

CLIMATE CHANGE AND SPECIES RANGE SHIFTS

Genetic divergence in forest trees: understanding the consequences of climate change

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Summary

1. Predicted climate change is heading in many respects into untested environmental conditions for trees and to the reshuffling of species distributions. We explore the consequences that these changes are likely to have on population differentiation of adaptive traits. Superimposed on the spatial redistribution of the species, will there be a redistribution of their genetic variation?

2. We base our predictions on a conceptual framework, whose elements are the extant differentiation, and the predicted divergent evolution of populations along purposely chosen altitudinal/latitudinal gradients. We consider simultaneously phenotypic and genetic divergence, but emphasize genetically driven population differentiation. We illustrate phenotypic and genetic patterns of variation with examples from well-studied northern and southern hemisphere tree genera *Quercus* and *Eucalyptus*.

3. Most phenotypic traits show very large *in situ* clinal variation with variation in altitude or latitude. Genetic clines detected in common gardens usually follow the observed *in situ* phenotypic clines, reflecting cogradients. Rare counter gradients have also been detected, where phenotypic and genetic clines exhibit opposing signs. These patterns suggest that plasticity and selection contributed in most cases synergistically to the extant differentiation.

4. We anticipate that microevolutionary processes will be different along environmental gradients. At the leading edge, availability of newly suitable habitats will trigger migration favouring genotypes equipped with colonists attributes. At the rear edges of the distribution, populations will be submitted to strong selective pressures favouring genotypes capable of withstanding drought and heat stress. Central populations will benefit from the plastic response of trees that will temporarily compensate for the maladaptation, until genetic adaptive variation will be restored by gene flow, mutation or recombination.

5. We make predictions about future differentiation along environmental gradients, by highlighting traits that are likely to diverge, the rate at which differentiation will take place, and the role of gene flow and hybridization. We envisage that parallel selection may maintain differentiation at extant levels, whereas divergent selection will promote substantial differentiation for traits facilitating adaptation to contrasting conditions along the environmental gradient. We anticipate that genetic divergence may occur very rapidly and will be enhanced by the multilocus architecture of most adaptive traits.

Key-words: altitude, clines, cogradients, countergradient, divergent selection, gene flow, genetic differentiation, hybridization, microevolution, plasticity

Introduction

Based on climatic predictions, key changes to be imposed on the extant forest ecosystems will involve increasing

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temperatures combined with varying degrees of increasing or decreasing precipitation. These changes are expected to modify the distribution of tree species. For example, over the next 100 years bioclimatic envelopes of forest species in Europe are predicted to be shifted northwards and

eastwards from 300 to <800 km (McKenney *et al.* 2007). Major latitudinal and/or altitudinal shifts in the climatic envelopes of forest tree species have been similarly predicted on most continents (Hughes, Cawsey & Westoby 1996; McKenney *et al.* 2011), although there are uncertainties at the regional scale (McKenney *et al.* 2011). Beyond predictions, latitudinal and altitudinal migration have been already observed at the leading edge (Lenoir *et al.* 2008). At the rear end of distributions, an increased risk of tree mortality due to drought and heat stress is predicted for many forests globally (Peñuelas & Boada 2003; Allen *et al.* 2010). Such effects are already seen in the contemporary tree flora of most continents (Calder & Kirkpatrick 2008; Ikeda *et al.*, in press). Tree mortality may lead to local extinction, but on the other hand mortality may open opportunities for more rapid generation replacement and enhance the probability of genetic adaptation (Kuparinen, Savolainen & Schurr 2010). Finally, these changes are heading in many respects into untested environmental conditions for trees due to superimposition of global climate change on elevated [CO₂]. Our concerns in this article are the genetic consequences resulting from such changes. Will climate change increase or decrease, or redistribute the phenotypic variation that we observed in extant populations along environmental gradients? Superimposed on the spatial redistribution of the species, will there be a likely redistribution of their genetic variation for adaptive traits? What are the likely consequences of these changes on the evolutionary responses of the species as a whole? We address here the effects of climate change on population differentiation. Anticipating the future organization of a species' genetic diversity has important fundamental and applied implications. On the one hand, it will allow identify key evolutionary processes shaping future diversity, but on the other, it may help to guide management actions including the need for investment in potentially expensive and untested translocation actions (Frascaria-Lacoste & Fernández-Manjarrés 2012).

To explore the redistribution of genetic differentiation, we will proceed in three steps. First, we limit our investigations on genetic differentiation occurring over altitudinal and latitudinal gradients. These environmental gradients have been most widely investigated in forest genetics, and our conclusions will be reinforced by the comparative analysis across different species (Read *et al.*, in press). The robustness of the observed population responses to these major environmental gradients are enhanced when parallel patterns are observed at a local, regional and global scale and across phylogenetically independent systems. Furthermore, changing latitude and altitude provide surrogates to help predict the microevolutionary, adaptive response to future temperate increases. Secondly, we consider a generic conceptual framework that would allow us to make predictions about future differentiation. Essential elements of the framework are the extant level of genetic differentiation between populations, and predictions of ongoing and future microevolution in different parts of the environmen-

tal gradient. We therefore overview the extant genetic-based responses of tree adaptive traits to these major environmental gradients and explore how these responses may be enhanced or constrained in the future. Understanding and predicting the microevolutionary response to such environmental changes is extremely complex as (i) trees are foundation species embedded in a complex network of intra- and interspecific biotic interactions (community context – Whitham *et al.* 2006; Ikeda *et al.* in press), which in cases may override abiotic responses (Pautasso *et al.* 2010); and (ii) evolutionary response to strong environmental gradients is likely to involve multidimensional changes to the phenotype and will be potentially constrained or enhanced by a network of multitrait interactions (Hellmann & Pineda-Krch 2007; Anderson, Panetta & Mitchell-Olds 2012). Finally, we attempt to assemble the knowledge gained from past and ongoing microevolution to make prediction about the future population differentiation along the altitudinal/latitudinal gradients. Each of the three steps will be illustrated by results obtained from well-studied northern hemisphere tree genera *Quercus* (Fagaceae family; commonly termed oaks), which are foundation species of many European forests, and the southern hemisphere genus *Eucalyptus* (Myrtaceae family) that dominates woodlands and forests of the Australian continent. We use these phylogenetically and geographically independent forest tree systems to illustrate our predictive framework, rather than attempt a detailed review of genetic divergence in trees. We additionally make comparisons between the two genera to investigate uncertainties of our predictions. *Quercus* and *Eucalyptus* show similarities in many evolutionary processes and population features. In both genera, species often co-occur in mixed stands or along ecotones, population sizes are often large, and interspecific hybridization is frequently reported. Most extant oak populations in central and Northern Europe stem from recent post-glacial colonization. While *Eucalyptus* occupancy of its current range on the Australia continent is more complex, many of the extant subalpine forests of southern-eastern Australia are similarly the result of recent post-glacial colonization of mountains from lower altitude refugia.

Conceptual framework for predicting future genetic divergence among populations

Our objective is to provide elements to predict future divergence (D_f) resulting from climate change (Fig. 1). Divergence accumulates as a result of environmental and evolutionary processes over a given time span (single or successive generations) acting on different populations distributed throughout heterogeneous environments, for example in a given spatiotemporal context. In northern temperate regions latitudinal and/or altitudinal distribution often frames the spatial context where evolutionary processes and mechanisms have mainly been investigated in trees (Alberto *et al.* 2013). Latitudinal and altitudinal

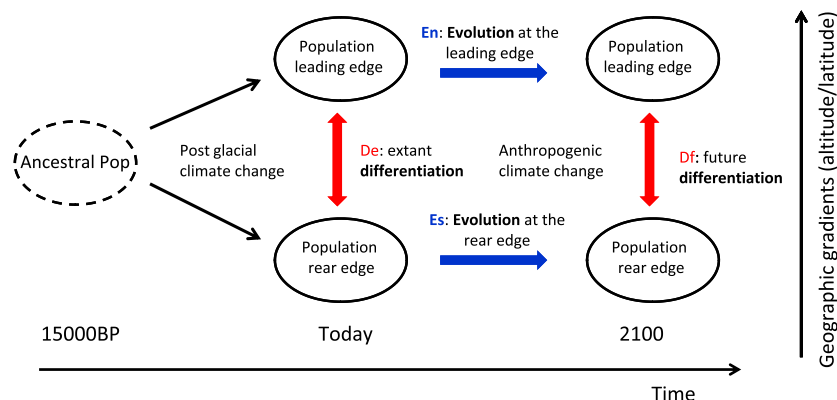


Fig. 1. Conceptual frame for predicting future adaptive differentiation in the context of climate change. Future adaptive differentiation (Df) triggered by climate change will be the result of three major contributions: (i) the level of extant differentiation (De), (ii) the evolutionary shifts occurring in different parts along the environmental gradient (De and Df) and (iii) the contribution of gene flow occurring along the gradient. Differentiation between extant populations has accumulated since their separation from their common ancestor, which in temperate zones is for many tree species a refugial population at the last glacial period (15000 BP). As a result De shares some common causes with Df as divergent selection due the climate change (natural warming for De and anthropogenic climate change for Df). This is why elements for predicting Df may be obtained from the patterns of distribution of genetic variation discernible in extant populations (co- versus countergradient variation for example).

environmental gradients are of special interest because they are driven partly by temperature variation and thus extant observed divergence between populations results from past environmental climate changes (Frenne *et al.* 2013; Read *et al.*, in press). Such gradients involve a holistic change in the selection environment, not only involving temperature, but multiple abiotic factors such as water availability, radiation and wind exposure; as well as the biotic environment (Potts & Jackson 1986; Montesinos-Navarro *et al.* 2011). Latitudinal/altitudinal gradients reproduce spatially the complexities of environmental variations that are likely to occur temporally over the next few decades. Substituting space for time offers therefore a unique experimental setting to explore past and future evolutionary responses to climate change (Anderson, Panetta & Mitchell-Olds 2012). In the southern hemisphere, Australian temperate forests systems are similarly structured by latitudinal and altitudinal gradients in temperature but superimposed on strong aridity gradients impacting water availability, drought and high temperature stresses and fire risk. While altitudinal and latitudinal gradients are both driven by temperature variation, they differ notably for other environmental cues, but we will mainly use examples from the former gradient. Populations sampled along altitudinal gradients are spatially closer, and thus are more likely to stem from a recent common ancestor and are more exposed to gene immigration from divergent populations. As a result, observed genetic differentiation is essentially driven by local but divergent adaptation. In what follows and to avoid any confusion about altitudinal or latitudinal limits between the two hemispheres, we will use the terms leading edge and rear edge to designate the limits of the natural distribution that are expanding or retracting due to climate change whether it is along an elevation or a latitudinal gradient. The time-scale that we propose

corresponds to the span that is generally considered by IPCC (from today to 2100).

In Europe, oaks are major components of broadleaved forest. They are widely distributed from the southern Mediterranean edges to the boreal limits. Throughout their distributions, oaks exhibit very large phenotypic and genetic variation that has been explored since decades either in provenance tests (Kleinschmit 1993) or by molecular methods (Kremer *et al.* 2012a). Oaks are ideal species for tracking past and contemporary evolutionary change. Their post-glacial history has been reconstructed in detail by a combination of genetic and historical approaches (Petit *et al.* 2002a,b). The variation in extant oak populations has been monitored extensively from the molecular to the phenotypic level, making it possible to document spatial and temporal differences in genetic diversity across Europe (reviewed in Kremer *et al.* 2010). More recently, a series of investigations disentangled environmental from genetic influences on functional traits along altitudinal gradients within two valleys in the Pyrénées (Vitasse *et al.* 2009a,b, 2010; Bresson *et al.* 2011) and provide experimental support to our predictions in this paper.

The southern hemisphere eucalypts (comprising genera *Eucalyptus* and *Corymbia* and more than 800 taxa) are the dominant trees of most native woodlands and forests of Australia, as well as being widely planted throughout the world (Grattapaglia *et al.* 2012). They are normally evergreen, broadly adapted and naturally occupy habitats from sea level to the alpine tree line, from temperate and arid zones to the high rainfall subtropics. Eucalypts range from towering dominants in wet forest, including the tallest angiosperm species in the world (Grattapaglia *et al.* 2012), to the small mallees and shrubs of dry and high country (McGowen *et al.* 2001). As with oaks, the genetic differentiation within numerous eucalypt species has also been

studied using quantitative (Potts & Wiltshire 1997) and molecular (Byrne 2008; Grattapaglia *et al.* 2012) genetic approaches. Being subject to domestication globally for more than a century, the literature abounds with reports of common environment, field trials demonstrating provenances differentiation and provenance \times environment interactions for fitness surrogates (Potts & Wiltshire 1997; Hamilton *et al.* 2011). Eucalypt species exhibit adaptations to a great diversity of abiotic and biotic stresses, including cold temperatures, drought and a multitude of pests and diseases (Teulière *et al.* 2007). Adaptive divergence within species in response to spatial variation in such stresses is well documented at multiple scales: from the steep local clines associated with exposure to the alpine (Potts & Jackson 1986; McGowen *et al.* 2001) or coastal (Foster *et al.* 2007) environments, through to broad-scale rainfall (O'Brien, Mazanec & Krauss 2007) and latitudinal (Dutkowski & Potts 1999; Stackpole *et al.* 2011; Hamilton *et al.* 2012) clines.

Mechanistically, future divergence (D_f) depends on the level of today's divergence (D_e) and on the evolutionary responses of populations located along the gradients (E_n and E_s) (Fig. 1). Essentially assessing D_f would require comparison of the level of divergent selective pressures between today and 2100. Will selection pressures be different along the gradient? And how will the divergent selection pressures be counterbalanced or enhanced by gene flow and other evolutionary forces? Predictions of E_n and E_s remain largely speculative: for obvious practical reasons, experimental data are lacking, and only theoretical expectations have been explored. The only component of D_f that can be immediately accessed is the extant genetic divergence (D_e) that can be assessed in common garden experiments that have been installed. We will provide examples of D_e for key growth and functional traits that have been extensively investigated in oaks and eucalypts. The main objectives are to overview extant divergence (D_e), to show how extant divergence can contribute to future adaptation (E_n and E_s) and finally to address the future divergence (D_f).

We make a clear distinction between phenotypic and genetic divergence. While phenotypic divergence can be monitored by *in situ* observations in extant natural populations, genetic divergence can only be detected in common environment or reciprocal translocation experiments (Gienapp *et al.* 2008). Phenotypic divergence between two populations in the wild results from their genetic divergence, for example differences in genetic composition of the two populations, and from environmental differences between the two sites. The former is caused by various evolutionary processes modifying gene frequencies and effects, while the latter results from the ability of the same population to respond differently to environmental changes, which is 'phenotypic plasticity' expressed here at the population level. While only genetic divergence is of evolutionary relevance and may contribute to future adaptation (De Jong 2005; Nicotra *et al.* 2010), the adaptive

role of plasticity cannot be entirely dismissed (Chevin & Lande 2010). Plastic responses of genotypes facing new environmental conditions may act as a transient stepping stone to later adaptation, once genetic variation supporting adaptation has been restored by gene flow, mutation or recombination (Ghalambor *et al.* 2007; Crispo 2008). Evidence for genetic-based adaptive differentiation along altitudinal/latitudinal gradients comes from the demonstration of repeated patterns of genetic differentiation across independent species, fitness differences in reciprocal plantings established along environmental gradients or in controlled environments, as well as demonstrated links with functional traits, and cohort analysis. Even when genetic-based divergence has been demonstrated in such experiments, proving that the observed divergence in a specific trait is adaptive and what specific selection forces has shaped this divergence in functional traits is not a simple matter (Conover & Baumann 2009), but is easier along altitudinal gradients for reasons mentioned earlier. Such divergence could be due to genetic drift, and, as environmental and geographical gradients are often linear and parallel, the effects of historical migration and gene flow need to be separated from those of natural selection in shaping the observed pattern of genetic variation (Kremer *et al.* 2002). This is further complicated by the highly integrated nature of the phenotype and the networks of genetic correlations among functional traits, which may arise through pleiotropy or linkage. Genetic divergence in a functional trait may thus arise indirectly through selection acting on a genetically correlated trait. Under such circumstances, further evidence is required to unravel the effects of direct and correlated responses, although if the genetic architecture remains unaltered both direct and correlated responses are an integral part of the microevolutionary response to climate change (Hellmann & Pineda-Krch 2007).

Extant phenotypic and genetic divergence along environmental gradients (D_e)

Large continuous phenotypic differences in multiple traits can be invariably observed in the wild as oaks and eucalypts traverse gradients in latitude (Dutkowski & Potts 1999; Kleinschmit 1993) and altitude (Potts & Reid 1985a; Bresson *et al.* 2011). In extreme cases, this may involve a transition from the tree to shrub habit in the more stressful environments (McGowen *et al.* 2001) and may even occur over short spatial distances (Fig. 3). Such changes in phenotype may be due to phenotypic plasticity, genetic divergence or a combination of both. While there is increasing focus on laboratory-based molecular approaches to understanding the genetic component to this variation, with the large size and longevity of trees, the tried and tested approach of provenance/progeny/clonal testing of germ-plasm transferred to common environment field trials is a well-established and widely used approach in forest tree studies and is our focus. In such trials, replication and randomization of genetic entries are the key to unravelling the

quantitative genetic architecture underlying variation in the tree phenotype, and multisite testing the key to understanding the relative importance of genetic and environmental contributions to the phenotypic differences observed in natural populations along environmental gradients. Although studies directly comparing phenotypic to genetic patterns are common for herbaceous plants, phenological and ecophysiological traits of trees measured in natural conditions have been rarely investigated in concert with measurements of their progeny or clones in common garden experiments (but see Cordell *et al.* 1998).

When both experimental approaches were undertaken, *in situ* phenotypic clines can be different from genetic differences observed under common environment conditions. For example, in temperate conifers, populations from northern latitudes flush later than population from southern latitudes, because bud burst is temperature dependent (reviewed in Alberto *et al.* 2013). However, under common environment conditions, northern populations flush earlier and southern populations later. Such patterns of variation have been called countergradient because phenotypic and genetic gradients exhibit opposite signs (Conover & Schultz 1995). In contrast, cogradients refer to phenotypic and genetic gradients that show parallel response to environmental gradients (Figs 2 and 3 for examples in oaks and eucalypts). In other words counter- and cogradients correspond therefore to cases where plasticity and selection contribute in antagonistic or

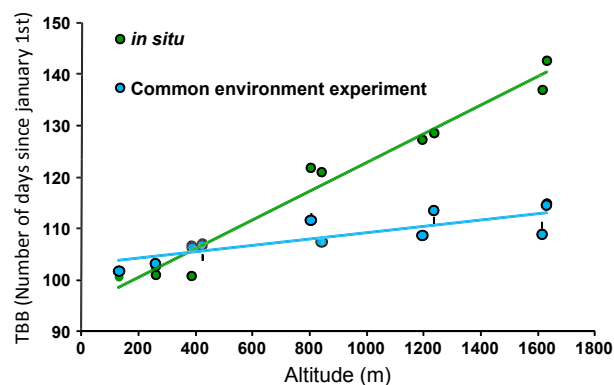


Fig. 2. Cogradients variation of the timing of bud burst in *Quercus petraea* (modified from Alberto *et al.* (2011) and Soularue & Kremer (2012)). The timing of bud burst (TBB) was recorded in sessile oak (*Quercus petraea*) stands located along two valleys on the northern side of the Pyrénées mountains, as the number of days since January 1st (Y axis). Similar observations were made on open-pollinated progenies collected in the same stands but raised under common environments at low altitude. *In situ* (green dots on the graph) and common garden assessments (blue dots) follow the positive linear variation as a function of altitude. This example illustrates a cogradients pattern of variation, because the slopes of the phenotypic and genetic clines share the same sign. Countergradient variation corresponds to cases where signs of the two slopes are opposite. In this example, the slope of *in situ* variation is much steeper, thus suggesting that plasticity prevails over genetic effects. In the *Eucalyptus* example (see Fig. 3), the two slopes are more similar.

in synergistic ways to adaptation. In most cases, adaptation will be accelerated by cogradients variation and restrained under countergradient variation (Crispo 2008; Conover, Duffy & Hice 2009).

Plasticity is a major cause of phenotypic differentiation observed *in situ* in functional traits between wild populations distributed along environmental gradients, affecting not only mean values but also relationships among traits (e.g. leaf traits in eucalypts – Warren *et al.* 2006). Phenotypic plasticity contributes to temperature acclimation for photosynthesis reported in *E. pauciflora* from the Australian Alps (Slatyer 1978), as well as for growth, plant form, internode length and leaf size of *E. gunnii* grown along an altitudinal gradient in Tasmania (Table 2). In a reciprocal transplant experiment in the Pyrénées mountains, all studied traits displayed significant altitudinal trends for sessile oak and beech. Most of the traits exhibited linear clinal variation (Vitasse *et al.* 2010), while a few (leaf size and $\delta^{13}\text{C}$, a surrogate of water use efficiency) show a quadratic response to altitude (Table 1). The degree of plastic response to an environmental change varies with genotype and plant trait (Hovenden & Vander Schoor 2006). However, for oak, no difference in the magnitude of phenological plasticity has been found among populations from different altitudes for phenological traits (Vitasse *et al.* 2010). In addition, the occurrence of countergradient clines for leaf senescence (Table 1) demonstrates,

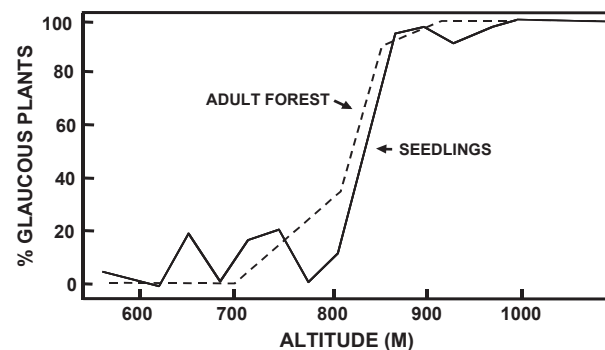


Fig. 3. Cogradients variation of leaf glaucousness in *Eucalyptus urnigera* (modified from Barber & Jackson 1957). Leaf glaucousness was assessed *in situ* (adults) in *Eucalyptus urnigera* along a steep altitudinal gradient on Mt. Wellington. The same assessments were made on open-pollinated progenies (seedlings) grown in a low-altitude nursery. The transition occurs from predominantly green to glaucous phenotypes over <200 m altitude and 1 km ground distance. The glaucousness is due to a waxy layer covering the surface of leaves which reflects radiation as well as prevents leaf surface wetting. These attributes are advantageous in protecting the plants from low-temperature damage in open high-altitude forest but disadvantageous in the lower light, competitive environment in the closed low-altitude forest. The glaucousness is under strong genetic control resulting in a cogradients and parallel trends in both the adults in natural forest and juveniles grown from open-pollinated progenies. When open-pollinated progenies were grown in a low-altitude common garden, monitoring over 47 years demonstrated strong selection against the high-altitude variants, but survival differences were not evident until 16 years (Potts & Reid 2003).

Table 1. Patterns of extant population differentiation in sessile oak (*Quercus petraea*) along altitudinal gradients

Traits	Phenotypic cline *		Genetic cline†		Ratio P/G‡	Genetic differentiation §	Reference
	Low altitude	High altitude	Low altitude	High altitude			
Phenological traits							
Time of leaf unfolding	– (early)	+ (late)	–	+	10.4	0.36	Vitasse <i>et al.</i> (2009a,b)
Time of leaf senescence	+ (late)	– (early)	–	+	–4.2	0.11	Vitasse <i>et al.</i> (2009b,c)
Length of growing season	+ (long)	– (short)	No clinal trend			na	Vitasse <i>et al.</i> (2009b,c)
Leaf morphological traits							
Leaf size	+ (high)	– (low)	Quadratic cline		na	0.28	Bresson <i>et al.</i> (2011)
Leaf mass per area	– (low)	+ (high)	No clinal trend		na	0	Bresson <i>et al.</i> (2011)
Stomatal density	– (low)	+ (high)	No clinal trend		na	0	Bresson <i>et al.</i> (2011)
Physiological traits							
Maximal stomatal conductance	– (low)	+ (high)	–	+	3.3	0.15	Bresson <i>et al.</i> (2011)
Maximum assimilation rate	– (low)	+ (high)	–	+	1.5	0.20	Bresson <i>et al.</i> (2011)
Leaf nitrogen density	– (low)	+ (high)	–	+	2.5	0.03	Bresson <i>et al.</i> (2011)
Carbon isotope discrimination	– (low)	+ (high)	–	+	1.8	na	S. Delzon (unpublished data)
Growth traits							
Apical growth	+ (high)	– (low)	+	–	na	0.14	Vitasse <i>et al.</i> (2009b)
Diameter growth	+ (high)	– (low)	+	–	na	0.08	Vitasse <i>et al.</i> (2009b)

*Data were obtained from observations made in two *Quercus petraea* stands located along two valleys on the northern slopes of the Pyrénées.

†Acorns were collected on individual trees in the stands located in the two valleys and raised in a common environment provenance/progeny test located on low altitude. Data of the provenance/progeny test were used to compute slopes of the genetic clines and genetic differentiation.

‡Ratio P/G is the ratio between the slope of the phenotypic gradient (P) to the slope of the genetic gradient (G).

§The Q_{st} value or Q_{st} analog (ratio of between population variance/total phenotypic variance).

Traits highlighted in grey exhibit countergradient variation.

however, that antagonistic effects between plasticity and genetic adaptation can constrain the overall phenotypic divergence among populations (Crispo 2008; Conover, Duffy & Hice 2009). These results suggest that there might be cases where the lack of phenotypic divergence does not necessarily mean absence of divergent selection between populations. Missing phenotypic divergence may hide the presence of cryptic genetic divergence, due to the antagonistic effects between plasticity and genetic divergence. Similarly, interactions with the test environment itself may also mask genetic divergence along a cline (Campbell & Sorensen 1978).

Present genetic differentiation observed in provenance tests results from the joint effects of divergent selection since establishment of the populations and historical/demographic effects that were associated with colonization and establishment. In European oaks, many examples have shown that present populations in central and Northern Europe may actually stem from different source populations that were genetically separated in different micro- and macrorefugial zones. Joint historical investigations based on palaeontology and phylogeography coupled with genetic surveys conducted in provenance tests have, however, shown that the joint effects of divergent selection and gene flow have erased any pre-existing historical genetic footprint (Kremer *et al.* 2002). Interestingly, divergent

selection during establishment was driven by climate change during the post-glacial warming along the altitudinal and latitudinal gradients examined. Recent studies highlighted high levels of phenotypic variability for leaf functional traits and phenology along altitudinal gradients for sessile oak (Vitasse *et al.* 2009b,c; Bresson *et al.* 2011). Overall, *in situ* observations showed that populations growing at high altitude had substantially later leaf unfolding, higher leaf mass per area, leaf nitrogen content and photosynthetic capacity and smaller leaf size than those at low altitude (Table 1). These patterns were maintained under common environment conditions for phenological and growth traits (Vitasse *et al.* 2009a; Alberto *et al.* 2011). However, a few ecophysiological traits (leaf mass per area and leaf stomatal density) displayed significant differentiation between populations from different altitudes in the wild (Bresson *et al.* 2011), but did not exhibit genetic differentiation under common garden conditions (Table 1).

In *Eucalyptus* (Fig. 3 and Table 2), phenotypic and genetic differentiation along altitudinal gradients is also usually clinal, involves multiple traits, and cline forms may be sufficiently distinctive to warrant subspecific recognition (Potts & Jackson 1986, McGowen *et al.* 2001; Potts, Potts & Kantvilas 2001). One of the best-known examples is the stepped cline that occurs in the continuous population of

Table 2. Patterns of population differentiation along an altitudinal gradient reported in *Eucalyptus gunnii*.

Traits	Phenotypic cline		Genetic cline		Reference
	Low altitude	High altitude	Low altitude	High altitude	
Phenological & developmental traits					
Flowering time (season)	Nonlinear		na	na	Potts & Reid (1985b)
Vegetative phase change	+ (early)	– (late)	+	–	Potts (1985), Potts & Reid (1985a,b)
Morphological traits					
Inflorescence and capsule size	+ (large)	– (small)	na	na	Potts & Reid (1985a)
Leaf size	+ (large)	– (small)	+	–	Potts (1985), Potts & Reid (1985a,b)
Leaf thickness	– (thin)	+ (thick)	–	+	Potts & Reid (1985a,b)
Petiole length	+ (long)	– (short)	+	–	Potts (1985), Potts & Reid (1985a,b)
Internode length	+ (long)	– (short)	+	–	Potts (1985); Potts & Reid (1985a,b)
Glauconsness (leaf and stem)	Nonlinear		Nonlinear		Potts & Reid (1985a,b)
Physiological traits					
Anthocyanin on young stems	na	na	+	–	Potts & Reid (1985b)
Drought susceptibility	Nonlinear		+	–	Potts (1985)
Frost susceptibility	Nonlinear		No clinal trend or nonlinear		Potts (1985), Cauvin & Potts (1991)
Insect leaf herbivory (Coleoptera)	– (low)	+ (high)	No clinal trend or nonlinear		Potts (1985)
Insect sap sucking (Homoptera)	+ (high)	– (low)	–	+	Potts (1985)
Growth traits					
Apical dominance	+ (high)	– (low)	+	–	Potts & Reid (1985a,b)
Diameter growth	+ (high)	– (low)	+	–	Potts (1985); Potts & Reid (1985a,b)
Height growth	+ (high)	– (low)	+	–	Potts (1985), Potts & Reid (1985a,b)
Lignotuber development	na	na	Nonlinear		Potts (1985), Potts & Reid (1985b)

Results are based on comparison of populations along an altitudinal gradient (referred to as the southern Plateau transect) on the Central Plateau of Tasmania and are compiled from publications reporting phenotypic variation in the wild (Potts & Reid 1985a), as well as genetic-based differentiation in glasshouse trials (Potts & Reid 1985b), reciprocal wild plantings along the altitudinal gradient (Potts 1985; a) and an exotic field test (Cauvin & Potts 1991). The trait highlighted in grey is the only possible example of countergradient variation. While glauconsness increases with altitude in *E. urnigera* (Fig. 3), in the *E. gunnii* levels peak at mid-altitudes along the present transect due to greater exposure to low temperatures and drought where populations grow on the edge of open ‘frost hollows’ subject to cold air drainage. Vegetative phase change reflects the timing of the ontogenetic transition from juvenile through to adult leaves. Na: not available.

E. urnigera on Mt Wellington, Tasmania (Fig. 3). Progeny trials indicate that with increasing altitude this phenotypic cline involves genetic-based changes, including increasing leaf glauconsness, frost resistance and reflectivity, and retention of the juvenile foliage; but decreasing seed germination rate, seedling growth rate, internode lengths and leaf length. The most obvious feature of the cline is the transition from green leaves in the closed forest at lower altitudes (from 610 m) to leaves that were uniformly glaucous near the tree line (up to 1050 m), with the transition occurring over a smooth altitudinal transition of 150 m (<1 km ground distance). This steep cline suggests marked changes in the relative fitness of green and glaucous morphs over short distances (Endler 1977). The change in leaf glauconsness is due to a dense layer of surface wax. Initially, the adaptive value of the glauconsness was argued to be due to the wax decreasing the wettability of leaves which reduced frost damage at higher altitudes, but the wax layer was disadvantageous in the closed forest at lower altitudes where there was competition for light as it reduced absorption of radiation. On another Tasmanian mountain system, parallel phenotypic clines in glauconsness occur in several eucalypt species continuously distributed along a latitudinal gradient involving a similar environmental change from an open, frost-prone habitat to wet, closed forest (Potts & Reid 1985a). These clines also

have a genetic basis (Potts 1985; Potts & Reid 1985b), arguing for a parallel adaptive response. For one of the species, *E. gunnii*, reciprocal plantings of provenances along both altitudinal and latitudinal gradients showed that most characters associated with extension growth (e.g. height, internode length, leaf size) exhibited marked phenotypic plasticity, whereas other traits which vary markedly between populations, such as leaf shape and glauconsness, exhibited little plasticity (Potts 1985; Table 2).

Overall reported combined *in situ* and common environment observations in oak and eucalypts argue that cogeographic clinal patterns along altitude/latitude are the general rule in trees despite a few exceptions (Tables 1 and 2), suggesting that plasticity has contributed synergistically with selection to adaptive divergence in the past. Similar results were obtained for functional leaf traits in other plant species and are reviewed in this issue (Read *et al.*, in press). Cases of countergradient variation appear rare (one trait in *Quercus* and *Eucalyptus*). The evolutionary significance of countergradient variation seems to be largely species and trait specific (Conover & Baumann 2009; Conover, Duffy & Hice 2009) and has not been investigated in trees. Traits where countergradient patterns could be expected are phenotypic responses to biotic or abiotic stresses. We suspect that different biotic or abiotic stresses affecting the same trait can act in different directions at the environmental

or genetic level. For example, areas of high disease or frost exposures and where damages are higher phenotypically are likely to be those in which populations exhibit higher genetic resistance – thus at some stage of the evolution of resistance to biotic or abiotic stresses a countergradient is expected – if only transitory. Such reasoning may explain why in conifers and beech (Alberto *et al.* 2013), bud burst is occurring earlier *in situ* in warmer areas, but late flushing trees exhibit higher fitness on those areas. Finally, phenotypic clines are usually steeper than genetic clines (ratio P/G on Table 1) thus reinforcing the contribution of plasticity of the overall phenotypic divergence of populations across the environmental gradient. Slopes of the genetic and phenotypic clines of growth traits show also congruent signs between *Quercus* and *Eucalyptus*. However, detailed comparisons are limited by the low number of common traits assessed in both species.

Predicted evolution of populations along altitudinal/latitudinal gradients (En and Es)

Evolutionary changes expected at different parts of the natural distributions are dependent on the local acting evolutionary forces triggered by climate change scenarios (Alberto *et al.* 2013). It is likely that microevolutionary processes and regimes will be different along the environmental gradients that we consider here. At the present leading edge of the distribution range, species distribution models based on maintenance of the climate niche predict potential range shifts through combined migration and colonization of newly available habitats (Beaumont *et al.* 2012; Cheaib *et al.* 2012). These demographic dynamics are caused by recurrent founder effects and associated by strong drift effects, which are likely to reduce the genetic diversity (Arenas *et al.* 2012) but to also facilitate the distribution of advantageous alleles enhancing adaptation to the new conditions. Local differentiation among newly established populations may therefore be predicted, (Le Corre & Kremer 1998) and adaptation will be facilitated by pollen flow from more central populations thus helping to track environmental change (Kremer *et al.* 2012b). At the leading edge, colonization rates are determined jointly by the time from seed to first reproduction, rates of reproduction and dispersal. Thus, populations established in new areas are likely to exhibit traits favouring reproductive success and dispersal. Reproductive success is primarily promoted by increased probability of fruit ripening (Morin, Viner & Chuine 2008). Therefore, populations and species having greater phenological sensitivity to temperature and lower chilling temperature requirements might have a certain advantage by producing higher quality and quantity of seeds in a warmer world. At the rear edge of distribution (either latitudinal or altitudinal), populations will be submitted to strong selective pressures as local conditions will be unsuitable to the maintenance of the species (Alberto *et al.* 2013). Population sizes may fall below critical thresholds where they may face a risk of extinction

(Aitken *et al.* 2008) or introgressive displacement (McKinnon *et al.* 2004). Rescue from such maladaptation is dependent on the level of standing variation that will enhance evolution and the maintenance of their demographic growth (Gomulkiewicz & Holt 1995; Gomulkiewicz & Houle 2009). Gene swamping by pollen flow from central northern populations is likely to reinforce maladaptation under such circumstances (Holliday, Suren & Aitken 2012). At the rear margins, the loss of habitats is mostly due to increased drought mortality and decreased reproductive success, as well as adverse biotic interactions (Alberto *et al.* 2013). In a recent study, Allen *et al.* (2010) demonstrated the global vulnerability of woody plant species to reduction in rainfall and increasing temperatures. The risky hydraulic strategy (low hydraulic safety margins defined as differences between naturally occurring xylem pressures and cavitation resistance) exhibited by many species might explain the massive drought-induced dieback observed in many biomes through the world (Choat *et al.* 2012). A fundamental question concerns the plasticity and genetic diversity of cavitation resistance within species. The tight link between cavitation resistance and water availability is the product of natural selection over many generations. Yet, the reported lack of genetic diversity within species in cavitation resistance (Lamy *et al.* 2011) suggests that it is unlikely that species will be able to adapt hydraulically to accelerated climate change, increasing the risk of population maladaptation at the xeric limit of the species distribution range.

In the central part of the distribution populations will undergo the interplay between selection (due to the changing environmental conditions) and gene flow mainly. Furthermore, central populations facing new environmental conditions will benefit from plastic response of trees that will momentarily compensate for the maladaptation, until genetic variation restored by gene flow or mutation will provide the necessary heritable variation to cope with climate change (Ghalambor *et al.* 2007). Transient facilitation of adaptation by plasticity will, however, only be possible for traits exhibiting cogradient variation. Theory predicts that the favourable contribution of gene flow to the adaptive tracking of climate change is dependent on the rate of environmental change, dispersal distance and migration rates (Polechová, Barton & Marion 2009), and should be positive under most predicted scenarios (Kremer *et al.* 2012b).

At this point, contemporary evolutionary changes in natural forest trees are mostly speculative and have only been explored through theoretical or empirical predictions. Observed genetic shifts or evolutionary responses at contemporary time-scales are notably lacking. Such changes can only be assessed through allochronic monitoring, *sensu* Hendry & Kinnison (1999). Allochronic methods that aim at assessing the same trait (at the same age) in two successive generations may be hardly possible due to obvious time constraints in long-lived species as trees, coupled with plastic and developmental changes that may occur over

the life span. However, under quantitative genetic principles, evolutionary change from one generation to the next under some form of natural selection can be predicted based on genetic parameters of the population assessed at the parental generation. Such reasoning is traditionally used in applied tree breeding (the so-called breeder's equation). In this case, genetic parameters are usually estimated in progeny tests stemming from specific controlled crosses and reared under controlled environmental conditions. However, our goal is to assess genetic parameters pertaining to evolution under natural selection 'in the wild' and open pollination. In the context of natural selection, evolutionary change of a given trait can be conceptually predicted based on two parameters: the heritability of the trait and the selection gradient (Lande & Arnold 1983). The selection gradient is a synthetic measure of the strength of natural selection, and heritability is a genetic parameter that corresponds to the ratio of the additive genetic variance to the phenotypic variance of the traits. Their estimations require assessment of proxies of fitness values of trees and the relatedness of trees, which can be obtained using parentage analysis *in natura* (Andrew *et al.* 2005), although most studies of wild populations of forest trees use open-pollinated progenies grown in field trials (Costa e Silva, Hardner & Potts 2010). Assessments of evolutionary change in the wild could ideally be complemented by selection experiments conducted under con-

trolled conditions mimicking global climate change. These experiments would consist in estimating the same genetic parameters by manipulating the level of stress to modify the selection gradient. Evolutionary change may be constrained or accelerated by negative or positive correlation between the target trait and other related traits (Eroukhanoff 2009; Walsh & Blows 2009), and these correlations may also be modified by climate change. It is therefore important that experiments aiming at estimating evolutionary change also account for concomitant changes in correlated traits. While ideally genetic parameters should be assessed *in situ*, we provide here estimates obtained within planted forests (progeny test) conducted in breeding programs, as proxies of 'real' *in situ* values (Tables 3 and 4).

Quantitative and molecular genetic studies of the genetic architecture of contemporary populations and genetic control of complex traits provide insights into the adaptive potential of populations (e.g. levels of additive genetic variation [Va] and narrow-sense heritabilities [h^2]) and the genetic constraints to the selective response (e.g. adverse genetic correlations and indirect genetic effects). Reported values of genetic or phenotypic variances suggest that significant intrapopulation diversity resides in extant populations of trees that can facilitate substantial evolutionary change in a few generations (Tables 3 and 4). Response to selection may, however, be constrained by adverse genetic

Table 3. Genetic variation of functional and adaptive traits in oaks

	Coefficient of phenotypic variation (range of variation)	Narrow-sense heritability	Number of QTLs (range of contribution to the phenotypic variance in %)	Reference
Phenological traits				
Time of leaf unfolding	0.23–0.45	0.25–1	19 QTLs (0–31)	Baliuckas & Pliura (2003), Saintagne <i>et al.</i> (2003), Derory <i>et al.</i> (2009), Alberto <i>et al.</i> (2011)
Time of leaf senescence	na	na	16 QTLs (0–25)	A. Kremer (unpublished data)
Length of growing season	na	na	17 QTLs (0–25)	A. Kremer (unpublished data)
Leaf morphological traits				
Leaf length	0.26	na	2 QTLs (5–9)	Saintagne <i>et al.</i> (2003), Gailing (2008)
Leaf surface (Ls)	0.20–0.24	0.42	1 QTL (8)	Brendel <i>et al.</i> (2008), Bresson <i>et al.</i> (2011)
Leaf mass per area (LMA)	0.07–0.15	0.50	4 QTLs (3–10)	Brendel <i>et al.</i> (2008), Bresson <i>et al.</i> (2011)
Stomatal density (SD)	0.09–0.19	na	No QTL detected	Brendel <i>et al.</i> (2008), Bresson <i>et al.</i> (2011)
Physiological traits				
Maximal stomatal conductance (Gwmax)	0.27	na	No QTL detected	Brendel <i>et al.</i> (2008), Bresson <i>et al.</i> (2011)
Maximal assimilation rate (Amax)	0.23–0.42	na	No QTL detected	Brendel <i>et al.</i> (2008), Bresson <i>et al.</i> (2011)
Leaf nitrogen content (%N)	0.09–0.18	0.50	6 QTLs (1–11)	Brendel <i>et al.</i> (2008), Bresson <i>et al.</i> (2011)
Carbon isotope discrimination	na	0.54–0.74	6 QTLs (3–30)	Brendel <i>et al.</i> (2008), Bresson <i>et al.</i> (2011)
Growth traits				
Apical growth	0.36–0.75	0.21–0.23	6 QTLs (6–17)	Saintagne <i>et al.</i> (2003)
Diameter growth	na	na	na	

QTLs were detected in *Quercus robur* full-sib crosses comprising from 120 to 210 offspring. Due to the limited family size and the access to only one pedigree, the reported number of QTLs is an underestimation of putative QTLs existing in natural populations. Furthermore, due to this sampling strategy, reported estimation of the contribution to the phenotypic variance is overestimated. Na: not available.

Table 4. Genetic variation of functional and adaptive traits in *Eucalyptus*

	No. estimates	Narrow-sense heritability [mean (range)]	Genetic architecture	References
Phenological and developmental traits				
Flowering time (season)	4	0.68 (0.60–0.81)	5 QTL (3–4%). Little genotype x year interaction	Hudson (2012), Jones <i>et al.</i> (2011)
Vegetative phase change	16	0.62 (0.26–0.74)	1–5 QTL (1–63%) Very little nonadditive variance	Jordan, Potts & Wiltshire (1999), Freeman (2006), Hamilton <i>et al.</i> (2011), Hudson (2012), Costa e Silva, Potts & Tilyard (2013)
Reproductive phase change	3	0.44 (0.37–0.50)	1–5 QTL (2–10%). Very little nonadditive variance	Jordan, Potts & Wiltshire (1999), Bundock, Potts & Vaillancourt (2008), Hudson (2012)
Leaf morphological traits				
Leaf size	1	0.35	na	
Leaf shape	3	0.27 (0.19–0.34)	na	
Ecophysiological & biotic traits				
Defensive chemistry	24	0.45 (0.04–0.48)	1–4 QTL per compound (8–53%), with colocation of QTL for multiple compounds common	Freeman <i>et al.</i> (2008a), O'Reilly-Wapstra <i>et al.</i> (2011), O'Reilly-Wapstra <i>et al.</i> (2013)
Frost susceptibility (leaf tissue)	5	0.43 (0.27–0.52)	na	Tibbitts <i>et al.</i> (2006)
Drought susceptibility	4	0.17 (0.14–0.20)	na	Dutkowski & Potts (2012)
Disease susceptibility	10	0.27 (0.13–0.60)	5 QTL (11–20%). Very little nonadditive variance, significant indirect genetic effects	Freeman, Potts & Vaillancourt (2008b), Hamilton <i>et al.</i> (2012), Costa e Silva <i>et al.</i> (2013), Costa e Silva, Potts & Tilyard (2013)
Herbivore susceptibility	12	0.11 (0–0.46)	na	O'Reilly-Wapstra <i>et al.</i> (2013) and (unpubl. data)
Growth traits				
Diameter growth	22	0.28 (0.17–0.39)	1–6 QTL (3–16%), 38% of QTL show QTLxE interaction. Significant nonadditive and indirect genetic effects, additive variance poorly estimated with open-pollinated progeny	Bundock, Potts & Vaillancourt (2008); Freeman <i>et al.</i> (2009, 2013), Costa e Silva, Hardner, and Potts (2010), Costa e Silva <i>et al.</i> (2013)

The table shows the number, mean and range of open-pollinated estimates of narrow-sense heritabilities and comments on the genetic architecture (including the published number of QTL detected within a full-sib family and % of phenotypic variation explained) for functional traits for one of the most studied eucalypt species, *Eucalyptus globulus*. Heritability data have been updated from Potts *et al.* (2004) with only additional sources cited. Heritabilities are within population, single-site estimates and unless indicated are derived from field trials. In addition to significant additive genetic variation residing within populations, significant population differentiation across the geographical range of *E. globulus* has been reported for all traits studied (Dutkowski & Potts 1999), which in many cases surpasses neutral expectations (Steane *et al.* 2006; Dutkowski & Potts 2012). QTLs were detected in *Eucalyptus globulus* full-sib families comprising from 112 to 467 genotypes.

correlations which may arise through pleiotropy or linkage. Constraints may also arise at the population level through extended 'indirect' genetic effects associated with, for example, competitive interactions among neighbours, although in other cases indirect genetic effects may amplify the population response to selection as recently argued for eucalypt disease infection (Costa e Silva *et al.* 2013). However, we anticipate that the prediction of differential evolution for different traits along the altitudinal/latitudinal gradient will be applicable to *Quercus* and *Eucalyptus*. The potential for rapid responses to selection in both genera is also supported by their large genetic diversity, both within (Tables 3 and 4) and between (Table 1 and 2; Figs 2 and 3) contiguous populations.

Predicted divergence of populations (Df)

Genetic-based adaptive differentiation has accumulated in trees for numerous phenotypic traits along latitudinal/altitudinal gradients despite strong homogenizing gene flow (Savolainen, Pyhäjärvi & Knürr 2007). What kind of predictions can we make about the future genetic divergence that will build up as a result of ongoing climate change? We may first question about the traits that are likely to be more differentiated along the environmental gradients that we have considered. We may then raise the issue about the rate at which differentiation will take place. We will explore how the interplay between the different evolutionary processes (mainly selection and

gene flow) may shape differentiation under climate change. Our reasoning is based on the conceptual frame sketched in Fig. 1 that predict that the future differentiation will result from existing differentiation and ongoing evolution within the spatiotemporal setting of the populations. Our predictions will also follow inferences drawn from comparative analysis of past and ongoing evolutionary trajectories.

WHICH TRAITS WILL SHOW LARGER DIFFERENTIATION UNDER CLIMATE CHANGE?

Traits that have differentiated in the past along the latitudinal/altitudinal gradients are candidate targets for divergent selection resulting from ongoing climate change. However, such reasoning might be misleading due to differences in past and future selection scenarios. First of all, care should be taken that the trait under consideration is submitted to the same causal selective agent in both scenarios. Today's altitudinal and latitudinal gradients encompass a large variability of environmental drivers (temperature, precipitation, radiation, atmospheric moisture) that may differently be impacted by ongoing climate change. Careful inferences on traits undergoing divergent selection should therefore be subjected to prior verification that the causal agent of the extant differentiation (De) will be acting under future environmental change on the same trait. Secondly, one should investigate that climate, although changing over time in each population, will actually also generate climate differences across the gradient. For example, if climate change is of the same magnitude at different sites along the latitudinal/altitudinal gradient, then the overall future climatic difference between any two populations sampled along the gradient may actually not vary over time. Hence, while there will be evolution of populations, divergence may stay the same. These predictions can easily be illustrated by phenological bud burst in the case of oaks. The shift of the date of bud burst is about 7 days per 1°C of warming of spring temperatures (Vitasse *et al.* 2009b). If the temperature increase due to climate warming is of the same magnitude along the gradient, each population will flush on average 7 days earlier, but there will be no difference in divergence between populations. Put into more trivial terms, larger differentiation can only be expected if larger environmental differences among populations build up along the gradient. Thus, if evolution within populations (En and Es) is parallel, then less or no change of differentiation is to be expected. The level of divergent environmental change is a key element to consider for predicting differentiation and anticipate which form of evolution will actually be triggered: parallel or divergent. The predicted lack of divergence for bud burst due to parallel selection assumes, however, that climate change will have no impact on dormancy release. Although the current chilling temperatures are likely sufficient to fully release bud dormancy for most temperate tree populations, they, however, seem to be already insufficient for

populations growing at the southernmost limit of the species distribution. In addition, the lack of chilling temperatures may increase in the coming decades with winter temperatures rising (Vitasse *et al.* 2011) and may lead to phenological divergence between populations.

We may also anticipate that new traits will exhibit divergence or will become subject to divergent selection. We mentioned in the previous paragraph that evolution towards different phenotypes will be triggered at both extremes of the latitudinal/altitudinal gradient. We anticipate that different fitness-related traits may respond differently under parallel or real divergent selection scenario promoted by climate change, thus modifying the correlation matrix of traits and thus modifying the evolutionary change for each trait individually. Recent results from process-based models suggested that northwards colonizations will be primarily promoted by increased probability of fruit ripening and flower frost survival, while the loss of habitats southwards will be mostly due to increased drought mortality (Morin, Viner & Chuine 2008). Fitness-related traits such as drought and heat tolerance are therefore expected to differentiate under climate change along latitudinal/altitudinal gradients. Global climate change is projected to produce longer and more frequent droughts, which have the potential to trigger widespread tree die-off, particularly at the warmer margin of the species distribution. We hypothesize that evolution of rear-edge populations which have a narrow hydraulic safety margin towards a more drought tolerant xylem (more cavitation resistant) may be limited due to the low genetic diversity (Lamy *et al.* 2011). On the other hand, habitats at the leading edge where freezing occurs during the growing season limit vessel/tracheid diameters and so water transport efficiency. Experimental work suggests that mean vessel and tracheid sizes need to be <30 µm to avoid embolism by freezing and thawing (Pitterman & Sperry 2003). Climate warming could therefore lift this low temperature constraint and favour larger vessel diameter leading to more efficient (but less safe) water transport. These limits to xylem conduit size caused by water (southern margin) and freezing (northern margin) stresses may likely promote substantial divergence in xylem-related traits.

HOW FAST WILL DIFFERENTIATION BUILD UP AS A RESULT OF CLIMATE CHANGE?

Extant levels of differentiation assessed in provenance tests do not inform about the rate of differentiation. They correspond to the divergence that has accumulated among populations as they diverged from a common ancestor, which is often thought to be a glacial refugial population (Fig. 1). With a few exceptions, most European tree populations have been in place for more than 6000 years after the post-glacial warming stabilized (Kremer *et al.* 2010). Similarly, in Tasmania, the cline of *Eucalyptus gunnii* on the central plateau is expected to have adjusted to the topography following the post-glacial warming. It is

unknown when or if today's estimates of population divergence (De) have reached asymptotic values after population establishment. Hence, De does not provide any clue about the pace of population differentiation. However, theoretical predictions suggest that divergence can build up very rapidly during the first generations after establishment. These predictions stem from analytical calculations (Hendry, Day & Taylor 2001) and numerical simulations under more realistic situations (Kremer & Le Corre 2012). The latter authors have shown that it takes <20 generations to restore differentiation of adaptive traits following any environmental change, even in the context of extensive gene flow. The rate increases with the strength of within-population selection. Rapid adaptive divergence is enhanced by the allelic associations across loci contributing to the trait, which are immediately captured by divergent selection. We may therefore anticipate that evolutionary responses to climate change may build up rapidly as well, especially for traits that depend on a very large number of loci that increase opportunities for beneficial associations across loci (Kremer & Le Corre 2012).

Finally, the rate of phenotypic differentiation will also be enhanced when plasticity and genetic effects act synergistically, suggesting that higher and faster differentiation is to be expected for species and traits exhibiting cogradients (Soularue & Kremer, in press). Thus, patterns of variation observed in extant provenance tests (co- vs countergradient variation) may provide qualitative predictions on the rate and direction of future differentiation. Experimental evidence suggests that adaptive genetic divergence underlies changes of the mean trait value, as cogradients prevail over countergradient variation (Tables 1 and 2). To the extent that cogradients may be maintained under new environmental conditions generated by climate change, we may anticipate that selection will generate genetic divergence in the direction of the observed *in situ* variation. In this respect, assessments made in experimental controlled environments mimicking climate change (Beier 2004) may allow predictions of future genetic divergence.

HOW WILL GENE FLOW CONTRIBUTE TO ADAPTIVE DIFFERENTIATION?

Under stable but selectively divergent environments, gene flow can constrain adaptive divergence at the margins of the natural distribution (García-Ramos & Kirkpatrick 1997). This is due to gene swamping of nonadaptive alleles coming from central populations into peripheral populations. Reaction norms of populations sampled along altitudinal (Vitasse *et al.* 2010), and latitudinal gradients (Rehfeldt *et al.* 2002) in trees show indeed that maladaptation is more pronounced in peripheral than in central populations. Under directional environmental change, expectations of the effects of gene flow are different depending on the location of recipient populations (Kremer *et al.* 2012b). For populations located at the lead-

ing limit (or at higher elevation), gene flow may actually enhance local adaptation because of gene swamping of pre-adapted alleles coming from more central populations (Visser 2008). However, for populations located at the southern limit (or lower elevation), gene flow will increase maladaptation, because pollen swamping will only import less adapted alleles (Holliday, Suren & Aitken 2012). Overall, as adaptation will be enhanced at one extreme and constrained at the other, the overall predicted effect of gene flow is an increase of adaptive differentiation across the distribution of the species. There is, however, no empirical evidence to support these predictions.

Hybridization may also play a significant role in both genera, which may be different along the gradients. Rear edges of the distribution in temperate oaks (either southern latitudes or lower altitudes), for example, have a larger diversity of oak species. Although northwards and upwards migration dynamics of these species triggered by climate change are poorly studied (but see Delzon *et al.* in press), hybridization is likely to facilitate immigration of pre-adapted genes from populations at the rear limit. Indeed, reproductive barriers between tree species are often incomplete, and the evolutionary role of interspecific hybridization in the dynamics of species range expansion and contraction has long been recognized in both oaks (Petit *et al.* 2004; Alberto *et al.* 2010) and eucalypts (Potts & Jackson 1986; Potts & Reid 1988; McKinnon *et al.* 2004). There is molecular evidence of selective filtering of introgression (McKinnon, Smith & Potts 2010) and even complete introgressive displacement of pioneer (Petit *et al.* 2004) and less competitive species (McKinnon *et al.* 2004) by cogeners. Such evidence argues that the generation of genetic variability in local tree populations through hybridization may supplement standing genetic variation and cases enhance the adaptive response to climate change. More hybridization is therefore predictable at the rear than at the leading end of the distribution, which may also increase the overall genetic divergence.

Conclusion

We overview the extant pattern of phenotypic and genetic divergence among oak and eucalyptus populations and anticipated different microevolutionary shifts across altitudinal/latitudinal gradients. We consequently attempted to predict future adaptive divergence and concluded that different regimes of divergent selection occurring between peripheral populations will mainly contribute to future differentiation. The extant geographical distribution of phenotypic/genetic variation that can be assembled from assessments in combined *in situ*/common environment experiments provided important clues for making future predictions. This is the first time that the predominance of cogradients is shown for a large set of functional traits in two important tree genera. The predominance of cogradients in trees suggests indeed that adaptive divergence is likely to follow phenotypic divergence for

most traits. Phenotypic responses of trees raised under controlled environmental conditions mimicking climate changes may therefore provide some hints on the direction of future genetic divergence. These predictions can be extended to other traits, not reviewed in our examples, if patterns of co- versus countergradient, and the maintenance of these patterns are investigated beforehand.

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