REVIEW ARTICLE

Uncovering the contribution of epigenetics to plant phenotypic variation in Mediterranean ecosystems

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ABSTRACT

Epigenetic signals can affect plant phenotype and fitness and be stably inherited across multiple generations. Epigenetic regulation plays a key role in the mechanisms of plant response to the environment, without altering DNA sequence. As plants cannot adapt behaviourally or migrate instantly, such dynamic epigenetic responses may be particularly crucial for survival of plants within changing and challenging environments, such as the Mediterranean-Type Ecosystems (MTEs). These ecosystems suffer recurrent stressful events (warm and dry summers with associated fire regimes) that have selected for plants with similar phenotypic complex traits, resulting in similar vegetation growth forms. However, the potential role of epigenetics in plant adaptation to recurrent stressful environments such as the MTEs has generally been ignored. To understand the full spectrum of adaptive processes in such contexts, it is imperative to prompt study of the causes and consequences of epigenetic variation in natural populations. With this purpose, we review here current knowledge on epigenetic variation in natural populations and the genetic and epigenetic basis of some key traits for plants in the MTEs, namely those traits involved in adaptation to drought, fire and oligotrophic soils. We conclude there is still much to be learned about 'plant epigenetics in the wild' and, thus, we propose future research steps in the study of natural epigenetic variation of key traits in the MTEs at different scales.

PLANT EVOLUTION FROM BEYOND GENETICS

It recently became clear that heritable phenotypic variation does not need to be based on DNA sequence polymorphism (Richards 2006; Bossdorf *et al.* 2008). Biochemical and structural epigenetic marks can provide differential access to underlying genetic information with phenotypic consequences. For example, cytosine DNA methylation is a common epigenetic signal that in plants occurs in any sequence context, associated with both genes and transposable elements (TE) and, in cooperation with histone modifications by acetylation, phosphorylation and methylation, which entail changes in chromatin structure, regulate gene expression and TE activity (Zhang 2008; Bannister & Kouzarides 2011; Feil & Fraga 2012; Springer *et al.* 2016). In cross-talk diverse classes of RNA (*e.g.* small RNAs and long non-coding RNAs) can also modify chromatin structure and silence transcription through formation of RNA scaffolds mediating the recruitment of histone and DNA methyltransferases (Holoch & Moazed 2015).

Plants exhibit clear-cut examples of spontaneous heritable epialleles and, compared to animals, feature specific epigenetic mechanisms (*e.g.* CHROMOMETHYLASE enzyme family) and show more frequent persistence of epigenetic information through meiosis (Zhang 2008; Feil & Fraga 2012). As plants cannot adapt behaviourally or migrate instantly, reversible epigenetic response mechanisms, which act under environmental

or developmental influence (Angers *et al.* 2010; Müller 2010; Dowen *et al.* 2012; Robertson & Richards 2015), may be particularly crucial for their individual survival and population persistence within the dynamic environments they experience (Fig. 1).

Moreover, considering the generally duplicated genomic landscape of angiosperms, epigenetic effects play a major role in their gene regulation (Springer *et al.* 2016). By regulating mobile element activity and silencing redundant genes, epigenetic alterations constitute an effective and flexible mechanism for stabilising cellular processes starting immediately after genome doubling and/or hybridisation (Mittelsten *et al.* 2003; He *et al.* 2010; Chodavarapu *et al.* 2012; Song & Chen 2015). Utilisation of epigenetic regulation of duplicated gene expression could be advantageous relative to classic genetic mutations for adaptation in polyploids during their early establishment and subsequent evolution (Madlung & Wendel 2013). Ecological differentiation associated with whole genome duplication events has been recently linked to DNA methylation in species like *Limonium* (Róis *et al.* 2013) and *Dianthus broteri* complex (Alonso *et al.* 2016a).

Branching off molecular biology, epigenetic research in model organisms has bloomed during the last decade, and our mechanistic understanding of epigenetic processes has improved significantly (*e.g.* Lister *et al.* 2008; Zhang 2008; Matzke & Mosher 2014; van der Graaf *et al.* 2015). More
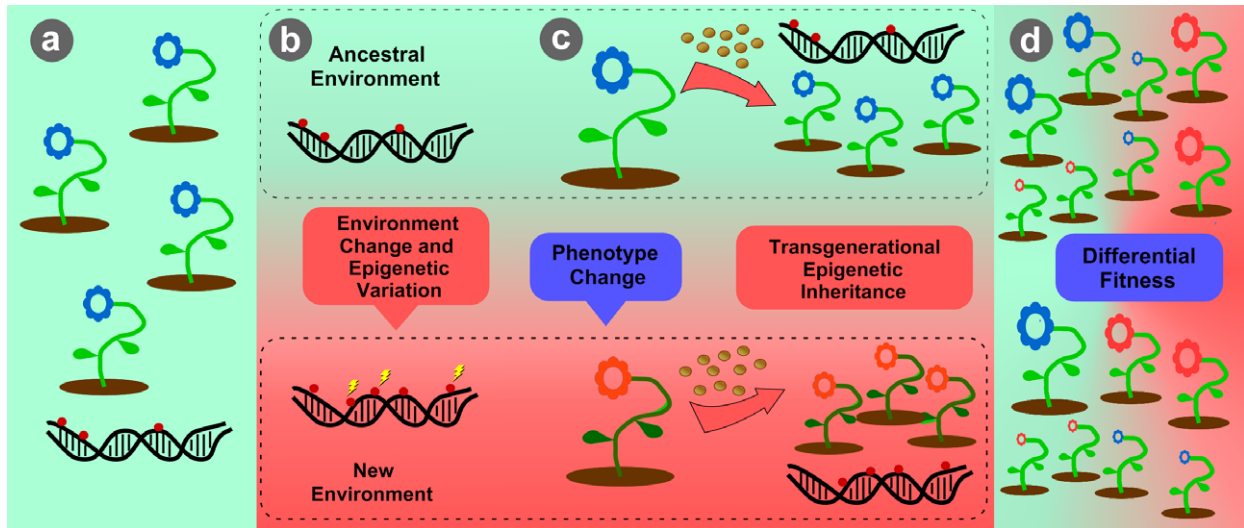
Fig. 1. Understanding transgeneration stress memory inheritance is crucial to evaluate the role of epigenetic responses to the changing and challenging MTEs. (a) Individuals within homogeneous environments may hold a certain epigenetic pattern here represented as cytosine DNA methylation (red balls). (b) Environmental changes can trigger chance responses in epigenetic patterns. (c) Epigenetic changes can be related to changes in phenotypic traits with functional relevance and can be at least imperfectly transferred to offspring. In changing environments, the next generation can find heterogeneous conditions that might or might not differ from those experienced by their parents. (d) Both increased epigenetic diversity and the association between epigenetic divergence and differential fitness are expected.

recently, a variety of methods, including techniques involving Next Generation Sequencing (NGS), have been developed to study DNA methylation and other epigenetic modifications in non-model organisms, which pave the way for studying epigenetics also in wild plant populations (Platt *et al.* 2015; Trucchi *et al.* 2016; van Gurp *et al.* 2016).

To understand the full significance of epigenetic variation and inheritance, it is imperative to place epigenetic processes in an environmental perspective and study their causes and consequences in natural populations (Bossdorf *et al.* 2008). However, to date the adaptive and evolutionary importance of epigenetic variation has only rarely addressed. Incorporation of epigenetics into evolutionary models is only starting to be attempted (Slatkin 2009; Tal *et al.* 2010; Geoghegan & Spencer 2012; Klironomos *et al.* 2013; Charlesworth & Jain 2014; Kronholm & Collins 2016), and more empirical information from natural populations is needed for accurate modelling of epigenetic dynamics.

The epigenetic sources of variation can be stochastic epimutations (Becker *et al.* 2011). However, in contrast to genetic mechanisms, a major portion of epigenetic variation is triggered by stress and environmental changes (Rapp & Wendel 2005; Turner 2009; Halfmann & Lindquist 2010; Kim *et al.* 2015; Meyer 2015) during a time when new phenotypes could be crucial for population survival. Moreover, if conditions return to their original state, spontaneous back-epimutations may restore original phenotypes. At the interface between genotype and environment, the overall rate of epimutation is much higher than that of genetic mutation (Charlesworth & Jain 2014; Furrow 2014), therefore, epigenetic diversity increases more rapidly than genetic variation in a changing environment. Being more flexible and dynamic, epigenetic information could therefore provide the substrate for phenotypic variation potentially visible to selection, and play a role in rapid adaptive mechanisms (Burggren 2016).

Despite the potentially high rate of back-epimutations, modelling studies have shown that if an environmental stress is maintained long enough, epigenetic alterations at a site can reach equilibrium frequencies within populations over less than a dozen generations (Slatkin 2009). Environmental fluctuations can trigger multiple simultaneous epimutations affecting complex adaptive traits, and novel epigenetic modifications can originate in more individuals simultaneously, which may facilitate fixation within a population or species (Flatscher *et al.* 2012; Burggren 2016). Finally, epigenetic mechanisms may partly defy well-understood population processes, like allelic drift and the prerequisite nature of recombination during adaptive change.

Several studies have already demonstrated a standing level of epigenetic variation within natural plant populations (*e.g.* Vaughn *et al.* 2007; Herrera & Bazaga 2010; Paun *et al.* 2010; Schmitz *et al.* 2013). While experiments have shown that environmental conditions can override epigenetic regulation (*e.g.* Pecinka *et al.* 2010; Verhoeven *et al.* 2010; Dowen *et al.* 2012; Wibowo *et al.* 2016), we now have evidence that natural selection acts on epigenetic variation similarly as on genetic components to result in novel adaptation (Herrera & Bazaga 2010; Paun *et al.* 2010; Furrow 2014; Platt *et al.* 2015; Kronholm & Collins 2016). Therefore, epigenetic information provides an additional source of natural variation, which may be particularly significant in small populations lacking genetic variability and/or occupying a fragmented landscape (Verhoeven & Preite 2014; Herrera *et al.* 2016).

Epimutations can have extensive morphological, physiological and ecological consequences, even in the absence of genetic variability (Johannes *et al.* 2009; Reinders *et al.* 2009). Even if most phenotypic differences between species are genetically determined, epigenetic inheritance can be of particular importance in the development of primary phenotypic divergence (Bossdorf *et al.* 2008). If adaptive and maintained long enough,

such phenotypic discontinuities can become genetically locked and trigger species divergence (Jablonka & Raz 2009; Flatscher *et al.* 2012). Modelling studies even suggest that epigenetic variation can facilitate jumps between fitness slopes, through reducing genetic barriers represented by valleys in an adaptive landscape (Pál & Miklós 1999). Therefore, epigenetic novelties have been one of the mechanisms put forward for saltational (mutationism) speciation (Hawkins *et al.* 2002; Jablonka & Lamb 2010), but empirical data are not yet available to support or reject such hypotheses.

ACCLIMATION AND TRANSGENERATIONAL STRESS MEMORY

Epigenetic changes can be transient, being reset between generations, but several spontaneous or induced epigenetic variants can be stably inherited across multiple generations (Jablonka & Raz 2009; Feng *et al.* 2010; Paszkowski & Grossniklaus 2011; Hagmann *et al.* 2015). The involvement of environmental stress in the formation of long-lasting epigenetic memories conferring heritable phenotypic traits cannot be easily experimentally addressed and therefore continues to be debated (Jablonka & Raz 2009; Burggren 2016; Crisp *et al.* 2016). Most research to date has focused on the intragenerational level, aimed to discover the epigenetic mechanisms involved in plant responses to strong environmental changes (individual acclimation) and their effects during successive stressful events experienced along the individual lifetime (individual stress memory or epigenetic priming). Current evidence for an epigenetic basis of phenotypic traits considered to be advantageous for plants growing in Mediterranean ecosystems will be reviewed in the following sections.

Evidence for transgenerational epigenetic priming or inheritance, *i.e.* when such individual stress memory also improves the response of the progeny (Fig. 1), has been experimentally gathered mostly in model and short generation time species (see Crisp *et al.* 2016; Herman & Sultan 2016 for reviews). The magnitude and potentially adaptive nature of extant epigenetic variation in Mediterranean plant populations (see below) supports the relevance of studying transgenerational inheritance. Transgenerational heritability of epigenetic markers is another feature not yet been analysed in detail. Multigenerational greenhouse experiments have proved that transmission of epigenetic markers occurs (*e.g.* Cortijo *et al.* 2014) but to a variable degree across plant species and genomic regions. For instance, a recent study highlights that fidelity can be variable at the intraspecific level: in *Helleborous foetidus*, wild plant individuals differed in the fidelity with which their epigenotypes are transmitted to progeny and such differences are associated with genetic variation (Herrera *et al.* 2014). In particular, reduced fidelity increased seed size variability and resulted in increased or reduced seedling recruitment, depending on the population analysed (Herrera *et al.* 2014). Thus, this study exemplifies divergent phenotypic selection on epigenetic transmissibility acting in the wild. The balance between time for epigenetic reset, fidelity in transgenerational transmission and the lapse between successive stress events may determine whether acclimation, individual memory or transgenerational memory would be the most successful strategy, and recurrent stressful environments might favour transgenerational memory.

The early evidence we currently hold urges complementing our gene- and genome-centred mechanistic view with a substantial consideration of epigenetic factors when seeking to understand population processes that drive the evolutionary process by mediating phenotypic evolution and adaptation. For this purpose, genome-wide heritable epigenetic components of natural variation, together with their fitness effects, should be comprehensively investigated in their environmental context. Such an approach has potential to help us understand how organisms respond to and interact with their environment. Research on natural epigenetic variation is notably timely in the current context of widespread environmental challenges, particularly in the Mediterranean zone where increased aridity and frequency of extreme climatic events are predicted (Matesanz & Valladares 2014). The interest here should in fact span several related domains, from conservation to theoretical evolutionary biology.

EPIGENETIC VARIATION IN THE MEDITERRANEAN-TYPE ECOSYSTEMS

The MTEs comprised five regions of the world (the Mediterranean Basin, California, central Chile, the Cape Region of South Africa and southern Australia) and have been largely recognised by their particular and unique climate, with bi-seasonality in temperature and precipitation: warm dry summers with associated fire regimes and mild wet winters, with large intra- and inter-annual precipitation variability, which promote unpredictable but recurrent abiotic stress (Davis *et al.* 1996; Rundel *et al.* 2016). These climatic conditions together with high heterogeneity in topography and soils have been hypothesised as the main drivers of the remarkable plant species diversity in the MTEs (Thompson 2005; Blondel 2006; Valente *et al.* 2010). In contrast to more stable biomes, the spatial heterogeneity and temporal environmental unpredictability in MTEs could lead rapidly to phenotypic diversity through epigenetic variation.

Epigenetic analyses of wild plant populations in MTEs highlight both extensive intraspecific epigenetic variation and its potentially adaptive nature in species differing in distribution range, habitat specialisation and life-history traits. In large and long-lived organisms like trees, phenotypic variation in response to abiotic stress can be crucial for acclimation to variable environments experienced by individuals throughout their lifetime (Bräutigam *et al.* 2013; Pascual *et al.* 2014). When such transient phenotypes can be transferred across generations through epigenetic signals they should finally result in adaptive phenotypic divergence without significant genetic differentiation (Pascual *et al.* 2014). In the following paragraphs we consider epigenetic studies conducted in MTEs that mostly involve perennial species of different lifespan (trees, shrubs and herbs). Preliminary analyses on a reduced sample of stone pines (*Pinus pinea*), collected from different Spanish populations and vegetatively propagated in a common garden, confirmed absence of genetic variability in this Mediterranean species (based on AFLP markers) but showed certain differentiation in methylation-susceptible markers between populations (Saéz-Laguna *et al.* 2014). In *Quercus lobata*, an oak endemic to the California valley with a neutral genetic variance spatially structured primarily by past and present climate, a few populations at its southern range limit

differed more in epigenetic than genetic markers (Platt *et al.* 2015). At the landscape scale, NGS epigenetic markers exhibited stronger association with climate than equivalent neutral genetic markers, supporting the potentially adaptive role of DNA methylation in this species, which also exhibited specific associations between certain epigenetic and genetic markers not spatially linked in the genome (Gugger *et al.* 2016). In contrast to the prevalent pattern, epigenetic diversity was not higher than genetic diversity in *Prunus avium* populations at their southern European rear-edge distribution limit, where weaker among-population epigenetic differentiation was also obtained (Avramidou *et al.* 2015).

In the narrow endemic *Viola cazorlensis*, scanning genomic analyses based on MS-AFLP showed that epigenetic diversity exceeds the substantial neutral genetic variation shown by this habitat specialist shrub (Herrera & Bazaga 2010). More interestingly, epigenetic variation was structured into distinct within- and between-population components despite neutral genetic variation not being spatially structured across populations, and suggested extensive gene flow among them (Herrera & Bazaga 2008). Nevertheless, populations of *V. cazorlensis* exhibited significant divergence in floral features associated with pollination success and the few anonymous genetic markers (AFLP loci) associated with these traits (*i.e.* adaptive genetic divergence; Herrera & Bazaga 2008). Also, divergence was larger in epigenetic markers (MS-AFLP loci), which accounted for 13% of the overall observed epigenetic variation (Herrera & Bazaga 2010). Still, most epigenetic variation remains at the within-population level where it has been related to substrate and variation in long-term herbivory experienced by *V. cazorlensis* individuals (Herrera & Bazaga 2010). At both within- and between-population scales evidence for the association between the methylation status of some methylation-susceptible loci and the allelic condition of some non-neutral, adaptive AFLP loci suggests that evolution could proceed through simultaneous, correlated selection on functionally linked epigenetic and adaptive genetic variation.

Finally, the widely distributed perennial herb *Helleborus foetidus* also exhibited greater epigenetic than genetic diversity along an ecological gradient in southeastern Spanish populations (Medrano *et al.* 2014). Moreover, global cytosine methylation was inversely related to differences in individual plant size and reproductive output (Alonso *et al.* 2014), and divergence in life-history traits, water use efficiency, plant size and fecundity was significantly associated with variation in epigenetic markers after accounting for genetic background, both at regional (ten sites pooled) and local (within sites) scales (Medrano *et al.* 2014). Such findings suggest that epigenetic variability within and across generations may widen the range of functional phenotypic traits allowing exploitation of contrasting environments despite a moderate genetic variance (Medrano *et al.* 2014).

Statistical association between the methylation state of specific loci and the allelic condition of specific genetic markers observed with different methodologies both in *Q. lobata* and *V. cazorlensis* confirm the complex relationship between genetic and epigenetic variation. However, the specific contributions of genetic and epigenetic variation to natural selection and evolution can be explored using spatially explicit models (Herrera *et al.* 2016).

KEY PHENOTYPIC TRAITS IN MEDITERRANEAN PLANTS

Mediterranean plants have evolved a number of morphological and physiological adaptations that determine their ability to survive and reproduce (Hernández *et al.* 2010). In addition, the Mediterranean climate has selected for plants with similar traits, resulting in similar vegetative growth forms (Verdú *et al.* 2003), although many of these adaptations have been suggested to be present in Pre-Mediterranean flora (*i.e.* exaptations; Bradshaw *et al.* 2011; Rundel *et al.* 2016). In the next paragraphs, we compile information about the genetic and epigenetic mechanisms behind key phenotypic traits involved in adaptation to drought, fire and oligotrophic soils, three characteristic environmental stresses of current Mediterranean climate. Some of these traits (*e.g.* sprouting, germination and dormancy) are directly related to plant reproduction and, thus, analysis of their genetic and epigenetic basis would be of particular interest to increase knowledge for plant evolvability and adaptation in MTE.

Adaptation to drought

Experimental studies have frequently found changes in methylation patterns of plants exposed to different abiotic stress treatments, including water availability and temperature (see Alonso *et al.* 2016b for literature review). One of the most severe stresses in the MTE is the long periods of drought during summer together with high temperatures. Plant growth and survival is compromised through exacerbation of water limitation (Medrano *et al.* 2009). The capacity to resist a water limitation period and to recover rapidly may be adaptive for Mediterranean plants regardless of their growth form and leaf habit, including also winter annual herbs. Such responses are regulated through complex genetic and epigenetic networks leading to rapid reprogramming of plant growth (Bertolini *et al.* 2013). The three main traits related to drought are leaf morphology, stomatal adjustment and the root system, with Mediterranean plants reflecting a continuum of leaf water relations and stomatal behaviour in response to water stress (Galmés *et al.* 2007). In this regard, natural intraspecific variation in several leaf traits related to water economy, including leaf size, specific leaf area (SLA), stomatal index, stomata size and density, and carbon isotope ratio, were more frequently related to epigenetic than to genetic markers in a large sample of wild *H. foetidus* individuals (Medrano *et al.* 2014), suggesting that DNA methylation may have a relevant role in promoting adaptation of widespread species such as this perennial herb along broad ecological gradients characteristic of Mediterranean mountains.

In addition, in a long-term field experimental study, *Quercus ilex* trees exposed to 12 years of rain partial exclusion exhibited epigenetic but no genetic differentiation, together with reduced variability in epigenetic markers compared to controls (Rico *et al.* 2014). This suggests that strong directional selection imposed by persistent stressful environmental conditions can alter standing epigenetic variation of long-lived plants by fixing epiallelic variants that confer tolerance to local stress. Tolerance to increasing heat stress in cork oak (*Q. suber*) involved a rapid initial change in cytosine methylation patterns (*i.e.* demethylation and *de novo* methylation at different loci) and a delayed increase in global cytosine methylation, together with

decreased acetylation of H3 histones, which exhibited contrasting specific patterning within leaf tissues (Correia *et al.* 2013). Unfortunately, these studies do not frequently report the phenotypic traits associated with treatment.

Leaf morphology

Light and water are main resources affecting leaf traits, controlling plant growth and survival, and determining the distribution of plants at global scale (Quero *et al.* 2006). Many experiments in crops have shown a general leaf size reduction caused by water stress (Bosabalidis & Kofidis 2002; Camposeo *et al.* 2011; Doupis *et al.* 2016; Liu *et al.* 2016). Congruently, MTEs contain a high proportion of species with small leaves and low SLA, the ratio of leaf area to leaf dry mass, suggesting its adaptive function (Ackerly 2004; Pérez-Harguindeguy *et al.* 2013; Sack & Scoffoni 2013). SLA is a trait directly associated with sclerophylly (*i.e.* thick cuticles), habit and leaf physiology. Variation in SLA determines stomatal conductance and photosynthesis rate (see above; Reich *et al.* 1997). Several studies suggest high genotypic variation in SLA with small to moderate heritability (Rebetzke *et al.* 2004; Rebolledo *et al.* 2012). The genetic and developmental basis of leaf morphogenesis and shape variation has been widely studied in *Arabidopsis thaliana* (Tsukaya 2005; Bar & Ori 2014) and other species (Bar & Ori 2015). However their environmental response pathways are less known and comprise multiple levels of genetic regulation (González & Inzé 2015). Leaf size is partially independently regulated through *class I KNOX* gene expression through hormone dynamics (Achard *et al.* 2006) and two transcription factor families, *CIN-TCP*s and *ARP/AS2* (Hay & Tsiantis 2006; Guo *et al.* 2008; Hepworth & Lenhard 2014). Reductions in leaf size in water-stressed environments are mediated by ethylene response factors and gibberellin catabolism in *Arabidopsis* (Dubois *et al.* 2013), whereas reduced gibberellin activity decreased leaf size and stomatal density in *Solanum lycopersicum* (Nir *et al.* 2014; Farber *et al.* 2016). In addition previous studies have suggested a role for abscisic acid (ABA) in the inhibition of leaf growth (Zhang & Davies 1990).

Epigenetic control of leaf traits (through methylation variation) in contrasting wild habitats has been suggested (Gao *et al.* 2010; Lira-Medeiros *et al.* 2010; Medrano *et al.* 2014). A recent study in *Polygonum persicaria* (Herman & Sultan 2016) has demonstrated the role of DNA methylation allowing adaptive transgenerational changes in leaf area in response to parental drought stress. In addition, histone modifications at drought stress-responsive gene regions induced changes in leaf morphology and physiology (Scippa *et al.* 2004; Kim *et al.* 2010; Zhang *et al.* 2016).

Stomatal adjustment

Stomatal adjustment is one of the fastest responses to drought in plants. Stomatal activity influences CO_2 absorption and thus impacts photosynthesis and plant growth. In response to drought, ion and water transport systems across membranes control turgor pressure changes in guard cells and stimulate stomatal closure (Osakabe *et al.* 2014). During prolonged water deficit (as in MTEs), plants produce new leaves with reduced stomatal conductance, *via* altered stomatal size and/or density (Franks *et al.* 2015). Although Mediterranean plants feature broad variation in stomatal regulation in response to water stress, a generalised decrease in stomatal conductance has been

found (Galmés *et al.* 2007). The mechanism of stomatal adjustment in response to water stress involves phytohormone (Daszkowska-Golec & Szarejko 2013) and hydraulic (Christmann *et al.* 2007) signals. The genetic control of stomatal adjustment in response to drought is well characterised in model species (reviewed in Osakabe *et al.* 2014). The *Arabidopsis* histidine kinase (AHK1) acts as an osmosensor and functions as a positive regulator of stress signalling (Wohlbach *et al.* 2008). The gene 9-cis-epoxycarotenoid dioxygenase 3 (*NCED3*), which catalyses a key step in ABA biosynthesis, is highly expressed in response to drought stress. Endogenous ABA stimulates a signalling pathway (involving Snf1-related protein and calcium-dependent protein kinases) that finally activates anion K^+ channels (*KAT1/KAT2*) and H^+-ATPase in guard cells, provokes a reduction of cell turgor and finally causes stomatal closure (Vahisalu *et al.* 2008).

In *A. thaliana,* stomatal index reduction associated with decreased humidity has been linked to increased abundance of siRNAs and hypermethylation of two genes involved in early differentiation of stomatal cells (*SPCH* and *FAMA*), which exhibit low expression in drought-treated wild-type plants but not in mutants defective in specific methyl transferases (Tricker *et al.* 2012). To our knowledge, only the study of Medrano *et al.* (2014) mentioned above has assessed the association between stomatal traits and epigenetic markers in the MTEs, thus more experimental studies on the effects of the seasonal dry summer on epigenetic patterns are needed.

Root system: Deep rooting versus shallow rooting

Root system morphology is a complex trait that is greatly influenced by environmental cues. A large and deep root system enhances survival in plants under drought conditions (Ho *et al.* 2004; Lynch 2013; Lynch *et al.* 2014). In fact, rooting depths of vegetation types vary on a global scale, with deepest rooting patterns occurring in seasonally water-limited ecosystems such as MTEs (Nardini *et al.* 2014). The occurrence of deep rooting in Mediterranean plants might allow mobilisation of significant amounts of water from deep to shallow soil layers ('hydraulic redistribution'; Brooks *et al.* 2010), conferring improved drought resistance than found in shallow root systems (West *et al.* 2012). In addition, the ability to regulate root system morphology in response to environmental cues can give plants a selective advantage (Forde 2009).

Root morphology is controlled through intrinsic developmental pathways and environmental response pathways (reviewed in Malamy 2005). The latter pathway is not yet fully understood, but the phytohormone ABA is known to stimulate primary root elongation and suppress lateral root branching in response to drought (Wang *et al.* 2010; Smith & De Smet 2012). The intrinsic genetic mechanisms of root development under drought remain partially unknown. Several studies have found quantitative trait loci (QTLs) controlling root architecture during osmotic stress. For example, Fitz Gerald *et al.* (2006) found two QTLs, called EDG1 and EDG2 (ELICITORS OF DROUGHT GROWTH), which contribute to natural variation in root systems under water stress. In addition, the transcription factor *OBP4* controls root growth in *Arabidopsis* in response to ABA and osmotic stress (Ramirez-Parra *et al.* 2016), whereas the *LONG CHAIN FATTY ACID SYNTHETASE 2* (*LACS2*) gene is involved in the synthesis of a cutin layer that suppresses lateral root emergence under water stress

(Macgregor *et al.* 2008). Epigenetic regulation of root growth under water deficiency has been studied in *A. thaliana* (Cortijo *et al.* 2014), where pericentromeric DNA hypermethylation (mostly located within transposons) causes enhanced root growth (Virdi *et al.* 2015). This hypermethylation is mediated *via* a plastid-targeting protein MutS HOMOLOGUE 1 (MSH1) which varies in expression in response to environmental stress and also induces root biomass variation in *Sorghum bicolor* (De La Rosa Santamaria *et al.* 2014).

Adaptation to fire

Fire affects global biodiversity through changes in the patterns and processes in ecosystems (Bowman *et al.* 2016). Recurrent wildfires are an integral part of MTEs and, together with drought cycles, have definitively marked the evolution and diversity of MTEs (Rundel *et al.* 2016). At intraspecific level, similarly to other local perturbations that are destroying adult plants, fires alter plant population structure and open new empty space where selection may favour certain phenotypes during post-disturbance colonisation that will lead to genetic divergence (*e.g.* Roberts *et al.* 2014) and a shift in genetic diversity (Banks *et al.* 2013). Mild perturbations may also promote epigenetic divergence and the appearance of new epigenotypes at local scales, as recently shown in re-established populations of *Lavandula latifolia* (Herrera & Bazaga 2016). However, as far as we know, the specific epigenetic response in plants associated with colonisation after fire has not yet been analysed.

At community level, there is some debate about the evolutionary origin of fire-related traits (Bradshaw *et al.* 2011). Fire regimes selected adaptive traits to tolerate and even promote fire (Keeley *et al.* 2011). Adaptations to fire in the MTEs are classified into two main fire response syndromes: resprouters and reseeders (Litsios *et al.* 2014). Here, we reviewed evidence about the genetic and epigenetic control of several proposed fire-adaptive traits associated with these two syndromes.

Serotiny
Serotiny is the capacity to release seeds in response to an environmental trigger rather than spontaneously at seed maturation (Wymore *et al.* 2011). This trait is considered an adaptation to increase recruitment after fire rather than improve adult plant persistence (Martín-Sanz *et al.* 2016). The level of serotiny is a heritable trait and is influenced by fire regime (Wymore *et al.* 2011; Hernández-Serrano *et al.* 2014). However, the genes responsible for this trait have not yet been identified. Recent studies have found several single nucleotide polymorphism (SNPs) associated with serotiny in two *Pinus* species (Parchman *et al.* 2012; Feduck *et al.* 2015). Congruently, with the scarcity of knowledge about the genetics of serotiny, no epigenetic mechanism for serotiny has yet been established. However, the high plasticity of serotiny (Martín-Sanz *et al.* 2016) may suggest a role for epigenetics that could provide an additional layer of complexity to this trait.

Seed dormancy and heat- and smoke-induced germination
Another trait related to the reseeder strategy is seed dormancy and its break by fire. Seed dormancy is an adaptive trait that promotes survival through unfavourable seasons by delaying seed germination (Gubler *et al.* 2005). Dormancy allows maintenance of a soil seed bank and delayed germination until

conditions are optimal for seedling establishment, thus maximising long-term success. In fire-prone ecosystems such as MTEs, other additional advantages of seed dormancy are reduced competition and increased resource availability after fire (Tormo *et al.* 2014).

Seed dormancy is a phylogenetically widespread trait, occurring in 15–20% of extant angiosperm orders, but shows phylogenetic clustering in MTEs (Bradshaw *et al.* 2011). Many Mediterranean species have physically coat-imposed dormancy, which require fire (heat or smoke) for release through coat damage (Thanos *et al.* 1992; Herranz *et al.* 1998; Paula & Pausas 2008; Paula *et al.* 2009; Reyes & Trabaud 2009; Moreira *et al.* 2010; Moreira & Pausas 2012, 2016; Santana *et al.* 2013).

The physiological mechanisms involved in initiation and release of seed dormancy involve complex interactions between environmental and genetic factors (Gubler *et al.* 2005). Hormonal and genetic controls have been widely studied (recently revised by Finkelstein *et al.* 2008; Gao & Ayele 2014; Nonogaki 2014) and there may be a universal mechanism of seed dormancy associated with hormone regulation. In the mother plant, ABA is known to induce primary dormancy during seed maturation, whereas gibberellins (but also a decrease of ABA level) break dormancy. In addition, other phytohormones, such as ethylene and nitric oxide, are involved in regulating secondary dormancy (Arc *et al.* 2013). Although the heat control of germination remains to be elucidated, some membrane proteins such as the heat-shock-activated MAPK (HAMK) could be involved in the perception of heat signals and the release of dormancy (Hilhorst 2007). Recently, several researchers have investigated the regulation of seed germination by chemical signals from burning vegetation (Nelson *et al.* 2012). For example, karrikins (KARs) are butenolide molecules found in smoke that enhance seed germination and seedling photomorphogenesis (Flematti *et al.* 2015). After being dissolved by rain in the months following a fire, KARs are absorbed by seeds buried in the soil. KARs trigger the signalling pathway through the KARRIKIN-INSENSITIVE2 (KAI2) receptor (Waters *et al.* 2014; Morffy *et al.* 2016).

On-going research on model plant species indicates that chromatin remodelling through histone ubiquitination, methylation and acetylation plays a significant role in regulating seed dormancy by maintaining active transcription of dormancy genes and, in combination with DNA methylation and small RNAs, silencing during dormancy release (Nonogaki 2014). However, the species-specific variation of epigenetic regulatory mechanisms is far from being understood and its study in species associated with fire-prone ecosystems would be key to transfer this knowledge to restoration planning.

Resprouting
Resprouting is the capacity of plants to regenerate after severe loss of biomass through sprouting from meristematic tissue (Clarke *et al.* 2013). Although resprouting capacity has been traditionally classified as a binary trait, it is better classified depending on the location and amount of buds (lignotuber, epicormic buds, rhizomes, etc.) and their degree of protection (Belligham & Sparrow 2000; Clarke *et al.* 2013; Pausas *et al.* 2016). Resprouting is an adaptive trait that increases fitness under a wide range of disturbances, including fire (Lamont *et al.* 2011). Resprouting initiation is caused mainly by fire, but also by herbivory or drought (Zeppel *et al.* 2015). Post-fire

resprouting allows colonisation of spaces previously occupied by other non-resprouters, as biomass regeneration is faster than through seedlings (Pausas & Keeley 2014). This trait is geographically widespread, occurring in very different lineages and ecosystems worldwide (Vesk & Westoby 2004). However, there is a high prevalence of post-fire resprouter species in fire-prone MTEs (Pausas & Keeley 2014; Pausas et al. 2016, 2017).

Resprouting is a complex trait, with multiple ontogenetic origins implied. Its high prevalence in different lineages and its existence in basal angiosperms could indicate resprouting is an ancestral character and its absence a derived one (Verdaguer & Ojeda 2005). Some studies show resprouting variation has a genetic basis (probably linked to the capacity to increase carbohydrate reserves) and a low, but significant, heritability (Cruz et al. 2003; Whittock et al. 2003; Verdaguer & Ojeda 2005). All knowledge about resprouting development comes from the study of axillary bud dormancy and vernalisation in *Arabidopsis* and crop plants. Once again, a complex phytohormone signalling pathway is involved in the dormancy of buds and their release as a consequence of environment interaction (Horvath et al. 2003). Auxins and ABA act as growth inhibitors, whereas cytokines and gibberellins promote cell growth (Anderson et al. 2012; Cooke et al. 2012). These hormones act through modulation of cell cycle genes (*e.g.* CYCD, CYCB and CDKB; Horvath et al. 2003) and regulation of expression of DORMANCY ASSOCIATED MADS-BOX (*DAM*) genes associated with dormancy induction and release in buds of several perennial plant species (Horvath et al. 2008, 2010; Abbott et al. 2015). Recent studies have shown the importance of epigenetics in the control of bud dormancy (reviewed in Cooke et al. 2012; Rios et al. 2014). The proposed model of epigenetic control involves silencing of DAM genes and changes in expression of cell cycle genes through DNA methylation, histone deacetylation or ubiquitination and *Polycomb* activity (Karlberg et al. 2010; Santamaría et al. 2011).

Adaptation to oligotrophic soils

The MTEs occur on a large variety of soil types, but are often characterised by medium-low fertility (Allen 2001). The most limiting nutrients in MTEs are nitrogen and phosphorus, which are directly related to plant growth (Sardans & Peñuelas 2013). These limitations have shaped the MTE flora through enrichment in low-nutrient-adapted lineages (Stock & Verboom 2012; Rundel et al. 2016). In addition, drought and low-nutrient stress are highly correlated in MTEs, as drought acts indirectly on plants by reducing the availability of soil phosphorus and potassium (Sardans & Peñuelas 2004, 2007). Hence, plant adaptations to low-nutrient soils and drought are intimately related. Transgenerational plasticity in adaptation to Californian serpentine soils of the invasive annual grass *Aegilops triuncialis* have been experimentally tested (Dyer et al. 2010). Increased fitness of progeny was found to occur through both accelerating phenology, such that exposure to summer drought is reduced, and down-regulating photosynthesis rate, which results in larger, more fecund plants. Adaptations to oligotrophic soils have been recently reviewed by Sardans & Peñuelas (2013). Some of these adaptive traits that enhance survival in poor soils have been reviewed in previous sections. For example, investment in root systems helps to enhance nutrient uptake (Osmont et al. 2007), changes in leaf

morphology (Sardans et al. 2006a) as well as resprouting capacity, which is modulated by nutrient content of the soil (Sardans et al. 2006b). In addition, plants in MTEs generally have other common traits related to nutrient-poor soils, such as slow growth and sclerophylly (Kooyman et al. 2016; Read et al. 2016). Mediterranean plants achieve high nutrient use efficiency through enhanced retranslocation of nutrients from leaves before senescence (*i.e.* nutrient resorption; Pugnaire & Chapin 1993; Fife et al. 2008). This nutrient conservation mechanism seems genetically controlled but exhibits high plasticity (Brant & Chen 2015), potentially indicative of epigenetic regulation. Molecular control of nutrient mobilisation is complex, involving degradation, sequestration, chemical modification and intracellular trafficking (Himelblau & Amasino 2001). Multiple genes involved in this mechanism have been elucidated, including proteolytic enzymes, ligases and multiple transporters (Buchanan-Wollaston et al. 2003).

Although there are some studies on soils of Mediterranean species and ecosystems (*e.g.* Dyer et al. 2010), responses to soil mineral imbalance have mostly been analysed in model and crop plants, which provide little information on the epigenetic regulation of such responses. Evidence for altered chromatin structure and cytosine DNA methylation patterns and RNAs production is steadily increasing, including confirmation of partial heritability (Sirohi et al. 2016). Additional evidence for epigenetic responses to salt/alkaline stress and heavy metal pollution in a wide range of species (see Alonso et al. 2016b for a literature review) further point to a potential role of epigenetic regulation in plant adaptation to oligotrophic soils that might be species-specific. A better understanding of the relevance of epigenetic control in adaptation to contrasting soil conditions could be gained by analysing some epigenetic feature (*e.g.* cytosine methylation, histone acetylation, small RNAs) in natural populations with different soil features (*e.g.* Lira-Medeiros et al. 2010) or by comparative analyses of phylogenetically related species with contrasting soil requirements.

NEW PERSPECTIVES FOR UNDERSTANDING THE EPIGENETICS OF KEY TRAITS IN MTES: A FUTURE AGENDA

Our knowledge of the epigenetic basis of complex traits is still limited. Most of the dedicated past research has focused on model organisms and crop species. In spite of recent advances and rapid progress in plant epigenetics reviewed here, there is still much to be learned about 'plant epigenetics in the wild', in particular in the MTEs. Numerous little-investigated research areas need to be explored in the near future to understand the full significance of epigenetic variation and inheritance. We propose here a '*to do list*' for the study of natural epigenetic variation of key traits in the MTEs at different scales:

1 *At the molecular scale* — Understanding of the genetic basis of plant phenotypic traits and plastic responses to specific environmental stressors has reasonably progressed in the last few decades (see *e.g.* Lachowiec et al. 2016). However, we still need to elucidate the physiological pathways, genetic basis and epigenetic regulation of more specific traits such as serotiny or nutrient resorption. The refinement of epigenetic markers based on NGS should allow much deeper analyses of both model and non-model species epigenomes.

Genome-wide association studies (epiGWAS; Trynka *et al.* 2013) are powerful (but challenging) tools to study complex traits that could be determined by variants at multiple genetic or epigenetic loci. Thereafter, fine-tuned studies on the epigenetic regulation of specific genes could be assessed to explore the species-specific variation of epigenetic regulatory mechanisms, which is in general far from being understood.

2 *At ecological scale* — Uncovering the adaptive function of phenotypic plasticity and transgenerational stress memory through epigenetics requires joint analyses of the functional phenotype, the population genetic structure and the epigenetic variation of wild-growing plants to better understand how epigenetic changes affect individual survival and reproduction in contrasting environments and after single or multiple stress events. As recently suggested (Herrera *et al.* 2016), contrasting genetic and epigenetic spatial structures can help to elucidate the role of local environmental induction of heritable epigenetic changes.

In addition, evidence for regulation of key phenotypic traits in MTEs should be gained through specific experimental designs altering epigenetic mechanisms (*e.g.* Verhoeven *et al.* 2010; González *et al.* 2016; Herman & Sultan 2016) and/or adding epigenetic analysis to studies of local adaptation through reciprocal transplant experiments (reviewed in Matesanz & Valladares 2014). For example, a better understanding of the relevance of epigenetic control in species adaptation to contrasted soil conditions could be gained by analysing some epigenetic markers in natural populations with different soil features (*e.g.* Lira-Medeiros *et al.* 2010).

3 *At evolutionary scale* — Clarifying the role of epigenetic inheritance promoting (or hampering) diversification and speciation remains a challenge for evolutionary biologists (Pfennig & Servedio 2013). Experiment designs that test increasing population persistence (*i.e.* adaptive divergence) due to differential frequency of heritable epialleles could help to evaluate the role of epigenetics in promoting diversification. In addition, comparative epigenetic analyses of phylogenetically related species with different habitat requirements or ploidy levels could help to uncover the contribution of epigenetics to evolutionary change.

4 *At community scale* — Epigenetic studies at community level, comparing MTEs *versus* more stable ecosystems, could be timely and could help us understand the global effects of environment and epigenetics in adapting to a changing world.

ACKNOWLEDGEMENTS

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