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MINI-REVIEW: ECOLOGICAL SOLUTIONS TO GLOBAL FOOD SECURITY

Phenological diversity provides opportunities for climate change adaptation in winegrapes

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Summary

1. Climate change poses an unprecedented challenge to agriculture. While growers have always struggled with year-to-year variation in climate – early rains or unusually hot summers – climate change provides a major directional shift in mean climate.

2. Across the globe, growing regions are warming and plants are shifting in both time and space. Current and future shifts pose a major challenge to researchers and growers alike, yet they also highlight a major avenue to adapt crops to climate change – by understanding and exploiting phenological diversity.

3. Using winegrapes (*Vitis vinifera* subsp. *vinifera*) as a case study, we review the phenological diversity present within one crop and its underlying environmental and genetic drivers. In winegrapes, harvest dates are strongly tied to temperature, but this sensitivity varies greatly, with different cultivars (or 'varieties') of grapes ripening much more or less for the same amount of warming.

4. *Synthesis.* This phenological diversity provides a mechanism to help growers adapt winegrapes to shifting climates – by planting different varieties that will grow well under current and future climate regimes. More generally, understanding phenological diversity – including its environmental vs. genetic components – offers a major avenue to use ecological knowledge to advance adaptation for winegrapes, and many other crops, to climate change.

Key-words: common garden, crop, genotype × environment interaction, phenology, temperature response, *Vitis vinifera* subsp. *vinifera*

Shifts in plant phenology – the timing of recurring life-history events such as leafout or flowering – are some of the most consistent biological indices of climate change. Diverse datasets show an advance in the timing of leafout and flowering in plant species of 4–6 days per °C (Wolkovich *et al.* 2012), translating into shifts of 2–5 days per decade as temperatures have risen across the globe over the last 30–40 years (Root *et al.* 2003; Menzel *et al.* 2006).

Studies of plant phenological shifts come from diverse records and plant types (Cleland *et al.* 2007). Many studies have examined the effect of climate on phenology using clones of one or more species (e.g. Schwartz 1994; Menzel & Fabian 1999) or particular varieties of certain crops (e.g. Chuine *et al.* 2004; Estrella, Sparks & Menzel 2007), which often have long records and reduced variation in phenology when compared with natural communities. This greater variation seen in natural communities includes genetic differences across different populations (or clones), which can make it harder to tease out the exact effect of climate because different genotypes may show different responses to shifting climate (e.g. one genotype may advance its phenology more or less than another genotype per degree warming). Yet ecological research has repeatedly highlighted that these intraspecific differences are critical to understanding and predicting responses to climate (Scheepens & Stocklin 2013; Giuliani, Kelly & Knapp 2014; Wang *et al.* 2014).

We argue that considering the insights from ecological research on shifting phenology with climate change (Inouye 2008; CaraDonna, Iler & Inouye 2014), and its decades of research on teasing out the genetic vs. environmental drivers of phenology (Vitasse *et al.* 2010; Kim & Donohue 2013; Frei *et al.* 2014), provide an important perspective for mitigating how crops will respond to climate change. Such an understanding would allow improved predictions of where and when to plant different crops in the future, and –

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importantly – how exploiting existing phenological variation within crops could help maintain high-quality crops in many of their current locations as climate shifts. Here we review this possibility in detail for one major crop that has both high economic value and high phenological variation – winegrapes.

Phenology and climate change in winegrapes

Winegrapes are one of the world's most lucrative crops – with a global market valued at nearly €30 billion (measured as total exports of wine, OIV, 2016). They are also highly sensitive to climate change. From Europe to Australia, harvest dates show advances of 1–2 weeks over the last several decades (Duchene & Schneider 2005; Bock *et al.* 2011; Webb *et al.* 2012; Cook & Wolkovich 2016). Variation in phenological trends is high, however, even within the same country or region (Fig. 1). Both environment – especially climate – and genetics (i.e. winegrape cultivar) contribute strongly to phenology. Thus, understanding and accurately predicting the timing of winegrape phenological events requires detailed understanding of the full suite of climate cues that drive phenology, and how these vary across cultivars, also known as varieties or cèpages.

Climate is the dominant driver of the temporal and spatial variation of winegrape phenology, with temperature playing the largest role (García de Cortázar-Atauri, Brisson & Gaudillere 2009). Drought stress also impacts phenology (Van Leeuwen *et al.* 2009; Martorell *et al.* 2015), but it triggers smaller phenological changes (Jones 2013) and is dependent on many factors. In contrast, temperature is a dominant driver across all stages (Parker *et al.* 2011; Jones 2013). Correlations between winegrape phenology and temperature are so strong that grape leafout and harvest dates have been used to reconstruct past temperature regimes (García de Cortázar-Atauri *et al.* 2010; Fila *et al.* 2016). Indeed, the coordinated interannual variation across regions (Fig. 1) is mostly driven by large-scale climate patterns. For example, 1816, which stands out as the latest or nearly latest harvest date in all three time series – with harvest occurring well into October in Bordeaux and Burgundy and nearly in November in the Lower Loire Valley – was coined the 'Year Without a Summer' as many crops failed and all harvests were severely delayed because of the eruption of Mount Tambora (Oppenheimer 2003). In contrast, the earliest harvest dates in the records all occur in recent decades as global climate change has led to widespread and significant warming across the globe (Stocker, Qin & Platner 2013). Thus, climate is clearly a major driver of phenology and creates coherency in interannual phenological patterns across regions. Climate, however, does not explain all phenological variation – as different grape cultivars grown under common climate conditions still show tremendous variation in the timing of different events (Figs 2 and 3).

Nearly all winegrapes fall under one subspecies (*Vitis vinifera* subsp. *vinifera*) of which thousands of different varieties exist (Olmo 1995; Galet 2015), with over 1000 in production across the globe today (Anderson & Aryal 2013). Each variety is a distinct genotype associated with a unique mix of traits such as berry colour and size, drought response and phenology. With some exceptions (e.g. Marselan or Pinotage), most varieties are relatively old (Olmo 1995; Lacombe *et al.* 2013) and the majority of popular winegrape varieties today, such as Cabernet Sauvignon, Chardonnay or Pinot Noir, have been in existence for many centuries (e.g. Haeger 2004). Because grapes are clonally propagated, these varieties have remained nearly unchanged over time. Recent genetic studies have shown that winegrape varieties span a relatively narrow amount of genetic diversity – with many varieties being siblings to one another (Myles *et al.* 2011; Lacombe *et al.* 2013, 2014).

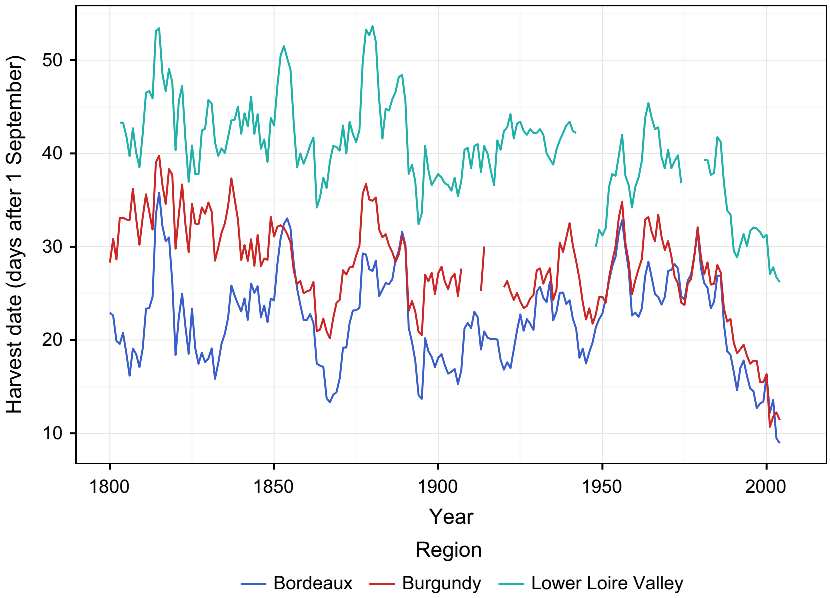

Fig. 1. Long-term trends in winegrape harvest dates from 1800 to 2007 across three major French winegrowing regions: Bordeaux (average growing season temperature: 17·7 °C; principal varieties: Merlot, Cabernet Sauvignon, Cabernet franc, Semillon, Sauvignon blanc, Muscadelle), Burgundy (average growing season temperature: 15·7 °C; principal varieties: Pinot Noir, Chardonnay, Gamay, Aligote) and the Lower Loire Valley (average growing season temperature: 15·8 °C; principal varieties: Cabernet franc, Chenin blanc). Harvest data from Daux *et al.* (2012); growing season temperatures and principal varieties from Johnson & Robinson (2013). [Colour figure can be viewed at wileyonlinelibrary.com]

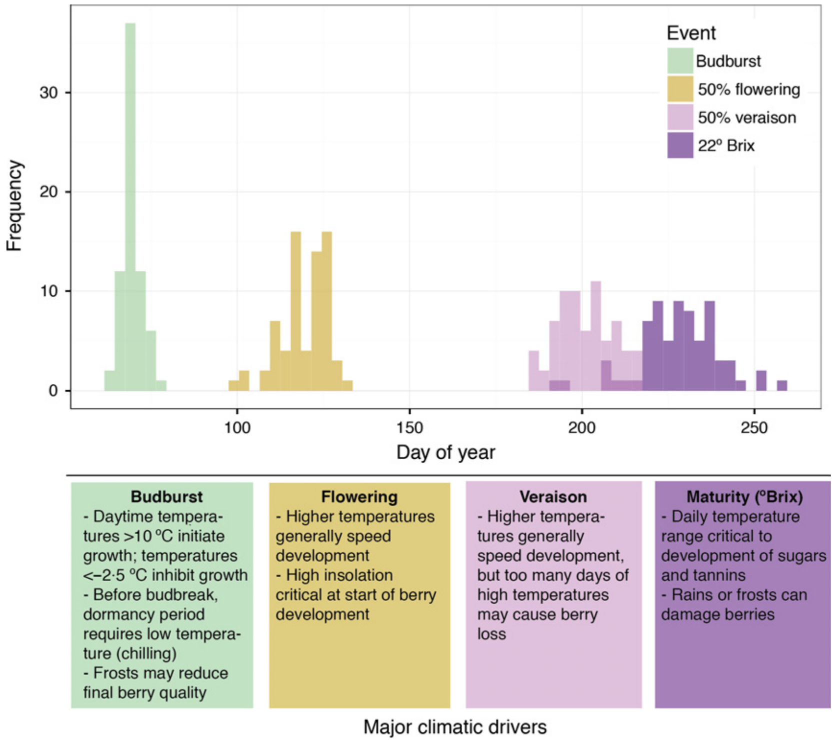

Fig. 2. The four major phenological events of winegrapes, measured under a common climate for 70 grape varieties: budburst (Eichorn-Lorenz stage 4), 50% flowering, 50% veraison (rapid sugar accumulation in grape berries) and maturity, measured as estimated day that 22° Brix is reached (top panel, data from 2015 from a common garden of grape varieties planted in Davis, California) and the major climatic drivers on each stage (summarized in Jones 2015) with additional information from Nemani *et al.* (2001). [Colour figure can be viewed at wileyonlinelibrary.com]

Despite their narrow amount of genetic diversity, the phenological diversity of winegrapes is remarkably high, even after controlling for environment (Figs 2 and 3). Winegrapes grown under common climate conditions consistently show that budbreak, flowering, and veraison (rapid sugar accumulation in grape berries, generally accompanied by a change in colour and/or softening) and fruit maturity (typically measured by sugar content) can vary by 3–6 weeks across different varieties (Boursiquot, Dessup & Rennes 1995).

Winegrowers use this phenological variation to their advantage. Because high-quality grapes generally require paced growth over a growing season such that they reach maturity only at the end of the season – after the heat of the summer, but before the frost or rains of autumn – growers tend to match the grape varieties that they plant to their local climate (Gladstones 2011). Though management and other local-scale factors (Coombe & Dry 1992; Dry & Coombe 2005) impact variety selection, there are general trends: growers in cooler regions tend to grow varieties that mature early, such as Riesling or Pinot Noir, while growers in hotter climates select late-ripening varieties, such as Furmint or Mourvedre (van Leeuwen *et al.* 2013). Therefore, some of the variation seen in phenology, especially variation within years (Fig. 1), likely reflects the different varieties grown in each region, with each region tending to plant a unique set of varieties with different ripening times.

Using standing genetic variation to inform phenologically based climate change adaptation

Current projections of future winegrowing regions suggest rapid and massive expansions in the future amount of land suitable for growing grapes (Hannah *et al.* 2013; Fraga *et al.* 2016). Already, winegrowing regions are moving north with climate change: in recent years, vineyards have expanded in southern England (Mosedale, Wilson & Maclean 2015) with hopes of being the ‘future Champagne’. Not surprisingly, these regions are tending to plant winegrape varieties that mature quickly. Yet, even as winegrape cultivation expands to higher latitudes, current winegrowing regions have the opportunity to continue producing high-quality wines by exploiting the phenological diversity of winegrapes.

Though work to date has tended to focus on phenology as an indicator of climate change, it may also provide a major opportunity for agronomic adaptation to climate change, through changing growing practices. Much as ecologists have exploited research on phenological variation across species’ ranges to suggest how assisted migration of certain genotypes could prevent some species’ declines with climate change (Taeger, Sparks & Menzel 2015; Aitken & Bemmels 2016), crop growers could follow a similar model of using genotypic variation to mitigate crop declines with climate change.

Most current projections of future winegrowing regions assume an extremely limited diversity of winegrape varieties will ever be planted and they generally ignore the possibility for regions to shift their planted varieties. Currently planted winegrapes show extreme phenological diversity (Fig. 2) and tolerate a variety of climates, with winegrapes grown successfully from the cool, short growing seasons of northern Germany and France to the long, hot growing seasons of southern Italy and the Greek islands (Anderson & Aryal 2013). Recent simple models of winegrape phenology highlight this variation in over 100 varieties (Parker *et al.* 2011, 2013). If growers could harness this diversity for climate change adaptation, it would allow vineyards to remain in

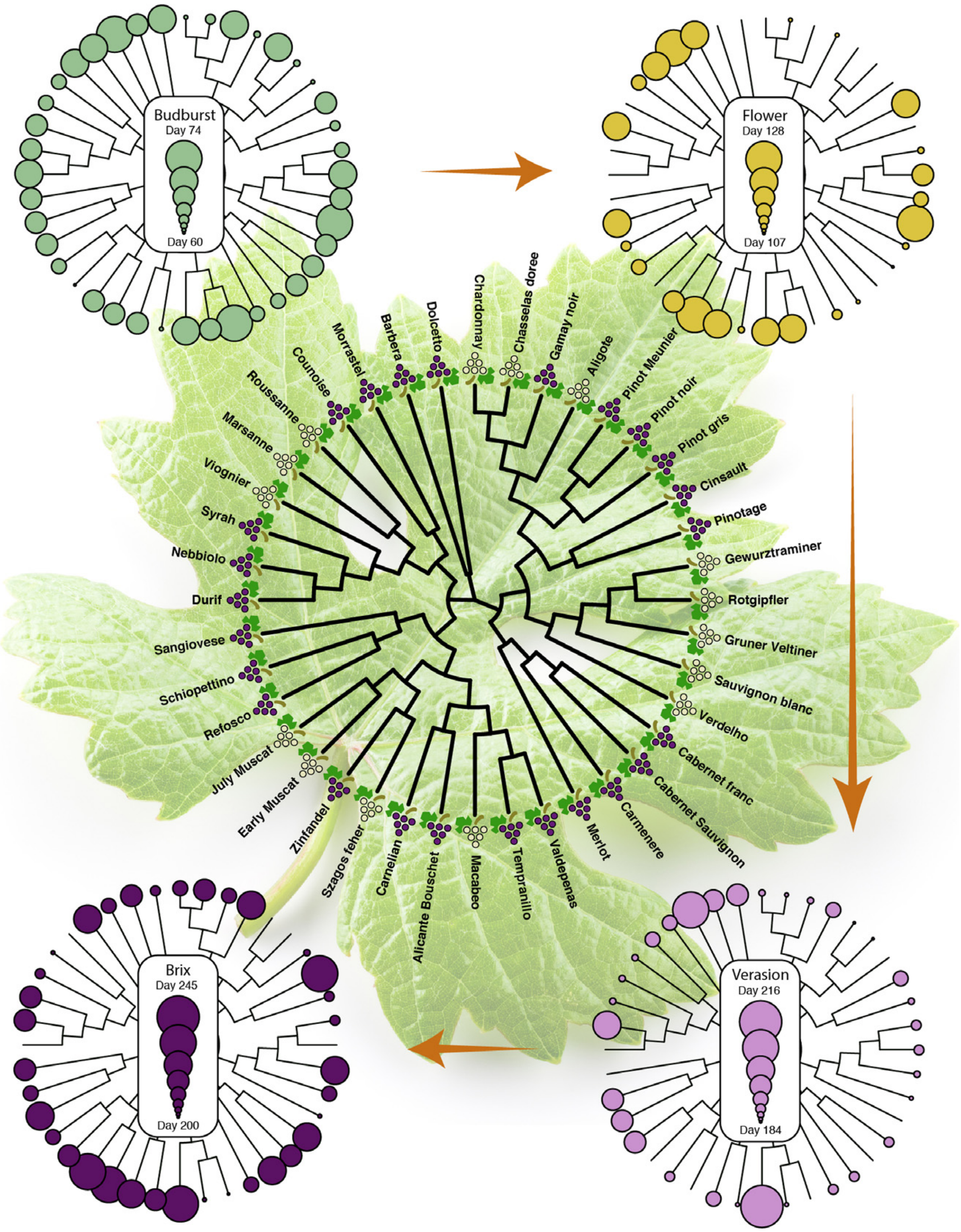

Fig. 3. How phenology maps onto phylogenetic relationships among different winegrape varieties. Proximity of varieties in the phylogenetic tree is proportional to the degree of genetic similarity (note that that the tree in the centre of the diagram is the same tree used to detail each event in the phenological series shown at the periphery of the central tree). Bubbles mapped onto the peripheral trees are proportional to the day of the year when a variety reached budburst (top-left, Eichorn-Lorenz stage 4), 50% flowering (top-right), 50% veraison (bottom-right) or 22° Brix (bottom-left). Tips without bubbles represent where data were unavailable for a particular stage and variety. Genetic and phenological data were collected in 2015 from a common garden of grape varieties planted in Davis, California. [Colour figure can be viewed at wileyonlinelibrary.com]

place, holding on to local knowledge of grape cultivation and winemaking, as well as the economic and cultural benefits that wine regions enjoy. Adaptation of growing practices could also prevent some of the potential expansion of vineyards into new, currently undeveloped regions (e.g. Hannah *et al.* 2013), thus, preventing unnecessary land use conversion. Doing so requires overcoming several major hurdles, some cultural and political, but many based on simple research needed to unlock the power of grape variety adaptation to climate change.

Major hurdles in climate change adaptation through phenology

Though winegrapes have been well studied by researchers for over a century, predicting which varieties are best suited to which climates remains more of an art than a science. Much of the reason for this discrepancy is data-related: developing models for particular varieties requires much more data than we currently have compiled. Such models require phenological data from the same varieties over a wide range of climates (ideally across both space and time) and multiple phenological stages.

While harvest dates are widely available, data on other stages are only readily available for roughly 100 or fewer of the >1000 varieties (Parker *et al.* 2011, 2013) and even for these varieties, the data have many limitations. Critically, data on dormancy are completely missing. Because observing when plants begin and (especially) end dormancy is extremely difficult (Rinne *et al.* 2011; van der Schoot, Paul & Rinne 2014), current phenological models are built on limited data and assumptions about how dormancy in winegrapes works – and the knowledge that release from dormancy must occur at some point before budbreak. Issues exist for other stages as well. For example, higher temperatures accelerate phenology up to a point (this exact point varies by crop and variety, but often occurs around 40 °C, see Parent & Tardieu 2012), after which any higher temperatures delay and eventually halt phenology (Wang & Engel 1998). Yet almost all data currently come from lower temperatures (often <30 °C). This is a major gap given that climate change is expected to push many regions into much higher temperatures, where data are lacking. Data concerns also extend to harvest dates, where growers' decisions about the maturity (or sugar) level to harvest at means that dates from different vineyards and different varieties may not be directly comparable. For example, a Chardonnay is generally harvested at a lower sugar content than a Cabernet Sauvignon, and sugar levels within varieties can vary from vineyard to vineyard and year to year – making comparison of the harvest dates without accompanying sugar data difficult (Webb *et al.* 2012).

With better data in hand, researchers could build greatly improved variety-specific crop models and begin to make robust projections for which varieties could be grown in which regions under future climate scenarios. These projections would in turn lay the critical groundwork for helping growers select what to plant in their vineyards in the future. Yet, given that more than 1000 varieties are planted today (Anderson & Aryal 2013), researchers need a better method than simple brute force data collection across all varieties to develop improved projections. We argue that in order to overcome this challenge, scientists will need a much better understanding of how environmental and genetic factors interact and determine the expression of phenological diversity in winegrapes.

Disentangling genetic vs. climatic factors to inform phenologically based climate change adaptation

Winegrape researchers know a great deal about the main environmental cues of different phenological events (see lower panel in Fig. 2); they have only begun, however, to study what controls these cues at the genetic level (Duchene 2016). Yet research across other plants and within grapes themselves suggests great promise for building a framework that predicts phenology – and possibly other traits – based on a variety's genotype. Such a framework could identify promising varieties not widely grown now that could be well adapted to new climates, and inform breeding new varieties. Research in model systems (e.g. *Arabidopsis* and *Populus*) provides compelling evidence that a suite of genes may shape multiple phenological events (Wilczek *et al.* 2010), and these genes are often conserved across diverse lineages. Furthermore, recent work shows how phenology can be robustly predicted based on the underlying genetic architecture (Chew *et al.* 2012). Given that we already have a partly annotated reference genome for winegrapes (Jaillon *et al.* 2007), and that most genetic tools can be easily transferred across the diversity of grapes (Myles 2013), the potential for rapid advances in grape research are high. Indeed, recent efforts to match parts of the winegrape genome to phenology and fruitfulness found several promising regions that explained up to 44% of observed variation (Grzeskowiak *et al.* 2013).

As in many crops, genetic data on winegrapes are accumulating rapidly (White *et al.* 2012), outpacing the collection of matching phenotypic data. Building high-quality phenotypic datasets thus appears to be the major current challenge to determining the genetic basis of phenology in most crops. While basic phenological observations are extremely simple – requiring only that someone note the phenological stage of a leaf, flower or berry cluster – to be useful they must be collected every 1–3 days, making the required time investment grow quickly with sample size. Furthermore, because phenology is strongly tied to climate, a common garden is required to isolate its environmental vs. genetic components. When combined with genomic data from the same plants, common garden phenological data can lead to insights into the evolution and genetic basis of phenology. This work can identify genes that strongly influence phenology (Grzeskowiak *et al.* 2013) and reveal how phenology has evolved during the history of domestication (Fig. 3). Nevertheless, robust estimates of the genetic component of phenology, as well as the genes involved in it, require data collected from across common gardens planted in different climates (McIntyre, Lider & Ferrari 1982; Vitasse *et al.* 2010; McKown *et al.* 2014; Migicovsky *et al.* 2016).

Yet we argue the goal of harnessing global data is well within reach. Many common gardens already exist in the research repositories of grape collections (e.g. USDA collections; Domaine de Vassal in France and many other government and institute-organized collections across winegrowing countries) but combining the resources of these international repositories will require researchers willing to bridge the gaps across variety synonymy issues and other hurdles. It will also require that funding agencies commit to unlocking the power of combined genetic and phenological data by providing support to combine the existing resources, collect additional needed phenotypic observations and related genomic data.

The two efforts – to improve phenological models of winegrapes through incorporating variety differences and to build a framework that allows researchers to predict the phenology of different varieties based on genetic differences – could advance together. Phenological observations collected from common gardens planted across climatic gradients would provide the raw material to build robust phenological models. It would also help identify the genetic basis of this phenological variation by allowing for large-scale statistical tests of associations between expressed phenology and genotype (Korte & Farlow 2013). Each component alone would greatly improve our ability to predict which varieties will grow best in which climates. But we argue that combining the two approaches would provide a major advance: it would allow greatly improved forecasting of responses to climate change across hundreds or even thousands of winegrape varieties, and could have major implications for breeding improved varieties for novel climates. Of course such models will only succeed in influencing growers if they are continually vetted with results from diverse varieties planted in common gardens across the globe.

Climate and agriculture: past and future

On a global scale, the earth's climate has been relatively stationary over the last several thousand years (Stocker, Qin & Platner 2013). Though weather varies each year to make some years cooler or hotter than others, the overall average has remained relatively unchanged. Over these years, humans have refined agricultural practices – identifying where certain crops grow best and others fail. For many crops they found certain cultivars that grew well in cooler climates with shorter growing seasons and others that needed longer, hotter seasons. In winegrapes, the marriage of climate to grape variety is critical to production of high-quality wines – so much so that many grape varieties have become tied to particular places, through tradition and sometimes law, such as Pinot Noir in Burgundy or Cabernet Sauvignon in Bordeaux and Napa.

Today stationary climate on a global scale is a thing of the past. While climate has shifted in certain regions in the past, humans have now altered the global climate to such an extent that the trend of warming in recent decades clearly stands out amidst the year-to-year variation, and this trend is manifested in the altered phenologies of many crops (e.g. Fig. 1). Even with major and sustained efforts to reduce greenhouse gas emissions, the globe will continue to warm for decades to come and humans must find a way to adapt their agriculture to our new non-stationary world.

We argue that understanding and exploiting phenological diversity of crops will be critical to meeting this new climate challenge. For many crops, diverse cultivars allow the crop to grow across diverse climate regimes, providing a major opportunity for adaptation. Many of these crops, including winegrapes (Myles 2013), are those where quality is emphasized over yield. By switching varieties as climates warm, growers may be able to stay in place and continue to grow the same crop for decades to come. But to do this requires (i) collecting better phenological data, (ii) researchers to translate these data into useful models of what will grow well under future climate regimes and (iii) the sharing of results with growers and producers. It also requires convincing producers, wine governance organizations and consumers of the value of matching variety to climate, and not a specific place, as our previous millennia of stationary climate allowed.

Authors' contributions

E.M.W. conceived of ideas, led writing of the manuscript and created Figs 1 and 2; D.O.B., M.A.W. and K.A.N. contributed to ideas, contributed critically to the drafts and gave final approval for publication; D.O.B. created Fig. 3.

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Data accessibility

Data from Daux *et al.* (2012) and Wolkovich (2017). Variety phenology. KNB Data Repository, https://doi.org/10.5063/f1rf5s05.

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