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Fifty years of genetic studies: what to make of the large amounts of variation found within populations?

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1 Introduction

Determining the sources and role of intra-specific genetic variation is a classical focus of evolutionary biology (Mitchell-Olds et al. 2007). Ever since the beginning of population genetic studies in forest trees, the observation of high levels of within-stand phenotypic and, later, molecular diversity has been a commonplace. In these sessile and long-lived organisms, the maintenance of adaptive genetic and phenotypic diversity within populations seems of paramount importance, because the environment is likely to change within their life span (Petit and Hampe 2006).

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Phenotype diversity has been recurrently reported in forest trees (Borghetti et al. 1988; Cornelius 1994; Aitken et al. 1996; Howe et al. 2003; Wightman et al. 2008; O'Reilly-Wapstra et al. 2013); variability in life history traits (in particular, phenology) and adaptation to stress have consistently been a major subject in forestry. Such studies have typically focussed on variation at the regional or species range level, in relation to large-scale environmental (mostly climatic) gradients (Savolainen et al. 2007; Alberto et al. 2013). Examples abound in several tree species: to quote only a few, we may mention studies on oak bud burst (Ducousso et al. 1996), poplar leaf phenology (Hall et al. 2007), spruce bud burst and bud set (Mimura and Aitken 2010), Scots pine bud burst and frost resistance (Hurme et al. 2000) and growth performance in Spanish cedar (Navarro et al. 2004). The question of the adaptive relevance of clinal genetic variation was explicitly addressed in most such studies or underlay their experimental setup. The amount of genetically based trait variance due to differentiation between populations, as measured by Q_{ST} (Spitze 1993; Prout and Barker 1993), varies from moderate to high depending on the trait; nevertheless, a substantial portion of variance is explained by family differences within populations, as Q_{ST} is generally far smaller than one (see review for forest trees in Latta 2004). At the molecular level, intra-population variance for nuclear loci generally accounts for around 95 % of total variance, as observed by Hamrick and Godt (1990) and largely confirmed by all subsequent studies (see review in Petit et al. 2005). Early molecular marker-based studies reported, in addition to large amounts of intra-population diversity, significant fine-scale spatial genetic structure (FSGS) in several species; the first such study was performed by Brunel and Rodolphe (1985) in *Picea abies*, followed by a steady stream of publications ever since. Processes leading to the establishment of FSGS have been studied in detail in trees, and modelling of such processes has often been carried out by tree population geneticists

(Hardy and Vekemans 1999; Smouse et al. 2001; Sagnard et al. 2007). Such detailed knowledge of FSGS has mainly insisted on neutral processes: it was implicitly assumed that genetic variation was a *marker* for tracing individual relatedness, not for adaptive processes, and the question of whether within-stand genetic variation may have any adaptive meaning was only seldom asked (but see, e.g. Epperson 1992). This was reasonable, given the nature of the markers used (almost always putatively neutral), but ignored growing evidence of quantitative trait aggregation within populations (e.g. Nanos et al. 2004).

2 The adaptive meaning of local variability

FSGS studies take explicitly into account the spatial distribution of genotypes. They are the (neutral) foundation of the study of “microgeographic” processes, which focuses on evolutionary mechanism occurring within spatially structured populations (Richardson et al. 2014). The “microgeography” keyword recurrently appeared in the plant population literature, starting in the 1980s. In its broader meaning, it refers to studies carried out at geographical scales compatible with substantial amounts of gene dispersal; this spatial scale generally corresponds to the occurrence of continuous populations.

On a landscape scale, two strategies have recently been developed to relate genetic and genomic patterns of diversity to landscape features. On the one hand, environmental features and the related neutral and adaptive processes that shape genetic divergence patterns were screened using multivariate methods (e.g. reviewed in Balkenhol et al. 2009; Wang and Bradburd 2014), while on the other hand, researchers aimed to identify phenotypes and loci under selection and environmental factors driving local adaptation (Sork et al. 2013). Recent landscape genetic studies came closer to analysing the causes of microgeographic genetic variation; nevertheless, the conceptual frame of reference of landscape genomics is to compare distinct populations sampled across a gradient or in contrasting environments, rather than looking at within-stand variation, and thus cannot help explain intra-population patterns. Yet, plant population biologists have known for long that the distribution of plant species, phenotypes and genotypes can be shaped by stark environmental contrasts even at very short spatial scales: Janis Antonovics et al. have published a long series of articles both from the theoretical (Dickinson and Antonovics 1973) and the empirical point of view on heavy metal tolerance in *Anthoxanthum odoratum* at local scales (Antonovics 2006 and all the previous papers of the “Evolution in closely adjacent plant populations” series quoted therein); oat (*Avena barbata*) was also the target of similar studies, based on isozyme data (Hamrick and Allard 1972); the long-term Park Grass Experiment has shown microgeographic adaptation in-the-

making (Gould et al. 2014); the “Evolutionary Canyon” was the subject of several studies on microsite adaptation to moisture gradients at the molecular level, mostly on cereal plants (Li et al. 2000 and citations therein); more recently, Delph and Kelly (2014) provided an interpretation of plant intra-population genetic diversity as clearly adaptive; and Pannell and Fields (2014) explicitly highlighted local scale processes in their recent review on local adaptation.

3 Microgeographic variation: a neglected field in forest science

Contrary to annuals and herbs, the study of microgeographic adaptation has drawn only little attention from forest geneticists. The reasons are unclear: an early focus on provenance variation may have contributed to the generalised thought that the genetic variation among populations is the one that matters (see, for example, Morgenstern 1996). Furthermore, the long life span of trees, during which not only broad climate patterns but also local environmental conditions can change, makes it difficult to identify the specific critical moments and conditions which shape within-stand genetic structure. Finally, perhaps estimates of dispersal distances convinced the forest genetics community that selection would be systematically overridden by gene flow at spatial scales smaller than the landscape, and the advent of neutral theories (Kimura 1985; Hubbell 2001) pushed forest scientists to favour a view in which selection is rarely observed. Even though microgeographic adaptation studies in trees have been historically rare, forest science has consistently (and sensibly) supported the idea that maintaining high within-population genetic diversity (or large population sizes, which is a prerequisite for intra-population diversity) is a major target in the conservation and management of tree populations (e.g. Lefèvre et al. 2013). Populations must maintain sufficient levels of diversity to ensure survival, but the understanding of the origin and mechanisms underlying the maintenance of such large amounts of diversity within forest stands is limited. Moreover, the “option value” of genetic diversity (i.e. the idea that given that we do not know which combinations of genetic variants will be favoured by future selection, the best strategy is to preserve as much diversity as possible; Koskela et al. 2013), while intuitive and strongly supported by quantitative genetics theory, has not been rigorously demonstrated. Proving experimentally that some level of genetic diversity increases fitness in forest trees is elusive, because one should be able to tear apart population-level and individual effects; to prove such effects, one should manipulate diversity and perform long-term monitoring of the evolution of fitness in multiple, distinct environments (Hughes et al. 2008), which can be extremely difficult with long-lived forest trees. At the heart of the study of population-level genetic diversity in trees, there

seems to lie a conundrum: we often explain its existence with purely neutral considerations, yet the “genetic diversity option value” tenet links long-term maintenance of forest stands (that is, their fitness) to their levels of genetic diversity. How can this be? Add to this that the heritable basis of several fitness-related traits has been known for decades, and the knowledge gap becomes self-evident: we know that there is ample within-stand diversity, we know that some substantial part of phenotypic diversity is heritable and we assume that diversity is the fuel of adaptation, but we do not know how to relate such variation to current or past adaptive processes in natural stands. So, how should this large genetic diversity be interpreted and managed? Has it got any adaptive meaning? How to prevent losing the portion that “matters”, if any? Keeping overall high levels of genetic diversity within populations, in accordance with option value arguments (see Jump et al. 2009), is sensible conservation-wise but suffers from two possible flaws: it does not provide any guidance in case we need to make “no regret” choices (a highly probable scenario given limited resources), and it assumes that all we know about past and current selection is useless to predict future evolution. To overcome these limitations, we need to understand to what extent standing genetic diversity is maintained by adaptive processes and how to develop targeted measures to preserve, or engineer, adaptation in a precise manner and over short time spans. Besides the fundamental endeavour of acknowledging the role of selection in shaping local variability patterns, such questions have also an applied side: managing diversity by “keeping as much as possible” is a blunt tool; if we have to act here and now to preserve forests in the context of rapid global change, we better hold a scalpel, to complement general genetic diversity preservation strategies with specific, more refined actions.

4 Microgeographic variation in forest trees: state of the art

What do we know about the adaptive significance of within-stand genetic diversity? How much of it is shaped by environmental variation and adaptation? First, let us look at the larger picture: are tree species distributed according to any environmental parameter varying at the geographical scale of individual trees? There are some reasons to think this is the case, at least in landscapes displaying microgeographic variation in parameters affecting tree fitness. John et al. (2007) have shown that soil properties can explain a non-negligible portion of the spatial distribution of tree species in tropical forests in Panama, Colombia and Ecuador. At higher latitudes, soil depth and clay content in typically sandy soils determines the presence of either *Pinus pinaster* or *Pinus pinea* in continuous mixed conifer forests in central Spain (Allué and Allué 1994). These examples illustrate that neutral processes

are not sufficient to explain species distributions, even at small spatial scales. It is not a big conceptual leap to imagine that the same holds true for genotypes within populations of a single species, given that within-population phenotypic variance can be as large as, or larger than, interspecific variance (Bangert et al. 2005; Shuster et al. 2006; Brousseau et al. 2013). Proofs that microgeographic environmental gradients and contrasts influence genotype and phenotype distribution are rare but consistent: examples are known from a variety of species and habitats. Table 1 summarises the microgeographic studies in forest trees described below. In Engelmann spruce (*Picea engelmannii*), Mitton et al. (1989) found association between genotypes at the phosphoglucosyltransferase (PGM) isozyme locus and drought stress in sub-populations separated by few tens of metres; the same research group found associations between isozyme genotypes at the glycerate dehydrogenase (GLY) locus and stomatal size, on the one side, and soil moisture, on the other side, in pinyon pine (*Pinus edulis*) over distances in the order of hundreds of metres (Cobb et al. 1994; Mitton et al. 1998); Kelly et al. (2003) found that a single birch (*Betula pendula*) stand could be sorted into genetic groups associated to temperature at seedling establishment, according to 358 amplified fragment length polymorphism (AFLP) markers. In a similar study, in European beech (*Fagus sylvatica*), Jump et al. (2006) found one AFLP marker (out of 254 screened) associated with spatial and temporal variations in temperature at seedling establishment and differentiation between sub-populations less than 3 km apart; in the same species, Pluess and Weber (2012) found three AFLPs (among 517) associated with moisture across populations separated by only 0.5 km, and Csilléry et al. (2014) identified contrasted signatures of selection for multi-locus single nucleotide polymorphism (SNP) combinations in a set of 546 SNPs from 53 climate response genes, in sub-populations sampled over an elevation gradient spanning less than 5 km. A similar study in Norway spruce (Scalfi et al. 2014) found two SNP loci (out of 384) associated with elevation; Brousseau et al. (2013) found extensive divergence for functional traits in contiguous sub-populations of tropical *Eperua falcata* and *Eperua grandiflora*, interspersed and located on seasonally flooded or vertically drained soils; in the same populations of *E. falcata*, Audigeos et al. (2013) found that genotypes and alleles were associated to soil type at eight out of 88 SNPs from seven candidate genes and for three of the same genes at the haplotype level. In a further study, six AFLP markers out of about 1,200 were found to be divergent between sub-populations of the same species, submitted to the same environmental contrasts (Brousseau et al. 2015). In *P. pinaster*, Vizcaíno-Palomar et al. (2014) found higher fitness (as evaluated by survival in the field) for seedlings sampled from a foreign population growing in harsher climate than for those from the local population but only in particular microenvironments (Vizcaíno-Palomar et al. 2014); in this same species,

Table 1 Summary of the studies about microgeographic genetic variation in forest trees

Species	Genetic marker	Phenotype	Environmental factor	Scale (km)	Citation
<i>Eperua falcata</i>	–	Functional traits	Soil moisture	<0.5	Brousseau et al. (2013)
<i>Eperua grandiflora</i>	–	Functional traits	Soil moisture	<0.5	Brousseau et al. (2013)
<i>Pinus edulis</i>	Isozymes	Functional traits	Temporal soil moisture variation	<0.1	Cobb et al. (1994)
<i>Pinus edulis</i>	Isozymes	Stomatal size	Soil moisture	<0.6	Mitton et al. (1998)
<i>Picea engelmannii</i>	Isozymes	–	Drought stress	<0.1	Mitton et al. (1989)
<i>Betula pendula</i>	AFLPs	–	Temperature at seedling establishment	<0.2	Kelly et al. (2003)
<i>Fagus sylvatica</i>	AFLPs	–	Elevational gradient and temperature at seedling establishment	<3	Jump et al. (2006)
<i>Fagus sylvatica</i>	AFLPs	–	Moisture	<0.5	Pluess and Weber (2012)
<i>Eperua falcata</i>	SNPs	–	Soil moisture	<0.4	Audigeos et al. (2013)
<i>Eperua falcata</i>	AFLPs	–	soil moisture	<0.4	Brousseau et al. (2015)
<i>Pinus pinaster</i>	SNPs	–	Elevational gradient	<1.8	Budde (2014)
<i>Picea abies</i>	SNPs	–	Elevational gradient	<2.6	Scalfi et al. (2014)
<i>Fagus sylvatica</i>	SNPs	–	Elevational gradient	<5	Csilléry et al. (2014)

Budde (2014) found association between individual genetic distance and small elevation differences in a continuous forest, independent of geographic distance. These studies indicate that microgeographic variation contributes to shape within-stand genetic structure. Most of them explicitly showed that local adaptation occurs and can be detected, provided that the necessary trait, genetic and environmental information are gathered. The approach shared by all these studies is straightforward: identify an environmental gradient or contrast and look for genotype- (or trait-) environment associations. Note that these gradients, although identified by a single variable, probably represent bundles of correlated variables (e.g. soil moisture is associated with soil fertility and concentration of particular compounds, and elevation is associated with water availability and soil structure).

The analysis of microgeographic adaptation can also be undertaken with trait heritability as a starting point, focussing on intra-population genetic variation for fitness-related traits. In this case, the rationale is that variance in such traits may indicate different coexisting optima—a sign of spatially or temporally variable selection and adaptation. Some pioneering studies have shown that natural forest populations studied in situ display heritability for fitness-related traits, such as chemical traits associated to herbivore resistance in eucalypts (O'Reilly-Wapstra et al. 2013) and white spruce (Mageroy et al. 2014), serotiny and growth traits in Mediterranean pines (Budde et al. 2014; Alía et al. 2014) and leaf functional traits in cork oak (Ramírez-Valiente et al. 2014). More results of the same kind are available in beech (Bontemps et al., in preparation). These studies show that there is a sizeable amount of additive variance in adaptive traits expressed in natural populations, which can be modelled by natural selection.

5 How much selection?

Is natural selection on adaptive traits enough to explain the divergence patterns described above? Or is it reinforced by life history or neutral processes? And what portion of within-population genetic diversity is typically maintained by natural selection? Phenological divergence by differential response to environmental cues can promote restriction of gene flow (Soularue and Kremer 2012), which in turn can promote adaptive divergence, which could reinforce isolation (isolation-by-adaptation; Nosil et al. 2008), and limitations to dispersal of both pollen and seeds may contribute to reinforce directional selection processes that would be otherwise too weak, such mechanisms would not only induce divergence at several (combinations of) adaptive loci but also promote divergence at the genome level, mimicking widespread selection. It is therefore very likely that most polymorphisms found in a population are effectively neutral and that most within-population divergence patterns are maintained by neutral processes (Ohsawa and Ide 2008). One of the biggest empirical (and methodological) challenges here is to distinguish genuine adaptive processes from neutral processes and from neutral processes enhancing or generalising (to the genome or to other traits) the effect of adaptive processes. Another limitation is that the intensity and direction of selection are likely to vary in time, both because different life stages can have different fitness optima and because environmental conditions change over the life span of an individual tree. These factors can seriously limit our ability to detect selection; however, if we are able to setup studies taking into account temporal data (e.g. Jump et al. 2006) and multiple life stages (e.g. Alía et al. 2014), the breakdown of effects of selection into

temporal and ontogenetic components should be possible. Note that forest trees, with their clear-cut life stages and long life cycle, are rather well-suited for such an approach.

The studies cited above prove that genetic diversity at the allelic, genotypic, multilocus or trait level is associated to environmental heterogeneity (Yeaman and Jarvis 2006). Detailed knowledge on how the environment varies in space and time is often lacking at fine spatial scales, and we may miss major relationships between genetic and environmental heterogeneity just because we have characterised the former but not the latter. The current and historical focus on large-scale patterns may actually be the result of constraints in the availability (and accessibility) of environmental data at the local scale. The amount of genetic variants found to be linked to microgeographic environmental variation is expected to increase as we acquire better data on environmental variables, i.e. microgeographic environmental data currently act as a “limiting factor”. A similar argument holds for genetic studies typically based on relatively few traits (<5) or genetic markers (<1,000). New phenotyping capacities (but see below) and the astonishing increase of genomic resources made recently available for forest trees will contribute to the identification of additional links between genetic divergence and environment. This will nevertheless fulfil only part of the task: as already stated above, part of the environment–genotype and environment–trait relationships that will be detected will occur by chance or due to neutral processes. We will need to finely assess false discovery rates and appropriately take demographic (e.g. dispersal) parameters into account. It is likely that the last word on adaptive processes will come from a combination of methods, necessarily including experimental approaches and/or functional validation steps which are often neglected in forestry field.

We do not know how common intra-population divergence may be, and it is likely that underpowered studies having sought environment-related genetic patterns, and having found none, have never been published. Yet compared to the common-sense intuition that adaptive patterns should be really hard to detect at such short scales, the few studies quoted above have found such patterns with relatively simple off-the-shelf methods and in a multiplicity of forest environments, from temperate to tropical. This may indicate that, if studied with sufficient power, more case studies may show habitat-related genotype and phenotype distributions, suggesting widespread microgeographic adaptation. Nevertheless, one should keep in mind that studies with very large sample numbers, genotypes, traits and environmental data are unlikely to arise soon, and therefore statistical power will be limited. Experimental design will have to take this into account, with special attention to the problem of multiple testing of potentially non-independent effects.

6 Perspectives

Accurately characterising microgeographic adaptive processes in such large, long-lived organisms as trees will not be an easy task, but if we are to explore the adaptive potential to future environmental change that resides in standing genetic variation, this goal is inescapable, because 95 % of a tree’s genetic variability resides within populations. The first goal will be to assess how common and how strong intra-population selection is. Next, we will need to turn this knowledge into policies, if we are to manage adaptive diversity; this requires the intermediate step of evaluating how easily we can drive adaptive processes. Several advances may help us acquiring a better understanding of microgeographic adaptive variation. One is obviously the widespread implementation of high-throughput genotyping methods (currently restricted to tree species with large commercial value), which will permit the fine screening of genomic variants. As it is likely that selection may target multilocus combinations rather than individual polymorphisms (Le Corre and Kremer 2012; Csilléry et al. 2014), methods to detect selection taking multilocus combinations into account should be sought. More efficient methods to characterise functional traits *in situ* will also be required to identify the major environmental axes along which genetic differentiation occurs, and there is a great need for the development of phenotyping methods that are able to handle large number of individuals and traits; some options were reviewed by Houle et al. (2010), but such methods are still restricted to model species. To make this task more feasible, broadly defined groups of “candidate” traits may be identified. An educated guess is obviously to start from those traits that can respond strongly and rapidly to environmental variables changing over microgeographic distances (e.g. soil hydromorphy, composition and fertility and biotic interactions, particularly with microorganisms). To quote only a couple of traits, leaf nitrogen content and specific area covary with soil composition and fertility (Ordoñez et al. 2009; Orwin et al. 2010). Furthermore, the identification and characterisation of the environmental factors underlying genotypic and phenotypic variation is crucial. Multivariate methods (such as redundancy analysis (RDA), partial Mantel tests or multiple regression of distance matrices (MRDM), reviewed in Balkenhol et al. 2009) have been mostly used to detect relationships between genetic structure and environmental factors at the landscape scale (Gram and Sork 2001; Eckert et al. 2010; Manel et al. 2012; Orsini et al. 2013), but they have already proven useful at a microgeographic scale (e.g. Andrew et al. 2012) and could be promising to test within tree populations (Budde 2014). Finally, population dynamics models integrating all aspects of dispersal and selection, including the genetic and environmental basis of traits and their impact on fitness (Oddou-Muratorio and Davi 2014), will be very useful to estimate the strength of selection processes and

to evaluate the efficiency of management policies over few generations. If we succeed in getting access to these pieces of information, and to merge them into a unified view of population processes, then we will hold a very powerful analytical and applied tool for forest evolutionary biology and ecology and for helping to manage forests in a sustainable way.

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