly depend on the rate of change of the environment, effective population size (influencing the amount of available genetic variance and the efficiency of selection), the spatial pattern of local adaptation (clinal vs. patchy heterogeneities), the genetic architecture of adaptive traits, the predominant gene flow direction (e.g. south-north versus north-south), and interaction effects between selection and demography (Kuparinen *et al.* 2010). For tree species and their typical life-cycle, the correlation between juvenile vs. adult traits would also matter. The answers to these questions will determine the relative contribution expected from pollen and seed dispersal to the response of species to the ongoing environmental changes.

Concerning more specifically the leading edge of a shifting species range, studies mostly based on thin-tailed dispersal kernels showed how a colonisation wave can result in unexpected foundation/drift effects determining the distribution of neutral or adaptive genetic diversity (surfing phenomenon, e.g. Travis *et al.* 2007, Excoffier *et al.* 2009). For neutral diversity, the shape of the dispersal kernel affects the spatial distribution of genes and the diversity of migrants (Fayard *et al.* 2009). Further studies are needed to understand how LDD affects the spatial dynamics of (i) selected genes within a range expansion in a

homogeneous environment, (ii) quantitative trait loci in a clinal pattern of local selection (iii) neutral and selected genes during a range expansion in a shifting environment. Additionally to theoretical results, specific case studies are also needed where realistic dispersal kernels are confronted to the true spatial distribution of selection pressures (e.g. Kuparinen *et al.* 2010).

3.7. Evolution of dispersal

Genetic variation for traits affecting dispersal is common in plant populations (e.g., Donohue *et al.* 2005). Accordingly, plant dispersal traits have been observed to evolve fast in response to environmental change (e.g., Cheptou *et al.* 2008), especially in the context of range expansion (Darling *et al.* 2008). Identifying how global change (including climate change) will alter selection pressures acting on dispersal is therefore crucial. Previous theoretical work has identified a wealth of factors influencing dispersal evolution (e.g., Clobert *et al.* 2001; Ronce 2007). Future studies should focus on questions addressing the evolution of the dispersal kernel for seed and pollen rather than the dispersal rate, preferably by focusing on identified factors and mechanisms determining dispersal distance in general and long-distance dispersal in particular (Nathan *et al.* 2008). This will also facilitate elucidating the interactions of the main evolutionary factors (local adaptation, non-equilibrium population dynamics, colonization, heterosis, etc.), with special attention on the consequences of range expansion for dispersal evolution (e.g., Travis *et al.* 2010), and on the joint evolution of seed and pollen dispersal (e.g., Ravigné *et al.* 2006).

4. Questions that can be addressed with existing data (data mining, meta-analysis)

4.1. Predicted patterns of long distance gene flow based on meteorological data. Interaction between climate, phenology and gene transfer.

For wind-mediated gene flow via pollen and seeds, available resources of weather data could help to determine the potential magnitude and spatial extent of propagule dispersal within certain landscapes, regions, or even continents. Such an analysis requires regional meteorological datasets, phenological observations over a wide region and a deeper understanding of the meteorological factors driving pollen and seed emission and spread. Regional and global weather reanalysis products, such as the North American Reanalysis (NARR) dataset (Mesinger *et al.* 2006), and the European ECMWF, combine large number of satellite and ground observations with model-based interpolation of wind, temperature, humidity, radiation and other meteorological data and can be used as meteorological information resources (Schueler *et al.* 2005). On-line interfaces for weather and radiation simulation tools can also be used to evaluate conditions across large migration ranges (Bohrerova *et al.* 2009). For pollen, phenological data are available from pollen monitoring networks (e.g. the European Aerobiology Network EAN) or from phenological observations (e.g. the European Phenological Network - <http://www.pik-potsdam.de/~rachimow/ejn/html/frameok.html>). Model-driven weather reconstructions, such as the data from the IPCC climate change scenarios (Solomon *et al.* 2007) can provide data for evaluation of dispersal potentials in past and future climates (Nathan *et al.* 2011; Kuparinen *et al.* 2009). Improved emission functions in relation to weather conditions and the distribution and covariance of terminal fall velocities and mass (Nathan *et al.*, in review) can be combined to determine annual and multiannual pollen and seed dispersal

patterns throughout large geographic regions (e.g. Muñoz *et al.* 2004, Thompson & Katul 2008, Nathan *et al.* 2011). ,

4.2. Meta-analysis of provenance tests

A “norm of reaction” is the phenotypic response of a genotype to a range of environments. Most work in this area is concerned with the role of climate change, as norms of reaction can be used to predict the effects of climate warming fitness of populations, to select populations that will grow well under both current and predicted climates (Aitken *et al.* 2008). Indeed norms of reaction can be considered as response functions and used as tools to predict the responses of a population when it is transferred to different environments (Rehfeldt *et al.* 1999; Rehfeldt *et al.* 2002). Dispersal of a genotype to a new environment can therefore be seen as a norm-of-reaction issue. Common garden experiments of trees – so called provenance tests in forestry - have been installed over decades during the last century for most economically important tree species and could be used to assess norms of reaction (Wright 1976). While these experiments were usually planted in many replications hosted by different countries through international initiatives, the data analysis was separately done and a global assessment allowing to construct the reaction norms needs to be implemented. The very few reports about reaction norms inferred from replicated provenance tests clearly underpin the methodological efforts required to standardize heterogeneous data sets (Wang *et al.* 2010).

4.3. Genetic architecture of traits (meta-analysis of progeny, clonal tests)

In addition to provenance tests, progeny tests (common garden experiments comprising open pollinated progenies colmelcted in one or a few populations) can be especially valuable to assess the genetic architecture of traits at the species level. “Genetic architecture” includes the numbers of genes, the nature of gene effect (additive vs. dominance), interactions between genes, and level of diversity. Genetic architecture has been investigated through QTL detection and genetic associations studies in a limited number of populations and its variation across populations remains to be explored (paragraph 2.2).

A major paradigm is that peripheral populations exhibit low genetic diversity and greater genetic differentiation. Eckert *et al.* (2008) reviewed 134 studies representing 115 species, and found this trend occurred ca. 2/3 of these studies, but the trend was not strong in most cases. They emphasize that little effort has been invested to test whether these geographical trends in putatively neutral variation at marker loci reflect quantitative genetic trait variation, which is likely to influence the adaptive potential of populations across the geographical range.

Gene flow between differently adapted populations may be a persistent source of genetic variation within populations; if so, there should be strong correlations between genetic variance within populations and the amount of heterogeneity in the environment. A model study is that of Yeaman and Jarvis (2006), which involved 142 populations of lodgepole pine, and concluded that gene flow and heterogeneous selection does play a role in the contemporary genetic structure of these pine populations.

4.4. Seasonal and geographic variation of pollination, reproduction and fruiting of trees (Data mining and construction of data bases)

Information on flowering phenology has been collected systematically for a long time based on local observations, allergy pollen monitoring services, through modelling approaches and satellite maps (e.g. Koch *et al.* 2009; Karlsen *et al.* 2006). In the context of gene flow in forest trees, the spatial range of synchronicity between flower receptivity and pollen shed determines the spatial range over which gene flow can occur. Therefore, combining information on pollen emission and flowering dynamics at both regional and continental scales from existing databases (e.g. EAN - <https://ean.polleninfo.eu/Ean/> ; EPN - <http://www.pik-potsdam.de/~rachimow/epn/html/frameok.html>) is likely to provide a proxy for upper boundaries of effective gene flow distances. However, timing data on fruiting and seed release are very rare. Forest seed harvest information from legal regulations (EU-directive [1999/105/EG](#)) can potentially be used to infer range wide fruiting patterns, but also seed ripening and harvest times.

Specific questions to be addressed would be:

- How large are species specific geographic distances over which dispersing pollen is likely to find receptive female flowers?
- How much annual variation there is likely to be in these distances?
- How much annual variation can be observed in pollen concentration and seed production patterns?
- Identification of species and key life-history traits associated to large versus small spatiotemporal flowering windows?
- Which species/populations might have non-overlapping pollen shedding and female flowering times? This can substantially promote the rate of LDD gene flow by reducing competition with local pollen.

5. Research needs

5.1 Theoretical approaches

5.1.1. Extend models of species range evolution to the case of trees and in the context of climate change

New ecological forecast models should be developed that allow better understanding of how evolution affects extinction rates and the size and structure of species ranges in the context of global change. Analytical models provide conceptual insights into how gene flow, adaptation and biotic interactions shape species ranges in stable or changing environments (Pease *et al.* 1989; Kirkpatrick & Barton 1997; Case & Taper 2000; Goldberg & Lande 2007; Polechova *et al.* 2009; Price & Kirkpatrick 2009). Extant models, however, rarely incorporate salient features of tree life cycles, such as distinct dispersal modes or overlapping generations, which may profoundly affect their evolutionary responses to climate change.

Seed and pollen dispersal may have different consequences for population divergence and maintaining within-population diversity (Lopez *et al.* 2008) but their joint influence has never been studied explicitly in the context of climate change. While seed migration obviously limits the rate of demographic expansion, long-distance pollen movement might fuel or constrain adaptation to new conditions. Exploring this question requires modelling dispersal as a more complex process than simple homogeneous diffusion. Such modelling studies are also necessary to identify the critical features of the pollen and seed dispersal

distribution that we would need to empirically estimate, thus determining how experimental and estimation effort should be allocated.

Long generation times may preclude evolution fast enough to match climate change (e.g., Savolainen *et al.* 2004). Contrary to this prediction, however, is the observation that most tree populations have established clear latitudinal or altitudinal patterns of local adaptation during range expansion during the relatively brief period since the last glaciation (Savolainen *et al.* 2007). Overlapping generations and long generation times might instead promote high levels of genetic diversity in tree populations during re-colonization (Austerlitz & Garnier-Gere 2003), potentially allowing rapid adaptation. Selection at the juvenile stage may be particularly strong in trees given low survivorship in large, diverse, cohorts of saplings. This may allow effective adjustment to changing climate (for empirical examples see Kelly *et al.* 2003, Jump *et al.* 2006; for simulations see Kuperinen *et al.* 2010). How demography and the pace of adaptation in a changing environment depend on variation in fitness expressed before versus after sexual maturity is an open question. Stage-structured models of species responses thus appear critical for understanding demographic and evolutionary consequences of climate change specifically for tree populations.

Trait-based, mechanistic models enable predictions of species ranges under current and future climates (e.g., Morin *et al.* 2008). For instance the Phenofit model (Chuine & Beaubien 2001) predicts tree distributions based on existing phenological responses to local climate, drought and frost tolerance. Microevolutionary phenomena described above have only started to be incorporated in ecological forecast models (Kearney *et al.* 2009; Kuperinen *et al.* 2010). In particular, the joint effects of genetic correlations among traits and gene flow on adaptation (see Guillaume & Whitlock 2007, Guillaume *submitted*) have not yet been explicitly incorporated in such process-based models. There is an urgent need to include evolutionary responses in mechanistic models to understand the long-term consequences of climate change for the demography, range and functioning of forests.

5.1.2. Develop new dispersal models combining mechanistic and genetic approaches

Assessment of dispersal and gene flow by pollen and seeds has been advanced by both mechanistic and genetic approaches. Mechanistic dispersal models describe seed and pollen movement based on the characteristics of the dispersal unit, the source plant, the dispersal vector and the environment (Nathan *et al.* 2008). Their focus on the physical movement phase must be augmented by incorporating viability during dispersal (e.g., Bohrerova *et al.* 2009) and post-dispersal establishment factors (e.g., Bohrer *et al.* 2005) to discern the successful dispersal events that form the effective dispersal kernel. Genetic methods usually assess effective dispersal by fitting phenomenological dispersal kernels to parent-offspring data within populations, or by estimating immigration rates into a certain population (Broquet & Petit 2009). Genetic methods can assess dispersal (movement) *per se* (e.g., Jordano *et al.* 2007), but the insights they can provide into the underlying mechanisms are inherently restricted.

These mechanistic and genetic tools for assessing dispersal have been developed and applied virtually independently, even if they have complementary features and high synergy potential. Exploring the combination of both kinds of approach is advisable for the analysis of long-distance dispersal. For example, the ability of mechanistic approaches to assess dispersal across multiple scales complements

the problematic extrapolation of genetic methods beyond the small scale in which individuals were sampled. Genetic methods, in turn, can provide data to validate mechanistically-derived kernels, and to add the required (and often hard to measure) component of post-dispersal establishment effects needed to assess effective dispersal. For instance, mechanistically derived predictions of the relative proportion of immigrant vs. local propagule deposition into discrete forest patches or populations can be tested against independent estimates obtained using genetic assignment. More promisingly, mechanistically derived propagule transport probability functions over different distances could be incorporated into the usual probabilistic (maximum-likelihood or Bayesian) migration rate estimation procedures based solely on genetic likelihoods, which might allow jointly estimating migration rates and mechanistic parameters determining dispersal over long distances.

5.1.3. Develop the connectivity network

Notwithstanding the important merits of the dispersal kernel concept, which dominates current research on dispersal and gene flow in plants and animals, it also bears some significant disadvantages that limit our ability to accurately assess gene flow patterns over multiple spatial scales. Studies using dispersal kernels to assess gene flow inherently assume isotropy (i.e., the same dispersal kernel for all directions); yet, this assumption is unrealistic for many systems in which the dispersal vector moves in a directional manner, such as seasonal winds in a prevailing direction, downward flow of rivers, and oriented movement of animals. Lagrangian dispersal simulations can account for dispersal anisotropy by incorporating turbulence patterns (Bohrer *et al.* 2008), and hourly, daily or seasonal variation in wind direction (e.g. Wright *et al.* 2008); this computationally-intensive approach, however, is practically limited to relatively short-term small-scale applications. An alternative approach maps the connectivity between sites based on large-scale datasets and/or models available for the primary dispersal vector. This approach has been applied, for example, to assess wind connectivity of plants among islands in the southern oceans (Muñoz *et al.* 2004) and to quantify wind resistance experienced by seabirds migrating across the Atlantic ocean (Felicísimo *et al.* 2008). In principle, this approach can be adjusted to many plant species in a variety of spatial scales, if the patterns of flow or movement of the dispersal vector can be estimated. Because some key vectors such as wind, inland water systems, ocean currents and migrating birds disperse many plant species, efforts to develop vector connectivity maps could advance the study of gene flow via pollen and seeds for a large number of species.

5.1.4. Infer evolutionary changes from differentiation analysis (diachronic vs allochronic monitoring of evolutionary changes)

Evolutionary changes account for changes that accumulated over time from a given source population to the extant population and can be assessed through allochronic monitoring, *sensu* Hendry and Kinnison (1999). Allochronic approaches can hardly be implemented in trees for obvious biological constraints (but see Fallour-Rubio *et al.* 2009). Therefore diachronic approaches were preferred, which consist in comparing different extant populations that have diverged from a common source population. This is traditionally implemented in common garden experiments, or provenance tests in trees. While allochronic approaches measure evolutionary rates, diachronic approaches measure differentiation rates. Differentiation rates can only be translated into evolutionary

rates if evolutionary trajectories and times scales since the common ancestor are known (Kinnison and Hendry, 2001). When dealing with responses to climate change for extant populations we are seeking for evolutionary rates, and their indirect estimates based on past differentiation rates should be taken with caution (Gienapp *et al.*, 2008). We suggest revisiting provenance tests with the aim to estimate evolutionary rates that occurred during the Holocene during natural warming using diachronic approaches combined to historical reconstructions. Indeed, during the past decade combined phylogeographical and historical approaches have reconstructed evolutionary trajectories of European trees since the last glacial maximum in different ecological contexts (Magri *et al.*, 2006; Cheddadi *et al.*, 2006).

5.2 Development of integrated simulation approaches

Efforts should be dedicated to foster development of integrated computer simulation platforms. To date, simulation approaches are very field-specific and very few efforts have been made to integrate ecological with evolutionary and genetics modeling (but see e.g. Kuperinen & Schurr 2007, Kuperinen *et al.* 2010). There is a need now for such integration to accurately predict the impact of environmental changes on species persistence over the next century and at the continental scale. Individual-based, population genetics simulation packages already exist (e.g. *Nemo*, Guillaume & Rougemont 2006; *Metapop*, e.g. Le Corre & Kremer 2003; *simuPop*, Peng & Kimmel 2005) that could be extended to include the ecological and spatially explicit layers needed. The approach advocated integrates information over all scales, from continental range variation of ecological factors determining the strength of local adaptation to the molecular scale of genetic variation determining the rate of adaptation in local populations. It will thus feed on all aspects of the developments advocated by this research plan.

A key aspect of the modeling approach advocated here is the overlay of predictions from different processes; ecological niche and bioclimatic envelope modeling, variation of gene flow over geographical ranges, and evolutionary adaptation of local populations. The basal layer, the climatic layer, defines how changes in climatic conditions over the species geographical range modify the localization of suitable habitats (e.g., Thuiller 2003; Thuiller *et al.* 2005). The second layer describes spatial variation of pollen and seed dispersal and should integrate information from the climatic layer to model the changes of seed and pollen movements caused by climate change through modification to the dispersal kernels (e.g., Kuperinen *et al.* 2009; Nathan *et al.* in review), pollen viability (Bohrerova *et al.* 2009) or the timing of pollination and female receptiveness. The third layer integrates information from the two previous ones to predict how local populations adapt to their shifting conditions (e.g., Kuperinen *et al.* 2010). Information from the climatic layer will set the strength of selection acting on different adaptive traits by telling how far from its local optimum a population might be. Information on gene flow from the second layer will inform on hybridization rates and fitness effects, depending on the geographical origin of the migrants (e.g., Savolainen *et al.* 2007; Lopez *et al.* 2008; Yeaman & Guillaume 2009). It will also inform on the potential for colonization of new habitats. Finally, the outcome of local adaptation should be interpreted in terms of growth and persistence of local populations and how it feeds back onto the predictions of the intensity of gene flow over larger geographical scales.

Simulation approach is amenable to sensitivity and power analysis by screening

and replicating simulations over large ranges of parameter space. Results could be validated with analytical results under simple case scenarios.

5.3 Experimental approaches

5.3.1. Develop new methods to trace pollen and seed

Experiments monitoring long distance pollen and seed dispersal *in natura* are necessary both to improve empirical knowledge and to validate outputs from mechanistic models (5.1.2). Field observations, based on physical or biological traps (e.g. bait plants) were often restricted to a limited spatial scale due to (i) overlapping of the pollen/seed shadows masking LDD (ii) dilution effect (LDD is a needle in a haystack) (iii) large number of putative sources (characterizing their positions and genotypes is time- and cost-intensive). Using highly polymorphic genetic markers like microsatellites solved the first point but it is necessary to conceive new experimental designs dealing with points (ii)-(iii).

For the time being, more focus should be placed on isolated populations or trees. They proved to be experimental configurations particularly informative about LDD (Robledo-Arnuncio *et al.* 2005; Slavov *et al.* 2009). Because they are less subject to dilution effect, female plants, male-sterile or self-incompatible isolated individuals are even more adequate as trap plants for investigating pollen pool composition. A challenge would be to develop new experimental methods enabling to place such plants at specific positions during the pollination period, e.g. potted plants (see Devaux *et al.* 2007 for an example on a crop species), flowering branches kept alive or flowering grafts.

Species at low density in the landscape, scattered species or relictual populations provide favourable spatial configurations to measure LDD thanks to a restricted number of sources easier to characterize exhaustively at a large spatial scale (Bacles *et al.* 2005; Slavov *et al.* 2009). Efforts should be made in the future to identify such situations and to provide statistical analyses integrating both within and inter-sites pollen dispersal (Robledo-Arnuncio *et al.* 2009; Robledo-Arnuncio *in press*). High precision aerial photographs and satellite images could be valuable tools to retrieve all sources at the regional scale and avoid biases due to ghost populations. Using transportable trap plants in these landscapes could be particularly pertinent.

An alternative solution to characterize pollen pool composition far from sources could result from single-pollen grain genotyping (Matsuki *et al.* 2007). Although technically complex, this method provides information about pollen origin without requiring a trap plant (and thus reduces dilution effects). Generalizing this method would enable to genotype pollen from volumetric traps of the aerobiology networks (4.1) or from volumetric traps set-up at specific sites in a landscape. It could also provide information about pollen carried by insects, birds or bats (Matsuki *et al.* 2008).

It should be noted however, that the same special demographic conditions of isolated populations, which facilitate LDD assessment, may result in LDD patterns different from those expected in more general settings (e.g. in large or continuously distributed populations), where for instance the dilution effect produced by local seed or pollen sources may reduce effective LDD proportions, relative to isolated populations. Modelling approaches may help to generalize observations in isolated populations.

Further, to experimentally trace pollen or seed movement at the continental scale, a joint use of weather data, weather forecasting models and field observation of pollen/seed pools seems the most promising way (see also 4.1 and 5.1.2). Large-scale spatial characterization of presence/absence of a species, phenology, and airflows were already used to identify temporal windows ideal for LDD and relate them to the actual presence of pollen grains in physical captors (e.g. Siljamo *et al.* 2008). A next step would be to measure the diversity of origins in the effective pollen pools through the genetic and/or phenotypic diversity of the seed produced (e.g. Nilsson 1995). This would require fully characterizing the amounts of pollen emitted throughout the sources, the viability of pollen during transport and the determinants of seed set (flower density, pollination success, see also 4.1). In addition, sources should be sufficiently genetically/phenotypically differentiated in space.

5.3.2. Assess evolutionary changes due to long distance gene flow via allochronic monitoring

We strongly recommend setting up experiments that would allow assessing evolutionary changes over a few generations in trees (Reznick and Ghalambor, 2004). Such experiments would not only permit to estimate evolutionary rates, but they would also offer the unique opportunity for testing evolutionary hypothesis regarding responses to climate change (Bell and Collins, 2008). Different options can be foreseen:

- (1) Testing for the effect gene flow on the changes of population means and variance (genetic and phenotypic variances) over one generation. A straightforward design consists in conducting full sib control "hybrid" crosses between distant and close populations in comparison to "pure" within population crosses. Offspring should then be raised under controlled conditions mimicking different climatic scenarios. While more difficult to implement, because of potentially small sample sizes and unaccounted for microenvironmental variation, an alternative experiment consists in conducting the study "in situ" by comparing "natural migrants" that have been identified by parentage analysis or assignment methods and "local residents".
- (2) Testing the effects of the strength of selection over successive generations. We suggest installing short generation tree population (birch or willow) within open top chambers, and let the population reproduce under such conditions. Strength of selection can be set by manipulating conditions within the open top chambers. Outlier pollen can be supplemented at each generation to mimic gene flow.
- (3) Measuring the strength of selection at various filtering stages over the life cycle. While filtering stages (i.e. stages with strong competition and selective mortality) are well known in trees especially at the young stage (from seeds to juvenile seedlings), the impact of each stage on the population mean, the genetic variance, the allelic frequencies at adaptive relevant SNPs have only seldom been assessed.

Besides experiments established *a priori*, alternative ways of tracking evolutionary changes at contemporary time scales can be foreseen in peculiar cases where tree population transfers are well documented and mapped (Lefevre, 2004; Fallour-Rubio *et al.* 2009). In some cases these transfers actually mimicked climate changes, as populations were moved from cooler to

milder climates. Well known examples are transfers of North American tree species to Europe, whose introduced populations have differentiated in so-called land races (Douglas fir, Herman & Lavender, 1999 or Northern red oak, Daubree & Kremer, 1993), or large scale transfers of native trees in Europe (König *et al.* 2002). The method consists in establishing common garden experiments comprising offspring collected in source and transferred populations. These investigations would ideally complement the provenance test analysis, as a few generations have usually elapsed since introduction, when climate change was already occurring. Additionally, transferred populations or species have usually been deployed over larger areas than provenance tests and the transferred material has been tested in a real forestry context, rather than in experimental plantations.

5.3.3. Assess evolutionary changes due to long distance gene flow via diachronic monitoring

A key issue in predicting and managing evolutionary responses to ecological change is what proportion of trait divergence results from selection on novel mutations, from standing variation within populations, or from the influx of novel alleles due to long distance dispersal. Dependence on novel mutations is likely to generate a substantial delay before adaptation occurs, and may particularly be the case where populations are small and habitat fragmentation is high throughout the range. By contrast, adaptation resulting predominately from standing variation or from gene flow from distant populations stresses the importance of maintaining large population sizes over long periods of time, and/or routine translocations of pollen or seed between distant populations to maximise effective population size.

Population genetic analysis of the alleles and loci responsible for trait divergence in different populations allow assessment of how far novel adaptations can spread from where they arise to where they are at high fitness throughout the species' range. Barriers to the spread of advantageous alleles throughout a range will be reflected by distinct alleles or genomic regions responsible for local adaptation to different places with similar environments. Such multiple genetic bases for similar phenotypes throughout a species' range implies that the spread of advantageous alleles is limited by gene or trait interactions, or by ecological or population patchiness. Similarly, comparison of the size of the region affected by selective sweeps at a given QT locus can provide information on the rate at which the allele increased in frequency, and how this varies in different populations and under different conditions.

Another key issue is whether adaptation occurs by the establishment of novel genotypes in new habitats (colonisation), or through the spread of individual alleles across many different genetic and ecological backgrounds. Genotyping of new migrants compared to resident individuals at different life stages will allow a distinction to be made between phenotypic variation arising due to recent colonisation, gradual influx of alleles from neighbouring populations, or a novel local mutation, or novel genotypes arising due to recombination between residents.

6. Consideration of case studies

We anticipate that interactions between gene flow and selection may lead to contrasting effects on population evolutionary responses depending on the spatial, geographic and community context. Variation in the strength and

direction of selection can also be expected across a species' range, as well as in the directions and magnitude of seed and pollen flow. There is therefore an urgent need to monitor evolutionary change and gene flow in different ecological settings and contexts, in order to explore how the key ecological and genetic parameters identified in theoretical models and in previous studies interact in real populations. Study areas that are likely to provide key insight include:

- (1) Leading edge vs. rear end populations of continuously distributed species (Hampe and Petit, 2005). Populations at the leading edge are likely to be sinks for "preadapted" genes from more southern populations, and gene flow may facilitate their adaptation. On the other hand, leading edge populations may also get at least initially adapted to migration and LDD (i.e. dispersal evolution). The opposite may be true for populations at the rear end, where gene flow from interior populations may actually increase maladaptation, as generally, gene flow from better adapted populations does not exist. At the same time however, rear end populations may harbour higher levels of standing variation, potentially allowing more rapid adaptation to changing conditions.
- (2) Continuous vs patchy distribution of populations. Drift is likely to mediate the selection-gene flow interplay in the case of isolated and fragmented populations speeding up either adaptation or maladaptation.
- (3) Insect pollinated species vs wind pollinated species. Earlier flowering is expected with increasing temperature, which may generate a mismatch between the flowering period and the time that pollinating insects are active. This may limit gene flow among populations. Studies should also explore levels of genetic variation in flowering time and flower morphology, as well as in pollinator ecology, and therefore the potential for selection to offset these effects.
- (4) Comparing gene flow and selection on latitudinal vs altitudinal environmental gradients. Although selection intensities on different latitudinal and altitudinal scales can be very similar (e.g. a change of 1 °K temperature on a latitudinal scale equals 145 km but 167 m on a altitudinal scale, Jump *et al.* 2009), the amount of gene flow at these gradients is likely to be strongly different leading to contrasting interactions between gene flow and selection balance

7. References

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