

## REVIEW

### SPECIAL ISSUE: THE ECOLOGY AND GENETICS OF POPULATION DIFFERENTIATION IN PLANTS

# Small spaces, big impacts: contributions of micro-environmental variation to population persistence under climate change

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## Abstract

Individuals within natural populations can experience very different abiotic and biotic conditions across small spatial scales owing to microtopography and other micro-environmental gradients. Ecological and evolutionary studies often ignore the effects of micro-environment on plant population and community dynamics. Here, we explore the extent to which fine-grained variation in abiotic and biotic conditions contributes to within-population variation in trait expression and genetic diversity in natural plant populations. Furthermore, we consider whether benign microhabitats could buffer local populations of some plant species from abiotic stresses imposed by rapid anthropogenic climate change. If microrefugia sustain local populations and communities in the short term, other eco-evolutionary processes, such as gene flow and adaptation, could enhance population stability in the longer term. We caution, however, that local populations may still decline in size as they contract into rare microhabitats and microrefugia. We encourage future research that explicitly examines the role of the micro-environment in maintaining genetic variation within local populations, favouring the evolution of phenotypic plasticity at local scales and enhancing population persistence under global change.

**Keywords:** climate change; ecophysiology; genetic variation; local adaptation; microenvironment; microhabitat; paleoreugia; plasticity; refugia.

## Introduction

Environmental conditions vary across the distribution of a species, both at the macroscale, such as across broad latitudinal or elevational gradients, and the microscale, such as microtopography within a local site. Macro- and micro-environmental variation

exposes natural populations to mosaics of resource availability, differing abiotic conditions, and a range of biotic interactions. In this review, we explore the extent to which local micro-environmental variation influences phenotypic plasticity, patterns of genetic

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variation and population persistence, especially in the context of global change. Fine-grained heterogeneity in topography, nutrient levels, water available and other environmental conditions creates microhabitats. Soil microhabitats can differ substantially in microbiotic diversity within small regions (Smith *et al.* 2011). Small-scale topographic features such as slopes and washes of ephemeral desert river beds can dramatically influence plant physiology (Ehleringer and Cooper 1988). In tropical forests, rooting phenotype differs substantially in species inhabiting canopy gaps versus understory sites (Paz 2003). Micro-environmental variation can influence tree and shrub recruitment and plant distribution patterns (Anderson 2009; Anderson *et al.* 2009). Furthermore, animal activities often create micro-environments that influence plant community composition, species diversity and phenotypic variation; for example, ant or kangaroo rat mounds (Guo 1998) or beaver dams (Wright *et al.* 2002) alter abiotic conditions such as soil moisture content, light availability or nitrogen content in the soil.

We define a plant's micro-environment as the small-scale abiotic and biotic conditions the individual experiences, which may differ from average conditions experienced by other individuals within the same population. Some locales may contain discrete microhabitats that can easily be distinguished from the surrounding environment, such as treefall gaps within a forest (Paz 2003) or elevated microsites within wetlands (Anderson 2009; Anderson *et al.* 2009). In other habitats, the micro-environment varies continuously across microtopographic and other gradients (Box 1; Fig. 1). Crucially, micro-environmental variation has the potential to buffer natural populations from the immediate effects of global climate change, thereby enabling populations to persist locally (De Frenne *et al.* 2013; McLaughlin *et al.* 2017).

In this review, we explore how micro-environmental variation influences the factors that contribute to phenotypic variation within natural populations, and the implications of this phenotypic variation for populations' responses to climate change. Phenotypic variation arises through genetic variation, environmental variation (plasticity) and genotype-by-environment interactions. Climate change has influenced all of these components of phenotypic variation (e.g. Franks *et al.* 2007; Nicotra *et al.* 2010; Wilczek *et al.* 2014; Anderson and Wadgyamar 2019). Industrialization and other human activities have disrupted the global climate (IPCC 2013), thereby decoupling previously correlated conditions (like temperature and photoperiod) that drive life history evolution (e.g. Wadgyamar *et al.* 2018b). Climate is a potent agent of selection on natural populations (e.g. Siepielski *et al.* 2017), and climate change is likely exerting novel patterns of selection by altering the abiotic and biotic environment (e.g. Van der Putten *et al.* 2010; Becklin *et al.* 2016). Some plant traits, like physiological parameters, are highly responsive to environmental conditions and will rapidly adjust to environmental change. In other cases, micro-environmental variation within contemporary landscapes may have already favoured adaptive genetic variation that could enable population persistence under climate change. To that end, this review examines how the micro-environment could influence how plant populations respond to novel stresses imposed by climate change. Specifically, we investigate plant physiology and phenotypic plasticity, along with genetic variation within populations through the lens of micro-environmental variation. We end by describing how micro-environmental variation could create microrefugia, which have conserved populations through geological episodes of climate change and which could be critical assets for conservation under rapid anthropogenic climate change.

## Physiology, climate change and micro-environment

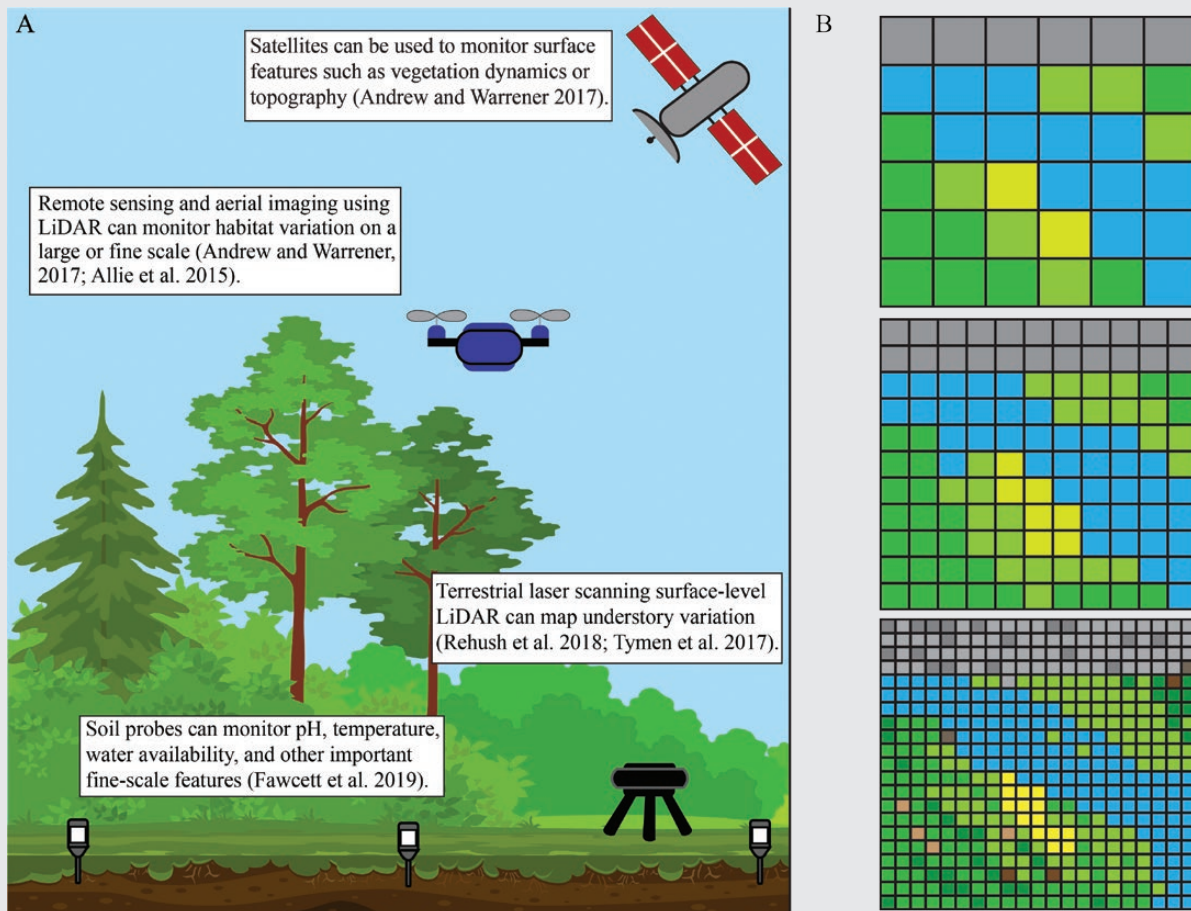
Anthropogenic climate change and other human activities are strongly influencing abiotic conditions as well as natural communities (Mitchell and Whitney 2018). Climate change has increased global temperatures, altered precipitation patterns and augmented the frequency of extreme weather events, with the extent of these changes differing across regions (Knapp *et al.* 2015; Borghi *et al.* 2019). Climate change and other anthropogenic forces act across broad scales, yet their effects on plants will depend on how they influence the local environments that individuals experience (Siepielski *et al.* 2017). The abiotic and biotic stressors plants encounter in their microhabitats affect physiological, phenological and morphological traits (Pereira 2016; Biswas *et al.* 2019). Water availability can vary substantially at fine spatial scales (Fig. 2), such as across an ephemeral riverbed along a well-drained slope (Free *et al.* 2013) or along elevational gradients (Kooyers *et al.* 2019). North- and south-facing slopes of mountainsides can experience stark differences in surface and air temperature (as much as 6 °C in the Swiss Alps) and soil temperature (3–5 °C in the Kluane region of Canada) (Scherrer and Koerner 2010; Dearborn and Danby 2017). Microhabitats can vary in light availability (Cervantes *et al.* 2005) and edaphic factors like metal concentrations (Ginocchio *et al.* 2004) and soil composition (Boege and Dirzo 2004). Thus, one plant may experience stress due to limited water availability, excessive waterlogging, thermal extremes or soil salinity, while a neighbour occupying a different micro-environment may experience more benign conditions. Understanding how microhabitats influence physiology will be essential to predicting the ecological and evolutionary responses to global change, and evaluating the potential for microhabitats to protect populations from some of the negative effects of this change.

Water availability plays a large role in the expression of physiological traits such as photosynthesis, water-use efficiency, stomatal conductance and stomatal density (Farooq *et al.* 2012). Water stress can reduce stomatal conductance and inhibit the biochemical pathways of photosynthesis (Tezara *et al.* 1999; Misson *et al.* 2010; Mathobo *et al.* 2017), but the extent to which a plant responds to drought and the type of response are a product of its genotype and its environment (Chaves *et al.* 2003). Even within biomes, precipitation patterns can determine plant species distributions (Engelbrecht *et al.* 2007), but it is more challenging to predict future precipitation under climate change than temperature patterns (Reside *et al.* 2019). Some models project that precipitation will increase at high latitudes, and that extreme conditions such as flooding or drought will become more pronounced in the tropics (Dore 2005; Schwartz *et al.* 2019). However, models differ in their projections about shifts in the intensity, frequency and duration of precipitation events (Trenberth 2011), making it challenging to predict how climate change will influence broad-scale precipitation patterns (Matte *et al.* 2019).

As models improve, predictions about regional-scale precipitation changes may become more accurate, yet understanding how these regional-scale changes influence local plant populations will be incomplete unless studies account for local micro-environments. Much research has examined plant responses to drought stress from the cellular to the organismal and even to the ecosystem level (Flexas *et al.* 2012; Pessarakli 2016), and experiments often attempt to scale from a few individuals measured under controlled conditions to the overall effect of drought on a region (Walker *et al.* 2018; Schwartz *et al.* 2019). Nonetheless, site-specific heterogeneity influences a plant's response to drought. For

**Box 1:**

Quantifying micro-environmental variation. (A) Discrete microhabitats have historically been identified by observing variation in species distributions, such as saguaro cacti seedlings growing under shade provided from nurse plants (Turner et al. 1966) or species growing on different soil types such as serpentine soil communities (Kruckeberg 1951) and gypsum outcrops (Meyer 1986). Researchers have quantified micro-environmental variation by measuring photosynthetically active radiation (PAR), pH, soil surface temperatures and soil nitrogen content in small regions of a landscape near plants of interest (Franco and Nobel 1989). Others have included soil-level details about microhabitat including microbe presence, isotopic composition of the soil (Smith et al. 2011) or soil texture (Misiewicz and Fine 2014). To characterize microhabitats regionally through time, one can deploy data loggers to track air and soil temperature, humidity, light levels, edaphic factors (e.g. pH, temperature, moisture) over multiple spatial and temporal scales (Fawcett et al. 2019). When combined with other thermal quantification techniques, such as infrared imaging, data loggers in the soil can be used to recover surface and air temperature variation across slopes of mountainsides (Scherrer and Koerner 2010). Recent technological advances have led to new techniques in remote sensing and identification of environmental variation. Counter-intuitively, remote sensing tools can provide fine-resolution information to help identify microrefugia as well as assess the quality and stability of the habitat when used with similarly fine-scale environmental data (Andrew and Warrener 2017). Landsat data have been used to monitor vegetation dynamics and may be used to detect and predict microrefugia (Andrew and Warrener 2017). Aerial Light Detection and Ranging (LiDAR) can detect microhabitat variation across a landscape and develop raster layers of soil composition for use in geographic information systems (Allie et al. 2015) while terrestrial LiDAR has been employed to map understory habitats to identify microhabitat variation within forest ecosystems (Tymen et al. 2017). New advancements in terrestrial laser scanning (TLS) can construct fine-scale 3D maps of object surfaces to the millimetre level (Rehush et al. 2018). Nevertheless, heterogeneity makes it difficult to use landscape features to predict microrefugia, so other fine-scaled observational tools are still necessary (Andrew and Warrener 2017). The tools required to delineate discrete microhabitats are becoming readily available and the computer algorithms designed to process the information are emerging quickly (Graham et al. 2019). These technological advances are beyond the purview of our paper; however, they are reviewed extensively elsewhere (Zellweger et al. 2019). (B) This hypothetical raster of a landscape illustrates the details that emerge from small-scale environmental data. As environmental data become more readily available, we can better inform our models with greater accuracy (Connor et al. 2019).







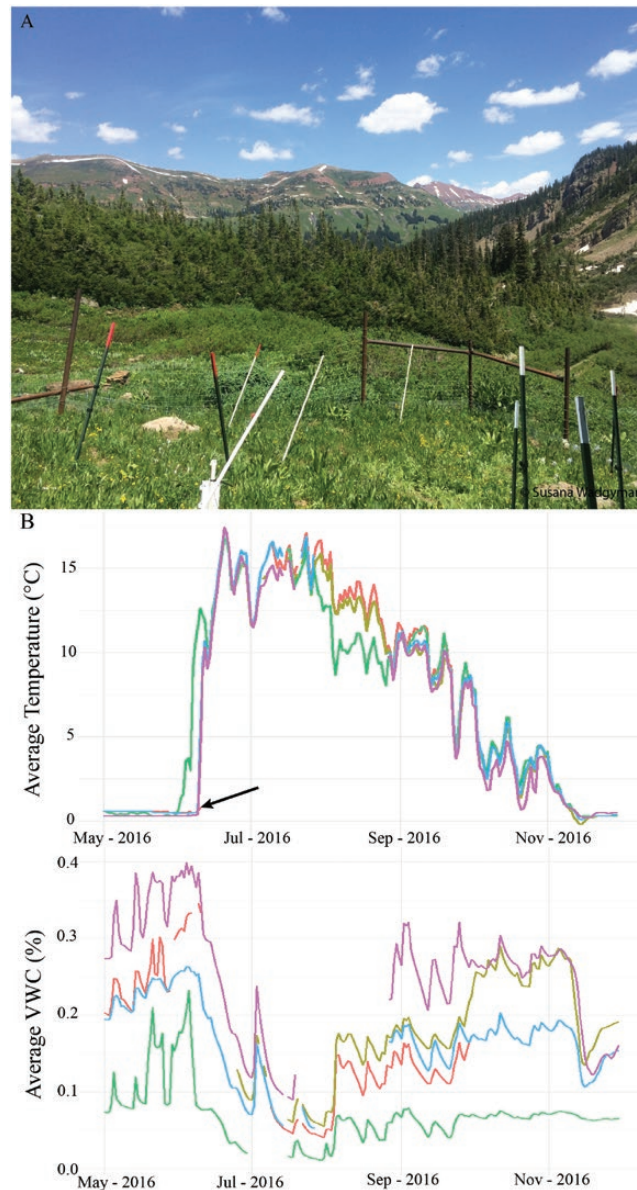
**Figure 1.** Examples of micro-environmental variation. (A) Soil ionic properties change drastically, as shown by zeolite outcrops in south-eastern Oregon, USA. (B) Slope and aspect influence light intensity along the Snake River, Idaho, USA. (C) Surface temperatures and soil depth are affected by the granite outcrops of Rock and Shoals, Georgia, USA. (D) The Tierra Amarilla Anticline of northern New Mexico, USA, is composed of sandstone and gypsum soils, which affect water availability to plants.

example, *Populus* species (Salicaceae) grown in a semi-arid environment showed substantial variation in stomatal size and density, attributed to small-scale climatic conditions in localized micro-environments (Pearce et al. 2006). Future experiments examining drought should incorporate micro-environmental variation if we are to assess the role of microhabitats in buffering against climate change. Recent technological advances have allowed us to consider this approach on a larger scale. For example, LiDAR analyses of a tropical forest's response to drought in Puerto Rico indicated that micro-environmental conditions such as solar radiation and moisture-bearing trade winds outweighed the effects of topography (slope, aspect and elevation) in forest recovery from drought, contrary to predictions (Schwartz et al. 2019).

In addition to affecting water dynamics, climate change is projected to continue to increase temperatures globally and cause more frequent heatwaves and temperature extremes (Hatfield and Prueger 2015). Thermal stress will disrupt the biochemical pathways related to photosynthesis (Kumarathunge et al. 2019), and can result in leaf senescence, decreased yield (in agricultural systems) and fitness (in natural populations), and inhibited root or shoot growth (Wahid et al. 2007). However, the degree of thermal stress depends on the species, phenological stage and the plant's ability to process temperature fluctuations on a daily basis (Żróbek-Sokolnik 2012). For example, seedlings from four species of Chihuahuan Cactaceae and three species from Asparagaceae showed species-specific effects on chlorophyll fluorescence and relative growth rate when grown in full sunlight (a heat-stress treatment) versus under the shade of mesquite nurse plants (*Prosopis laevigata*,

Fabaceae) (Pérez-Sánchez et al. 2015). Attempts to generalize the relationship between temperature and tree mortality on a regional scale in the Sierra Nevada Mountains (Paz-Kagan et al. 2017) as well as characterize plant traits on a global scale have repeatedly indicated physiological mechanisms for coping with temperature stress are species- and habitat-specific (Liu et al. 2017). Temperature varies substantially with micro-environmental conditions such as wind, light intensity, water supply and daylength (Kozłowski et al. 1991). These factors are often considered environmental noise (Bertolli and Souza 2013). However, modelling environmental variability has increased crop breeder's ability to predict and select for phenotypes across heterogeneous landscapes (Jarquín et al. 2014; Monteverde et al. 2019; Rincent et al. 2019). Additionally, when ecological niche models account for fine-scale environmental data, they can generate more robust predictions of species distribution patterns in contemporary (Pradervand et al. 2013) and future climates (Lenoir et al. 2017). By quantifying micro-environmental variation such as temperature, we can develop more effective models of individual physiology and ecosystem processes under climate change (Pincebourde et al. 2016; Tymen et al. 2017).

The effects of the abiotic stresses discussed above have mostly been evaluated in isolation; however, elevated  $[CO_2]$ , increased temperature and disrupted precipitation patterns interact to alter plant physiology (Xu et al. 2013; Ficklin and Novick 2017; Chiang et al. 2018). Open-air and growth chamber manipulations have revealed that increasing  $CO_2$  can induce higher photosynthetic rates (Farquhar 1997; Ainsworth and Rogers 2007; Bagley et al. 2015; Dusenage et al. 2019), and reduced



**Figure 2.** Micro-environmental variation can affect soil temperatures and water availability across small geographic areas. Here, we present soil temperature and volumetric water content as logged by five soil probes within 2 m of one another buried at a depth of 10 cm within a common garden site at the Rocky Mountain Biological Laboratory (A; elevation 3340 m). (B) Each color represents one probe. The data loggers record measurements at 15-min intervals; this figure displays data from the 2016 growing season. The arrow indicates the final day of snowmelt in the garden. Missing data can occur from gophers tampering with the soil probes. Although the probes are within close proximity to one another, there is a significant difference in mean annual soil temperature and volumetric water content across the garden site. By measuring small-scale differences in habitats, we can understand more about the environmental heterogeneity of regions and how these factors will affect plant populations. Climatic data displayed can be found in [Supporting Information—Table S1](#).

stomatal conductance (Kirschbaum and McMillan 2018), which could increase plant growth rate in an environment with more carbon dioxide (Xu et al. 2016). Warming temperatures can also enhance photosynthetic capacity of leaves (Linkosalo et al. 2016); however, an increase in carbon production may not necessarily augment biomass (Morrison and Lawlor 1999). Conversely, increasing temperatures are projected to intensify drought stress (Ficklin and Novick 2017), and elevated  $[\text{CO}_2]$  combined with hotter temperatures may exacerbate heat stress (Warren et al. 2011), potentially counteracting any fitness gains from higher photosynthetic rates. Plant responses to simultaneous changes in temperature, aridity and  $\text{CO}_2$  concentration may differ substantially from predictions generated by studying each factor in isolation (Zandalinas et al. 2018). Plant physiological

and demographic responses to changing abiotic conditions depend on habitat heterogeneity and biotic interactions across microhabitats (Tomioolo et al. 2015; Kleynhans et al. 2016). As such, experiments considering the effects of climate change should account for the fine-grained interactive responses between abiotic and biotic conditions (Price et al. 2013). Multifactorial experiments provide robust tests of how climate change factors interact in contemporary landscapes (Eller et al. 2011). These interactive forces will likely vary across the landscape.

Micro-environmental variation could potentially protect local populations from the adverse physiological effects of climate change (Silva et al. 2013). Uriarte and colleagues (2018) monitored seedling growth and survival within a tropical forest in Puerto Rico over a 9-year period, finding that moist



microhabitats buffered individuals against the negative effects of fluctuating rainfall and solar radiation. Likewise, in the semi-arid rangelands of Mongolia, fine-grained variation in the environment maintains functional trait variation within local communities, which could potentially enhance population persistence under novel precipitation patterns and increased temperatures (Lang et al. 2019). Thus, fine-scale environmental heterogeneity may mitigate the effects of climate change if climatically benign microsites exist locally (McLaughlin et al. 2017).

#### Future directions

Micro-environmental variation affects plants from the cellular to the organismal level by influencing temperature, nutrient availability and water availability. Modelling fine-grained environmental variation could lead to a more profound understanding of the dynamics that shape physiological plasticity and influence the genetic structure of populations across landscapes (Thuiller et al. 2008). Challenges arise when models use large grid sizes that overshadow fine-scale heterogeneity (Thuiller et al. 2008). Nevertheless, recent approaches have sought to address these difficulties with a combination of fine-grained environmental data and more readily available coarse-grained data sets (Mertes and Jetz 2018). Additionally, researchers are developing advanced geographic information system data sets that incorporate fine-scale environmental variation (Graham et al. 2019). We encourage future multifactorial experiments that evaluate the consequences of changing micro-environmental conditions on plant physiology. Such studies can test the hypothesis that fitness gains from elevated  $[\text{CO}_2]$  are counterbalanced by fitness losses from increasing temperatures, novel precipitation regimes and micro-environmental stresses. Additionally, multifactorial manipulations may reveal ways in which micro-environments could ameliorate the effects of climate change.

The increasing availability and cost-effectiveness of applying large-scale genomic, transcriptomic and epigenomic analyses to non-model organisms (Singhal 2013; Ellegren 2014; Richards et al. 2017) will also improve our understanding of physiological responses to microhabitat variation in natural plant populations. Differences in gene expression may underlie plant responses to variation in moisture regime, temperature, soil types and other environmental gradients (e.g. Sork 2017; Gould et al. 2018; Tripathi et al. 2019). Likewise, epigenetic variation may differentiate plant populations inhabiting different microhabitats (Richards et al. 2012; Herrera and Bazaga 2016), suggesting that epigenetic mechanisms could also contribute to physiological responses to climate change. In particular, future genomic, transcriptomic and epigenomic studies could identify the molecular bases for physiological responses of natural populations to projected future climatic conditions, and whether different microsites may potentially strengthen or dampen these responses.

In addition to affecting the abiotic conditions that directly influence plant physiology, climate change will also alter biotic interactions among species, including competition, pollination, herbivory and host-pathogen dynamics (Box 2). We summarize predictions regarding many of these biotic interactions in Box 2, yet an exhaustive consideration of the impacts of climate change on community dynamics is beyond the scope of this review. Nonetheless, microsites have the ability to alter biotic interactions over small spatial scales (Fransen et al. 2001; Collins and Foré 2009; Soliveres et al. 2015). Studies aiming to predict how climate change will affect community dynamics ought to

include consideration of microhabitat variation and its potential to strength, weaken or fundamentally alter the impacts of climate change on biotic interactions.

#### Genetic variation within populations

As climate change intensifies, the persistence of local populations depends on the extent of heritable genetic variation in traits subject to novel selection imposed by climate change (Hughes et al. 2008; Bellard et al. 2012; Salmela 2014; Wilczek et al. 2014; Ravenscroft et al. 2015; Becklin et al. 2016; Sheth et al. 2018). Many plant species have adapted to local abiotic and biotic conditions across habitat types or broad spatial scales where gene flow is limited (Leimu and Fischer 2008; Lowry et al. 2008; Hereford 2009; Wadgyamar et al. 2018a). In addition, micro-environmental variation can exert divergent selection across small spatial scales even within natural populations, resulting in microgeographic adaptation (Schmitt and Gamble 1990; Argyres and Schmitt 1991; Lechowicz and Bell 1991; Antonovics 2006; Dittmar and Schemske 2017). Could microhabitats maintain sufficient genetic variation in functional traits for populations to adapt to climate change (Bridle and Vines 2007; Richardson et al. 2014; Becklin et al. 2016; Gossmann et al. 2019; Razgour et al. 2019)?

If microhabitat heterogeneity causes the magnitude and direction of selection to vary extensively, pockets of genetic variation could be maintained within local populations, as long as localized selection is strong enough to overcome gene flow (Steiner and Berrang 1990; Argyres and Schmitt 1991; Richardson et al. 2014). For example, *Impatiens* species (Balsaminaceae) in the forest understory demonstrate adaptive differentiation between populations located at very fine spatial scales (10–50 m) (Schemske 1984; Schmitt and Gamble 1990; Argyres and Schmitt 1991). Indeed, local populations have differentiated genetically in response to micro-environmental variation in edaphic conditions (Lechowicz and Bell 1991). Additionally, temporal variation can maintain genetic diversity within populations (Salmela et al. 2013; Salmela 2014; Salmela et al. 2016). For example, in *Pinus sylvestris* (Pinaceae), populations encountering variable yearly growing seasons have greater genetic variation in reproductive phenology than populations in more stable conditions (Salmela et al. 2013; Salmela 2014).

Discrete microhabitats that differ substantially in abiotic or biotic conditions from the surrounding environment can contain individuals with alleles or traits that are not common in the rest of the population (Richardson et al. 2014; Prentice et al. 2015). For example, populations of the outcrossing grass *Anthoxanthum odoratum* (Poaceae) occur in both heavy metal contaminated soils and pasture habitats, separated by a distance of <20 m (Antonovics 1972, 1976, 2006). Common garden experiments have revealed that populations from these two soil types in close proximity are genetically differentiated in metal tolerance (Antonovics 1968, 2006; McNeilly and Antonovics 1968), and plants from contaminated soils flower earlier than plants in nearby, relatively benign pasture soil (Antonovics 1968, 2006; McNeilly and Antonovics 1968; Antonovics and Bradshaw 1970). Similarly, in reciprocal transplant experiments, populations of *Leptosiphon parvifloris* (Polemoniaceae) from serpentine soils flowered earlier than populations from sandstone soils in both habitat types, indicative of genetic differentiation across short spatial scales, as these habitats can be separated by a distance of <10 m (Kay et al. 2011; Dittmar and Schemske 2017). Reproductive phenology also differs between *Ricotia lunaria* (Brassicaceae) populations inhabiting contrasting microsites within the Evolution Canyon model system in Lower Nahal Oren, Mount Carmel, Israel (Kossovser et al. 2009; Nevo 2012;

**Box 2: Overview of environmental shifts impacting plant communities as a result of climate change.** As the effects of climate change progress, plant communities will encounter novel biotic and abiotic. Below is a synopsis of the most pertinent challenges they will face and a non-exhaustive list of references.

Effect	Prediction	References
<b>Abiotic</b>		
[CO <sub>2</sub> ]	Increased: CO <sub>2</sub> concentrations are increasing by ~20 ppm per decade due to anthropogenic forces.	IPCC (2013), Bereiter et al. (2015), Lüthi et al. (2008)
Temperature	Increased: Globally, temperatures will increase, and more frequent heat waves and temperature extremes will become the norm. Night-time temperatures are projected to increase more than daytime temperatures. Soil temperatures are warming faster than air temperature.	Hatfield and Prueger (2015), Karl et al. (1991), Zhang et al. (2016)
Precipitation	Altered: High latitudes will experience an increase in precipitation. All areas are projected to see an increase in extreme conditions such as flooding or drought associated with altered precipitation patterns.	Dore (2005), Schwartz et al. (2019), Trenberth (2011)
Soil	Altered: Cation exchange capacity will be altered, and soils will become more acidic. C and N cycling in the soil will be affected by increased temperatures.	Allen et al. (2011), Rengel (2011)
<b>Biotic</b>		
Resource competition	Altered: Certain species will gain a competitive advantage under climate change, whereas others will be at a disadvantage, which could shift community dynamics.	Urban et al. (2012), Blois et al. (2013), Gilman et al. (2010), Alexander et al. (2015)
Plant community composition	Altered: Woody shrubs will encroach upon grasslands and move poleward. Novel plant communities may arise due to differing migratory potential.	Gilman et al. (2010), Bond and Midgley (2012), Blois et al. (2013), Pearson et al. (2013), Urban et al. (2012)
Pollinator–plant interactions	Disrupted: Flowering phenology and pollinator activity respond to different environment cues, and potentially become unsynchronized. Flowering may decrease due to insufficient vernalizing temperatures.	Hegland et al. (2009), Byers (2017), Inouye (2019), Byers and Chang (2017)
Herbivory	Increased: Insect herbivores could adapt quickly to effects of climate change, consume more plant material as C:N ratios in leaves increase and expand ranges into herbivore-naïve plant communities. Increased opportunities for mammalian and insect herbivory across longer growing seasons.	Liu et al. (2011), Rasmann et al. (2014), Robinson et al. (2012), Becklin et al. (2016)
Below-ground interactions	Altered: Soil microbial community composition can be affected by drought conditions and carbon levels determined through leaf litter. Precipitation patterns can also determine top-soil microbial diversity.	Kaisermann et al. (2017), Pugnaire et al. (2019), Sheik et al. (2011), Eisenhauer et al. (2012)

Qian et al. 2018). *Ricotia lunaria* inhabits both the warm, dry, open savannah-like south-facing slope and the lush, green, shaded temperate north-facing slope, which are separated by only 100 m at the base (Nevo 2012). In common garden environments, populations from the south-facing slope flowered earlier than those on the north-facing slope, and showed upregulation of drought-response genes (Kossover et al. 2009; Nevo 2012; Qian et al. 2018). Thus, fine-grained spatial heterogeneity in the landscape can selectively favour adaptive genetic variation within populations.

The genetic difference in flowering of metal-tolerant *A. odoratum*, serpentine-adapted *L. parvifloris* and drought tolerant *R. lunaria* may become more relevant under climate change. The early onset of flowering often enables plants to escape from drought stress, which is expected to increase in severity as a result of climate change (Franks 2011; Dai 2013;

Weis et al. 2014). Furthermore, in some species, climate change favours advanced flowering (Franks et al. 2007; Munguía-Rosas et al. 2011; Anderson et al. 2012; Bemmels and Anderson 2019). As a result, populations of *A. odoratum*, *L. parvifloris*, *R. lunaria* and other species that are adapted to rare edaphic conditions could contribute to the continued local persistence of their species in the context of climate change (Richardson et al. 2014).

Genetically diverse populations may have increased adaptive potential under environmental change, which is increasingly important as human activities continue to fragment natural habitats and climate change alters abiotic and biotic conditions. For example, *Festuca ovina* (Poaceae) is a widespread perennial grass that grows across the various microhabitats on the island of Öland (Sweden) (Prentice et al. 1995, 2015). In addition to one native copy of the gene coding for the enzyme PGIC (*PgiC1*), some *F. ovina* populations also have

an additional expressed transgene copy (*PgiC2(f)*) horizontally derived from the genus *Poa* (Poaceae), which may help them adapt to micro-environmental variation in pH and soil moisture (Vallenback et al. 2008, 2010a, b; Prentice et al. 2015). PGIC plays a key role in glucose metabolism, and polymorphisms in PGIC are associated with variation in environmental factors such as temperature and salinity (Riddoch 1993; Prentice et al. 2015). In this system, the populations harbouring the transgene along with the native copy could have enhanced capacity to adapt to an increasingly fragmented landscape under climate change (Prentice et al. 2015).

To generate robust predictions of evolutionary responses to environmental change, studies can examine how populations respond genetically to climatic manipulations through time (e.g. Davies and Snaydon 1976; Panetta et al. 2018), resurrect historical lineages for comparison with current populations (e.g. Franks et al. 2008; Gómez et al. 2018) or expose contemporary populations to historical, current and predicted future conditions (e.g. Anderson and Wadgyamar 2019). Longitudinal studies are uniquely situated to evaluate adaptive potential in future climates if they monitor populations in treatments relevant to climate change. As part of the long-standing Park Grass Experiment, *A. odoratum* (Poaceae) was maintained in a mosaic formation of plots differing in nutrient levels for ~60 years (Davies and Snaydon 1976; Silvertown et al. 2006). The plots were spaced closely such that gene flow was expected to occur; nevertheless, reciprocal transplant experiments found that populations of *A. odoratum* were adapted to their local nutrient conditions, indicating that adaptation in this species can be rapidly achieved via standing genetic variation (Davies and Snaydon 1976; Silvertown et al. 2006). Thus, fragmented populations of *A. odoratum* may be able to adapt to rapid deterioration of environmental conditions due to climate change. Resurrection studies that compare populations before and after episodes of climate change (e.g. Franks et al. 2018; Hamann et al. 2018) can also accomplish similar objectives of assessing adaptive potential of natural populations. For example, Franks and colleagues (Franks et al. 2007; Hamann et al. 2018) documented rapid adaptation of drought escape in the mustard *Brassica rapa* (Brassicaceae) by comparing lineages collected before and after severe droughts in California. Despite rapid evolution of flowering time and other traits associated with drought escape, contemporary generations express lower fitness than historical generations, suggesting that climate change may quickly outpace adaptive evolution, even for short-lived species (Hamann et al. 2018). Taken together, these approaches provide powerful tests of the adaptive potential of natural populations under climate change.

#### Future directions

The genetic variation present within locally adapted populations may enable populations to withstand environmental changes associated with climate change (Razgour et al. 2019). In contrast, if limited gene flow restricts migration, locally adapted populations could be increasingly vulnerable to novel climatic conditions (Anderson and Wadgyamar 2019). Studies that account for fine-scale micro-environmental variation could identify populations potentially harbouring sufficient genetic variation to persist under climate change. Indeed, Sexton and colleagues (2013) found that environmental factors had a greater influence on genetic structure within populations than geographic distance across 70 published studies. Landscape genetic analyses using individual-based sampling that incorporate micro-environmental variation can provide

insight into the ways in which heterogeneous landscapes affect genetic variation (Wang and Bradburd 2014). Local populations may already include individuals that are adapted to conditions consistent with climatic projections for the area. These pre-adapted lineages could contribute disproportionately to adaptive responses to climate change (Fig. 3).

The rate of adaptation in a population is proportional to its additive genetic variance for fitness (Fisher 1930; Shaw and Etterson 2012); thus, high genetic variance in fitness could aid populations in adapting to climate change. However, empirical studies assessing the additive genetic variance for fitness and evolutionary potential of natural populations are rare (Hendry et al. 2018; but see Sheth et al. 2018; Bemmels and Anderson 2019). Estimates of the additive genetic variance for fitness can be statistically and methodologically difficult to obtain (Hendry et al. 2018), but studies aiming to predict evolutionary dynamics under climate change should estimate these parameters for populations exposed to projected future climates whenever possible. Researchers should also quantify whether differences in additive genetic variance for fitness exist between populations from heterogeneous and homogenous environments to gain further insight into whether historical exposure to micro-environmental variation has influenced populations' future adaptive potential.

In many cases, estimates of additive genetic variance for fitness may be unattainable, but researchers can examine genetic variation in functional traits relevant to climate change across a variety of microhabitats. For example, flowering phenology is highly responsive to climatic variation, and climate change may impose selection favouring earlier flowering (Sherry et al. 2007; Cleland et al. 2012; Wadgyamar et al. 2018b; Bemmels and Anderson 2019). Other functional phenotypes that could generate novel insights about climate change responses include foliar traits related to adaptation to increased temperatures and drought stress (specific leaf area, leaf water content, stomata size and density, water-use efficiency), and traits related to herbivore defence and resistance, as herbivory may increase with warmer temperatures (Anderson and Gezon 2015; Arnold et al. 2019). Additionally, drought stress can favour the evolution of smaller flowers (e.g. Galen 2000) to reduce water loss. As pollinators typically prefer larger flowers (e.g. Sandring and Agren 2009; Parachnowitsch and Kessler 2010; Krizek and Anderson 2013; Lavi and Sapir 2015), drought-mediated selection for smaller flowers could fundamentally alter plant-pollinator interactions in outcrossing species. Genotypes from distinct microhabitats displaying trait differentiation can be exposed to contemporary and projected future conditions in common gardens and other experiments under field conditions (e.g. Bemmels and Anderson 2019) to assess the degree to which a trait is genetically or environmentally determined, to evaluate genetic variation in complex traits, and to test the adaptive nature of these traits. Additionally, global change is not expected to uniformly influence the microclimate of different soil types (Hamidov et al. 2018). The selective pressures existing across distinct soil types can vary, possibly resulting in key adaptations to future environmental conditions.

Genomic scans have successfully identified signatures of selection in many populations (Jump et al. 2006; Manel et al. 2010; Yeaman et al. 2016; Leempoel et al. 2018). Intriguingly, these studies have occasionally detected signatures of local adaptation at very fine (i.e. microsite-level) spatial scales, including in *Salix herbacea* (Cortés 2017) and in animals (e.g. a salt-marsh fish, Wagner et al. 2017). Researchers can make additional inferences about adaptive population divergence





phenotypic plasticity and thus be better equipped to respond to changing climates than populations from stable, homogenous environments. However, not all examples of plasticity are adaptive (Langerhans and DeWitt 2002; Price *et al.* 2003; Ghalambor *et al.* 2007; Chevin and Lande 2015). When plasticity causes traits to shift in a direction antagonistic to the direction of selection, plasticity can be maladaptive. Maladaptive plasticity can arise as a response to environmental stress (Ghalambor *et al.* 2007; Chevin and Lande 2015). For example, stem elongation to escape from the shade of competitors is usually an adaptive phenotype (Dudley and Schmitt 1996; Schmitt *et al.* 1999; Weinig and Delph 2001). However, when the competitors are too tall to overcome, stem elongation can result in a fitness cost for the organism, resulting in maladaptive plasticity (Weinig 2000; Steinger *et al.* 2003). Whether plasticity in response to climate change will be adaptive or maladaptive may depend on the specific trait and environmental context.

Adaptive plasticity evolves in fine-grained heterogeneous environments with high levels of gene flow, which can hinder local adaptation (Schlichting 1986; Sultan 1987; Mooney and Agrawal 2008; Baythavong and Stanton 2010). For example, in the Australian woody shrub *Dodonaea viscosa* (Sapindaceae), populations separated by short geographic distances and connected by extensive gene flow experience extensive variation in temperature, aridity and precipitation (Baruch *et al.* 2018). Substantial variation in functional traits among populations in close proximity results from phenotypic plasticity rather than local adaptation in this species, allowing *D. viscosa* to have a higher potential to acclimate to climate change (Baruch *et al.* 2018). Similarly, in the salt marsh plant *Borrichia frutescens* (Asteraceae) on Sapelo Island in Georgia, USA, populations located only 20–50 m apart are likely connected via pollen flow and can differ dramatically in phenotype (e.g. height) depending on salt concentration (Richards *et al.* 2010). In *B. frutescens*, trait variation across salt gradients arises from phenotypic plasticity rather than from genetic adaptation (Richards *et al.* 2010). High levels of plasticity in *D. viscosa* and *B. frutescens* could indicate that they can respond to rapid environmental fluctuations as a result of climate change within a single generation. The existence of gene flow over heterogeneous microhabitats is a hallmark for the evolution of adaptive plasticity, though quite often, a mix of genetic adaptation and plasticity occurs in nature (Wadgyamar *et al.* 2017a). In systems where gene flow between populations inhabiting different microsites is low, genetic adaptation may be more likely to evolve than phenotypic plasticity, and the response to climate change may be delayed.

Thus far, we have focused on within generation plasticity. However, trans-generational plasticity can also contribute to trait expression when the parental environment strongly predicts the environment that the offspring will experience; in those cases, parents can provision their progeny with extra-genetic information that can enhance offspring fitness in parental environment. Thus, trans-generational plasticity could accelerate phenotypic responses to environmental conditions (Wolf and Wade 2009; Holeski *et al.* 2012; Baker *et al.* 2019). Trans-generational plasticity is expected to be favoured under stable environments but has the potential to be maladaptive if progeny encounter conditions that differ from those experienced by their parents (Galloway 2004; Visser 2008; Wadgyamar *et al.* 2018b). The maternal environment influences offspring responses to shade and herbivory (Galloway 2004; Bell and Galloway 2007; Galloway and Etterson 2007; Colicchio *et al.* 2015; Colicchio 2017) and even simulated climate change (Wadgyamar *et al.* 2018b). Epigenetic variation may be one mechanism by which plant

phenotypic plasticity can rapidly evolve (Zhang *et al.* 2013). More multigenerational experiments are needed to further assess the origins and populational-level effects of trans-generational plasticity (Donelson *et al.* 2018), especially in the context of climate change.

#### Future directions

As a result of climate change, plant populations face rapid shifts in abiotic and biotic stress (Box 2), which may outpace adaptive evolution and migration for many species (Loarie *et al.* 2009). Plasticity could enable local populations to express appropriate trait values rapidly, thereby mitigating the immediate effects of climate change (Nicotra *et al.* 2010). Theory suggests adaptive plasticity evolves in populations that experience fine-scaled temporal and spatial heterogeneity. Future studies should determine whether populations can manifest optimal phenotypes under simulations of projected climates, within a single generation and in a trans-generational context. Transcriptomic and epigenomic studies will be crucial in gaining a mechanistic understanding of how individual plants may plastically respond to changing climates, and whether these plastic responses may be passed to subsequent generations and promote rapid adaptation (Zhang *et al.* 2013).

#### Microhabitats as microrefugia: a paleobotanical perspective

Microhabitats influence plant physiology, potentially buffer against environmental change, promote the maintenance of adaptive genetic variation and contribute to the evolution of phenotypic plasticity. However, we do not know whether the small spatial scale of these effects is relevant to predicting long-term responses to global climate change. Do microhabitats facilitate species persistence over centuries to millennia, or are they ephemeral reservoirs for populations doomed to extinction? Microrefugia are microhabitats that allow populations of formerly widespread species to persist locally through periods of inhospitable conditions until a return to favourable regional climates (Rull 2009; Hannah *et al.* 2014). Because microrefugia distinguish local from regional environments and may potentially encompass an entire local population, the spatial extent of microrefugia is likely to be somewhat larger than that of the fine-scale, within-population microhabitat variation that has been the primary focus of our review. However, our discussion of microrefugia continues our consideration of the effects of small-scale environmental variation, in which heterogeneous landscapes create isolated habitats of limited spatial extent that differ markedly from their surroundings.

Empirical paleobotanical and phylogeographic studies have revealed that microrefugia sometimes facilitated survival through major, long-lasting climate shifts such as Pleistocene glacial cycles (Mee and Moore 2014). Pleistocene glaciation induced major changes in plant distributions globally, including latitudinal and elevational shifts, and range contractions and expansions (Bush and Colinvaux 1990; Hewitt 1999, 2000; van der Hammen and Hooghiemstra 2000; Davis and Shaw 2001; Carnaval *et al.* 2009; Dupont 2011; Qiu *et al.* 2011). Traditional paradigms for understanding the distributions of warm-adapted species during glacial periods have emphasized the importance of large refugia where regional-scale climates were suitable for species persistence (Hewitt 1999, 2000; Harrison *et al.* 2001; Soltis *et al.* 2006; Carnaval *et al.* 2009). In temperate forest plants, recent evidence has increasingly challenged this viewpoint and highlighted evidence for long-term persistence of populations

in small, scattered microrefugia within areas where regional climates were generally unable to support persistence (Stewart and Lister 2001; Willis and van Andel 2004; McLachlan et al. 2005; Provan and Bennett 2008; Rull 2009; Bemmels et al. 2019). The concept of microrefugia has also been applied to understanding Pleistocene distributions of animals (Schmitt and Varga 2012), as well as plants from alpine (Patsiou et al. 2014), boreal (Väliranta et al. 2011) and tropical biomes (Leal 2001; Collins et al. 2013).

The precise ecological and edaphic characteristics of microrefugia have rarely been identified (Rull 2009; but see Delcourt et al. 1980; Delcourt and Delcourt 1984). However, for a site to serve as a microrefugium, local environmental conditions must be decoupled from regional climates (Dobrowski 2011; Hylander et al. 2015; McLaughlin et al. 2017). Decoupled environmental conditions are particularly likely to arise in topographically complex environments, where slope, aspect and landscape position strongly affect local climates (Dobrowski 2011; Hylander et al. 2015). Hydrologic microrefugia may also exist where local sites are more mesic than surrounding areas (McLaughlin et al. 2017). Beyond facilitating population persistence, microrefugia may also have evolutionary consequences (Mosblech et al. 2011; Mee and Moore 2014). Small populations are subject to strong genetic drift, suggesting that populations in microrefugia could exhibit reduced genetic diversity and increased inbreeding, and be strongly genetically differentiated from one another and from larger populations in areas of stable regional climates (Mosblech et al. 2011; Mee and Moore 2014). Range expansion from microrefugia following a return to favourable climates may therefore have important consequences for genetic diversity in recolonized areas. Regions recolonized by populations that expanded from one or a small number of microrefugia might be expected to exhibit low genetic diversity. Alternatively, simultaneous recolonization from numerous genetically differentiated microrefugia could result in higher overall genetic diversity than would be expected given recolonization from a single, large refugium (Mosblech et al. 2011).

Microrefugia are also likely to differ in selection regimes relative to other areas where populations persist, suggesting that survival in microrefugia may drive the evolution of local adaptation (Mee and Moore 2014). Local adaptation is widespread in contemporary plants (Leimu and Fischer 2008) and was likely also prevalent in ancient populations (Davis and Shaw 2001), including microrefugia (Mee and Moore 2014). However, low genetic diversity, high genetic drift and inbreeding depression associated with small populations may reduce the ability of microrefugial populations to adapt to local environments (Leimu and Fischer 2008). In contrast, small population sizes could favour the evolution of specific traits, such as self-fertilization to avoid inbreeding depression (Mee and Moore 2014). Collectively, the independent evolution of populations inhabiting different microrefugia whether due to neutral genetic phenomenon or as a result of selection, and subsequent differential survival and extinction of these populations, may not only allow species to persist through periods of climate change, but may also lead to evolutionary change in the species as a whole (Stewart 2009).

#### Future directions

A general consensus on the relevance of microrefugia to species persistence through extended periods of climate change remains elusive (Hewitt 1999; Stewart and Lister 2001; Tzedakis et al. 2013; Rull 2014) for at least two major reasons. Firstly, microrefugia are difficult to detect using traditional paleobotanical and phylogeographic tools (Tzedakis et al. 2013), and their existence is often inferred but rarely explicitly documented (Rull 2009).

Multiple lines of evidence including fossil evidence, genetic studies and species distribution models have widely been used to infer the presence of refugia, but each approach has a variety of limitations and potential biases; the strengths and weakness of these approaches have been reviewed elsewhere (Tzedakis et al. 2013; Gavin et al. 2014). Secondly, even in exceptional cases where macrofossils provide physical evidence of localized species presence in a putative microrefugium (e.g. Delcourt et al. 1980; de Lafontaine et al. 2014), macrofossils do not necessarily represent populations that persisted through an entire period of climate change and left descendants in modern populations. Instead, these populations might eventually have gone extinct (Stewart and Lister 2001; Hannah et al. 2014) or otherwise failed to contribute to range recolonization after a return to favourable climates (Mandák et al. 2016).

Future research into microrefugia would benefit from combining these multiple lines of evidence (e.g. fossil evidence, genetic studies and species distribution models) to strengthen confidence in the identification of microrefugia (de Lafontaine et al. 2014; Gavin et al. 2014). In addition, explicitly testing whether small, isolated populations left descendants in modern populations would help clarify that these populations indeed contributed to long-term species persistence, rather than serving as evolutionary dead-ends (Hannah et al. 2014). Genomic data may be combined with recent advances in statistical phylogeography (e.g. Carnaval et al. 2009; He et al. 2013, 2017) to test these hypotheses and to reveal novel and detailed geographic and ecological insights into the roles of microrefugia. For example, modelling methodologies that incorporate genetic, climatological, spatial and ecological information, and that can be statistically evaluated using Approximate Bayesian Computation (Beaumont et al. 2002), can provide a robust hypothesis-testing framework. These types of models have been used to identify the latitude and longitude of refugia from which eastern North American hickories recolonized formerly glaciated regions, revealing that one species expanded from northern microrefugia while another species did not (Bemmels et al. 2019); to determine that differences in microhabitat affinity drove different responses to glaciation in two co-distributed Rocky Mountain sedges (Massatti and Knowles 2016); and to demonstrate that postglacial range shifts that tracked summer drought regimes at a regional scale better explain genetic structure in a Californian oak than shifts constrained by microhabitat availability (Bemmels et al. 2016). As modelling techniques improve, statistical phylogeographic approaches will no doubt continue to provide quantitative support for or against the importance of microrefugia, especially in cases where qualitative interpretation of traditional data sets has been controversial (Tzedakis et al. 2013).

Growing evidence that Pleistocene microrefugia likely existed for some, but not all, plant species also highlights the species-specific nature of responses to climate change (Stewart 2009; Stewart et al. 2010; Papadopoulou and Knowles 2016). Why some species persisted in microrefugia but others did not remains poorly understood and is an area in need of further study. Theoretical arguments suggest that both the climatic conditions necessary to generate microrefugia and the ability to persist in them could depend strongly on species' individual ecological niches. In particular, microrefugia are likely to arise only when species' ranges are limited by climatic factors that are not strongly correlated with other aspects of regional climate (Hylander et al. 2015). Traits such as high stress tolerance, long lifespan, asexual reproduction or selfing mating systems, and low genetic load could increase the probability that small plant



populations will persist in these environments (Hampe and Jump 2011; Mosblech *et al.* 2011). Empirical evidence has suggested that for temperate woody plants, traits that may have facilitated survival in microrefugia include small seeds, wind dispersal, vegetative reproduction and generalist habitat affinities (Bhagwat and Willis 2008). In addition, microrefugia are more frequently proposed to have existed for mesic and generalist temperate trees than for dry-adapted species (Bemmels *et al.* 2019), but patterns are too preliminary to draw firm conclusions. Finally, the ability to persist in microrefugia may also depend on biotic interactions with other community members, such as competitors, pollinators and pathogens. Climate change may influence the potential geographic distributions of each of these community members differently (Stewart *et al.* 2010; Hylander *et al.* 2015), leading to non-analogue communities and novel biotic interactions (Jackson *et al.* 2000). For example, lowered CO<sub>2</sub> concentrations during glacial periods could have led to the increased competitive advantage of conifers over broadleaf deciduous trees on a wider variety of microsites, due to the greater carbon-use efficiency of conifers (Jackson *et al.* 2000). However, the potential role of biotic interactions in mediating survival in microrefugia has as yet been underexplored.

### The role of microrefugia in plant conservation

Given that microrefugia have helped facilitate persistence of some plant species in response to historical climate change, could they also play a role in plant conservation in the face of ongoing global change? Benign habitats located within or near the current distribution of a species could provide refuge for local populations in the face of climate change. These refugia could enhance population persistence for populations that lack the genetic variation needed to adapt to novel climates quickly or that have limited migratory potential (Olson *et al.* 2012). Refugia can occur within short distances of current distributions and therefore be accessible to species with spatially restricted seed and pollen movement (Hylander *et al.* 2015). In addition, some refugia will occur in areas that form part of current distributions and will consist of relictual populations (Rull 2009). Because climate change may rapidly alter conditions across broad geographic areas, many of the most readily accessible future habitats within or near current distributions may only exist at small local sites where conditions are decoupled from regional patterns (Hylander *et al.* 2015), highlighting the potential importance of microrefugia.

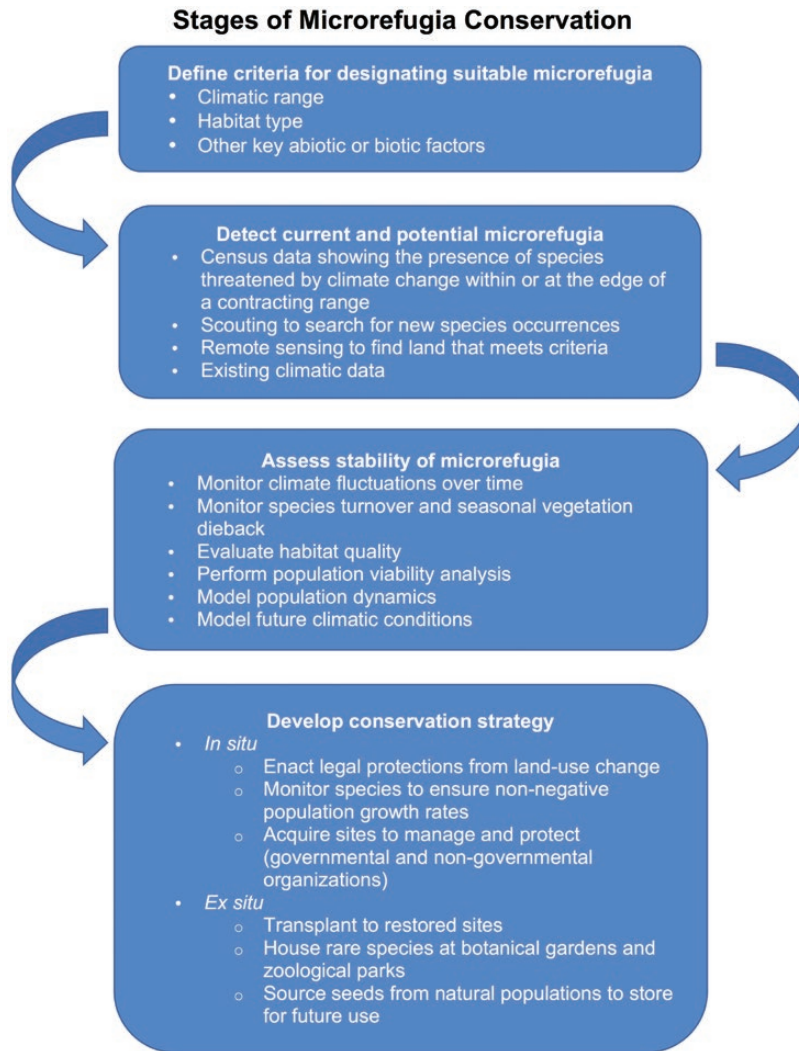
Conservation planning that incorporates a potential role for microrefugia should be informed by data on functional trait variation within these microsites. Within plant species, functional traits that influence fitness often vary across environmental gradients; this intraspecific trait variation arises through a combination of long-term adaptation to local environments, phenotypic plasticity, genetic drift and other demographic processes (Ackerly *et al.* 2002; Kooyers *et al.* 2015; Wadgymar *et al.* 2017a, b). Plant phenotypes can also vary across micro-environmental gradients within local sites (Blonder *et al.* 2018). For example, in an alpine plant community in the Colorado Rocky Mountains, moist fine-textured soils with high phosphorus and nitrogen levels were associated with long root systems and rapid growth rates at the micro-environmental scale (Blonder *et al.* 2018). Species' distributions within micro-environments were not only influenced by abiotic conditions, but also by competition with other species in the community (Blonder *et al.* 2018), which can vary in magnitude due to nutrient patchiness in heterogeneous soils (Fransen *et al.* 2001; Bliss *et al.* 2002; Garcia-Palacios *et al.* 2012). Combining abiotic

data that captures micro-environmental variation in a region with demographic and trait data (e.g. Oldfather and Ackerly 2019) from observational and experimental studies will improve predictive models of community structure and dynamics, as the micro-environment can determine species distributions (Blonder *et al.* 2018).

In addition to refugia's role as a climatic haven, these areas might host unique habitat types that support rare species with specific habitat requirements (Wintle *et al.* 2019). For example, tall and short grass prairies in the mid-Western United States were heavily converted to agriculture in the 18th century because of their rich soils (Camill *et al.* 2004). As a result, the native prairies of Minnesota have become rare and occupy <1 % of their original range (Camill *et al.* 2004). Throughout the region, these grasslands only exist now as small and isolated patches, yet prairie specialists require these rare patches for persistence (Camill *et al.* 2004). Rare habitat types are especially susceptible to fragmentation and degradation, as they are uncommon in the landscape. Because these habitats are also likely to contain rare species, these fragments are of high conservation priority and are crucial to the species' future success (Wintle *et al.* 2019). Small, isolated populations typically have restricted genetic variation, and communities in fragmented landscapes may have high prevalence of invasive species (Wintle *et al.* 2019). Given that >50 % of the world's terrestrial habitats now exist in a state of intermediate to very high human modification (Kennedy 2018), conservation biology will increasingly require managing populations confined to small habitat patches such as these, highlighting the need for research into the viability of populations in microrefugia and other small populations.

Pervasive anthropogenic habitat fragmentation alters microclimatic conditions within a landscape, thereby increasing the difficulty of identifying potential refugia (Latimer and Zuckerberg 2017). Given an increased impact of edge effects, isolated forest fragments experienced greater temperature fluctuations than large continuous forests. Additionally, current microrefugia are threatened by land-use change (Davies *et al.* 2017). Areas that have been identified as a current or potential refugium are seldom given protection, legal or otherwise. Because microrefugia are still not regarded as holding much conservation value, they face greater risk of disturbance. Restoring degraded sites so that they may serve as refugia is a viable option for plant conservation (Braidwood *et al.* 2018). Threatened plants may be transplanted to sites within or at the edge of the species' range to ensure their survival during periods of climate change that may cause local extinction (Braidwood *et al.* 2018).

Current methods show promise for successfully identifying stable refugia—areas that are habitable in the long term and are not subject to the environmental fluctuations that surrounding areas may experience (Tang *et al.* 2018). Some areas with a high level of endemism may be climatically stable future refugia (Harrison and Noss 2017). Centres of endemism typically occur in regions that are not subject to large fluctuations in climate, like coastal zones, because these conditions enable the persistence of rare taxa (Harrison and Noss 2017). Mountainous regions typically have high topographical and climatic diversity; this heterogeneity not only fosters biodiversity, but it also could create climate refugia (Harrison and Noss 2017). Models for predicting species' risk of extinction that combine current and past species distributions, climate, topography and edaphic data are more accurate than models that only take climatic factors and species distribution into account (Niskanen *et al.*



**Figure 4.** Proposed framework to identify and conserve plant microrefugia for species threatened by climate change. Microrefugia conservation is a fluid process that may not always follow these discrete steps. Multiple viable approaches exist, and steps may differ when the goal is to protect ecological communities rather than individual species.

2016). By accounting for micro-environmental variation, models can generate more robust predictions about extinction under climate change (Niskanen et al. 2016). It is possible to construct reliable models for predicting the locations of climate refugia given sufficient and appropriately small-scale and species-specific biotic and abiotic data for the local environment (Niskanen et al. 2016). For example, Tang and colleagues (2018) combined current and historical species abundances and distributions with climatic data from relictual populations to identify refugia and determine the relative stability of refugia in the face of climate change. Ecological niche models showed that mild winter temperatures generate long-term stable refugia in East Asia (Tang et al. 2018). Monitoring endemic species richness across the landscape will also help conservationists prioritize refugia (Tang et al. 2018).

#### Future directions

Conceptually, microrefugia could play a critical role in plant responses to anthropogenic climatic changes by enabling populations to endure without the need to migrate long distances to track rapidly changing climates (Neilson et al. 2005; Rull

2009; Feurdean et al. 2013). Conservationists still debate which criteria to use when identifying refugia, making it challenging to implement policy or management practices (Ashcroft 2010). For example, it is uncertain whether refuges will be of higher conservation value if they best reflect the historical climate of a region or the fundamental niche of the species inhabiting the region (Ashcroft 2010).

Developing management strategies for protecting habitats can be difficult when current warming trajectories greatly differ from historical patterns (Morelli et al. 2016). McLaughlin and colleagues (2017) argue that identifying species-specific hydraulic refugia is not only essential for plant population persistence but also beneficial in understanding the hydraulic effects of climate change. Topographic heterogeneity creates variation in water availability across landscapes, and benign micro-environments could serve as hydraulic microrefugia for plants that require mesic habitats when the environment becomes warmer and more arid (McLaughlin et al. 2017). Conservationists have not yet agreed upon procedures for using microrefugia to conserve plants, nor are there many policies in place to protect microrefugia. Numerous strategies to identify

and preserve microrefugia exist, but the most effective option depends on the conservation goals (Fig. 4). For example, to conserve a species threatened by drought, it may be more important to find a hydraulic refuge than a refuge with a suitable and stable climate (Fig. 4). After deciding how to define a refuge, there are multiple options for detecting stable locations that meet this criterion (Fig. 4). National-scale conservation laws may not be sufficient to protect threatened species if they do not account for the specific needs of organisms on a regional scale (Rossi et al. 2015).

Early efforts to preserve rare and endemic species in microrefugia hold great promise. In Valencia, Spain, researchers have established microrefuges, which are small (up to 20 hectares), actively managed areas intended to protect species and habitat types for the long-term persistence of plant populations (Laguna et al. 2004). Strategically located microrefuges protect more critically endangered taxa than larger natural protected areas (Laguna et al. 2004) while also harbouring more species than neighbouring plots of the same size without a microrefuge (Fos et al. 2017). Thus, managing *in situ* microrefugia is an effective conservation method.

If microrefugia are indeed havens for biodiversity, then biodiversity within microrefugia would be relatively high, even when very little land has been sampled. In a recent meta-analysis, Stein and colleagues (2014) found a significant and positive relationship between environmental heterogeneity and species richness across taxa, spatial scales and regions. Accounting for fine-resolution heterogeneity in landscapes can help identify and preserve microrefugia, especially for species imperilled by climate change. This process will become easier as researchers continue to collect demographic and trait data across diverse ecosystems to assess and predict how species, especially rare species, respond to global change.

## Conclusions

Climate change is rapidly altering ecological and evolutionary dynamics of natural communities and populations. Here, we argue that plant responses to novel suites of conditions may depend on the extent of abiotic and biotic micro-environmental variation in the landscape. Local micro-environments may already reflect climatic projections for a region if some microhabitat patches experience warmer temperatures or more or less arid conditions than average for a given site. Given that fine-grained spatial and temporal heterogeneity in environments can favour the evolution of phenotypic plasticity, pre-existing plasticity to the micro-environment may buffer local populations from decline as the climate continues to change. However, existing plasticity may not be sufficient to stabilize populations long term if future climates exceed the range of variability of historical climates. In those cases, adaptive evolution could be necessary to enable population persistence. We posit that micro-environmental variation could favour the evolution of adaptive genetic variation within local populations owing to different selective regimes over very small spatial scales. In that case, local populations might already harbour sufficient genetic variation to avoid extinction under climate change. Finally, benign local environments that reflect historical climates have sometimes facilitated survival through geological climate change, and these types of environments (e.g. natural depressions with cooler temperatures) could serve as microrefugia under anthropogenic climate change, enhancing plant conservation

as climate change continues. We encourage research that explicitly incorporates microhabitat variation into studies of plant responses to climate change. Ultimately, evolution in response to historical levels of micro-environmental variation might have generated enough adaptive potential to maintain populations in the short term, allowing us more time to enact effective conservation policy.

## Supporting Information

The following additional information is available in the online version of this article—

**Table S1.** Climatic data from a high-elevation meadow location near the Rocky Mountain Biological Laboratory (latitude: 39.0315806; longitude: -107.07846, elevation: 3340 m) from the period 1 May 2016 to 31 December 2016. The Decagon 5 TM sensors recorded soil temperature and soil volumetric water content at 10 cm depth at 15-min intervals. Data are displayed in Fig. 2.

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## Contributions by the Authors

All authors conceived of this project, wrote sections of the manuscript, and edited the manuscript. J.T.A. provided data in Fig. 2B.

## Conflict of Interest

None declared.

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## Literature Cited

- Ackerly D, Knight C, Weiss S, Barton K, Starmer K. 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia* 130:449–457.
- Ainsworth EA, Rogers A. 2007. The response of photosynthesis and stomatal conductance to rising [CO<sub>2</sub>]: mechanisms and environmental interactions. *Plant, Cell & Environment* 30:258–270.
- Alexander JM, Diez JM, Levine JM. 2015. Novel competitors shape species' responses to climate change. *Nature* 525:515–518.
- Allen DE, Singh BP, Dalal RC. 2011. Soil health indicators under climate change: a review of current knowledge. In: Singh BP, Cowie AL, Chan KY, eds. *Soil health and climate change*. Berlin, Heidelberg: Springer Berlin Heidelberg, 25–45.
- Allie E, Pelissier R, Engel J, Petronelli P, Freycon V, Deblauwe V, Soucemarianadin L, Weigel J, Baraloto C. 2015. Pervasive local-scale tree-soil habitat association in a tropical forest community. *PLoS One* 10:e0141488.
- Alpert P, Simms EL. 2002. The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? *Evolutionary Ecology* 16:285–297.
- Anderson JT. 2009. Positive density dependence in seedlings of the neotropical tree species *Garcinia macrophylla* and *Xylopia micans*. *Journal of Vegetation Science* 20:27–36.



- Anderson JT, Gezon ZJ. 2015. Plasticity in functional traits in the context of climate change: a case study of the subalpine forb *Boechera stricta* (Brassicaceae). *Global Change Biology* 21:1689–1703.
- Anderson JT, Inouye DW, McKinney AM, Colautti RI, Mitchell-Olds T. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings. Biological Sciences* 279:3843–3852.
- Anderson JT, Landi AA, Marks PL. 2009. Limited flooding tolerance of juveniles restricts the distribution of adults in an understory shrub (*Itea virginica*; Iteaceae). *American Journal of Botany* 96:1603–1611.
- Anderson JT, Wadgymar SM. 2019. Climate change disrupts local adaptation and favours upslope migration. *Ecology Letters* 23:181–192.
- Andrew ME, Warrenner H. 2017. Detecting microrefugia in semi-arid landscapes from remotely sensed vegetation dynamics. *Remote Sensing of Environment* 200:114–124.
- Antonovics J. 1968. Evolution in closely adjacent plant populations. 4. Manifold effects of gene flow. *Heredity* 23:507–524.
- Antonovics J. 1972. Population dynamics of the grass *Anthoxanthum odoratum* on a zinc mine. *The Journal of Ecology* 60:351–365.
- Antonovics J. 1976. The input from population genetics: “the new ecological genetics”. *Systematic Botany* 1:233–245.
- Antonovics J. 2006. Evolution in closely adjacent plant populations X: long-term persistence of prereproductive isolation at a mine boundary. *Heredity* 97:33–37.
- Antonovics J, Bradshaw AD. 1970. Evolution in closely adjacent plant populations. VIII. Clinal patterns at a mine boundary. *Heredity* 25:349–362.
- Argyres AZ, Schmitt J. 1991. Microgeographic genetic structure of morphological and life history traits in a natural population of *Impatiens capensis*. *Evolution* 45:178–189.
- Arnold PA, Kruuk LEB, Nicotra AB. 2019. How to analyse plant phenotypic plasticity in response to a changing climate. *The New Phytologist* 222:1235–1241.
- Ashcroft MB. 2010. Identifying refugia from climate change. *Journal of Biogeography* 37:1407–1413.
- Bagley J, Rosenthal DM, Ruiz-Vera UM, Siebers MH, Kumar P, Ort DR, Bernacchi CJ. 2015. The influence of photosynthetic acclimation to rising CO<sub>2</sub> and warmer temperatures on leaf and canopy photosynthesis models. *Global Biogeochemical Cycles* 29:194–206.
- Baker BH, Sultan SE, Lopez-Ichikawa M, Waterman R. 2019. Transgenerational effects of parental light environment on progeny competitive performance and lifetime fitness. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 374:20180182.
- Baruch Z, Jones AR, Hill KE, McInerney FA, Blyth C, Caddy-Retali S, Christmas MJ, Gellie NJC, Lowe AJ, Martin-Fores I, Nielson KE, Breed MF. 2018. Functional acclimation across microgeographic scales in *Dodonaea viscosa*. *AoB Plants* 10:ply029; doi:10.1093/aobpla/ply029.
- Baythavong BS. 2011. Linking the spatial scale of environmental variation and the evolution of phenotypic plasticity: selection favors adaptive plasticity in fine-grained environments. *The American Naturalist* 178:75–87.
- Baythavong BS, Stanton ML. 2010. Characterizing selection on phenotypic plasticity in response to natural environmental heterogeneity. *Evolution* 64:2904–2920.
- Beaumont MA, Zhang W, Balding DJ. 2002. Approximate Bayesian computation in population genetics. *Genetics* 162:2025–2035.
- Becklin KM, Anderson JT, Gerhart LM, Wadgymar SM, Wessinger CA, Ward JK. 2016. Examining plant physiological responses to climate change through an evolutionary lens. *Plant Physiology* 172:635–649.
- Bell DL, Galloway LF. 2007. Plasticity to neighbour shade: fitness consequences and allometry. *Functional Ecology* 21:1146–1153.
- Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15:365–377.
- Bemmels JB, Anderson JT. 2019. Climate change shifts natural selection and the adaptive potential of the perennial forb *Boechera stricta* in the Rocky Mountains. *Evolution* 73:2247–2262.
- Bemmels JB, Knowles LL, Dick CW. 2019. Genomic evidence of survival near ice sheet margins for some, but not all, North American trees. *Proceedings of the National Academy of Sciences of the United States of America* 116:8431–8436.
- Bemmels JB, Title PO, Ortego J, Knowles LL. 2016. Tests of species-specific models reveal the importance of drought in postglacial range shifts of a Mediterranean-climate tree: insights from integrative distributional, demographic and coalescent modelling and ABC model selection. *Molecular Ecology* 25:4889–4906.
- Bereiter B, Eggleston S, Schmitt J, Nehrbass-Ahles C, Stocker TF, Fischer H, Kipfstuhl S, Chappellaz J. 2015. Revision of the EPICA Dome C CO<sub>2</sub> record from 800 to 600 kyr before present. *Geophysical Research Letters* 42:542–549.
- Bertolli SC, Souza GM. 2013. The level of environmental noise affects the physiological performance of Glycine max under water deficit. *Theoretical and Experimental Plant Physiology* 25:36–45.
- Bhagwat SA, Willis KJ. 2008. Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? *Journal of Biogeography* 35:464–482.
- Billington HL, Pelham J. 1991. Genetic-variation in the date of budburst in Scottish birch populations - implications for climate change. *Functional Ecology* 5:403–409.
- Biswas SR, Mallik AU, Braithwaite NT, Biswas PL. 2019. Effects of disturbance type and microhabitat on species and functional diversity relationship in stream-bank plant communities. *Forest Ecology and Management* 432:812–822.
- Bliss KM, Jones RH, Mitchell RJ, Mou PP. 2002. Are competitive interactions influenced by spatial nutrient heterogeneity and root foraging behavior? *The New Phytologist* 154:409–417.
- Blois JL, Zarnetske PL, Fitzpatrick MC, Finnegan S. 2013. Climate change and the past, present, and future of biotic interactions. *Science* 341:499–504.
- Blonder B, Kapas RE, Dalton RM, Graae BJ, Heiling JM, Opedal OH. 2018. Microenvironment and functional-trait context dependence predict alpine plant community dynamics. *Journal of Ecology* 106:1323–1337.
- Boege K, Dirzo R. 2004. Intraspecific variation in growth, defense and herbivory in *Dialium guianense* (Caesalpiniaceae) mediated by edaphic heterogeneity. *Plant Ecology* 175:59–69.
- Bond WJ, Midgley GF. 2012. Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 367:601–612.
- Borghi M, Perez de Souza L, Yoshida T, Fernie AR. 2019. Flowers and climate change: a metabolic perspective. *The New Phytologist* 224:1425–1441.
- Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. In: Caspari EW, Thoday JM, eds. *Advances in genetics*. Cambridge, MA: Academic Press, 115–155.
- Braidwood DW, Taggart MA, Smith M, Andersen R. 2018. Translocations, conservation, and climate change: use of restoration sites as protorefuges and protorefugia. *Restoration Ecology* 26:20–28.
- Bridle JR, Vines TH. 2007. Limits to evolution at range margins: when and why does adaptation fail? *Trends in Ecology & Evolution* 22:140–147.
- Bush MB, Colinvaux PA. 1990. A pollen record of a complete glacial cycle from lowland Panama. *Journal of Vegetation Science* 1:105–118.
- Byers DL. 2017. Studying plant-pollinator interactions in a changing climate: a review of approaches. *Applications in Plant Sciences* 5:1700012.
- Byers DL, Chang SM. 2017. Studying plant-pollinator interactions facing climate change and changing environments. *Applications in Plant Sciences* 5:apps.1700052.
- Camill P, McKone MJ, Sturges ST, Severud WJ, Ellis E, Limmer J, Martin CB, Navratil RT, Purdie AJ, Sandel BS, Talukder S, Trout A. 2004. Community- and ecosystem-level changes in a species-rich tallgrass prairie restoration. *Ecological Applications* 14:1680–1694.
- Carnaval AC, Hickerson MJ, Haddad CF, Rodrigues MT, Moritz C. 2009. Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science* 323:785–789.
- Cervantes SE, Graham EA, Andrade JL. 2005. Light microhabitats, growth and photosynthesis of an epiphytic bromeliad in a tropical dry forest. *Plant Ecology* 179:107–118.
- Chaves MM, Maroco JP, Pereira JS. 2003. Understanding plant responses to drought—from genes to the whole plant. *Functional Plant Biology* 30:239–264.
- Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026.
- Chevin LM, Lande R. 2010. When do adaptive plasticity and genetic evolution prevent extinction of a density-regulated population? *Evolution* 64:1143–1150.

- Chevin LM, Lande R. 2015. Evolution of environmental cues for phenotypic plasticity. *Evolution* **69**:2767–2775.
- Chevin LM, Lande R, Mace GM. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biology* **8**:e1000357.
- Chiang F, Mazdiyasn O, AghaKouchak A. 2018. Amplified warming of droughts in southern United States in observations and model simulations. *Science Advances* **4**:eaat2380.
- Cleland EE, Allen JM, Crimmins TM, Dunne JA, Pau S, Travers SE, Zavaleta ES, Wolkovich EM. 2012. Phenological tracking enables positive species responses to climate change. *Ecology* **93**:1765–1771.
- Colicchio J. 2017. Transgenerational effects alter plant defence and resistance in nature. *Journal of Evolutionary Biology* **30**:664–680.
- Colicchio JM, Monnahan PJ, Kelly JK, Hileman LC. 2015. Gene expression plasticity resulting from parental leaf damage in *Mimulus guttatus*. *The New Phytologist* **205**:894–906.
- Collins AF, Bush MB, Sachs JP. 2013. Microrefugia and species persistence in the Galápagos highlands: a 26,000-year paleoecological perspective. *Frontiers in Genetics* **4**:269.
- Collins B, Foré S. 2009. Potential role of pollinators in microhabitat structure within a population of *Echinacea laevigata* (Asteraceae). *The Journal of the Torrey Botanical Society* **136**:445–456.
- Connor T, Viña A, Winkler JA, Hull V, Tang Y, Shortridge A, Yang H, Zhao Z, Wang F, Zhang J, Zhang Z, Zhou C, Bai W, Liu J. 2019. Interactive spatial scale effects on species distribution modeling: the case of the giant panda. *Scientific Reports* **9**:14563.
- Cortés AJ. 2017. Local scale genetic diversity and its role in coping with changing climate. In: Bitz L, ed. *Genetic diversity*. Rijeka, Croatia: InTech, 19–38.
- Dai A. 2013. Increasing drought under global warming in observations and models. *Nature Climate Change* **3**:52–58.
- Davies AL, Smith MA, Froyd CA, McCulloch RD. 2017. Microclimate variability and long-term persistence of fragmented woodland. *Biological Conservation* **213**:95–105.
- Davies MS, Snaydon RW. 1973. Physiological differences among populations of *Anthoxanthum odoratum* L. collected from the Park Grass Experiment, Rothamsted. II. Response to aluminium. *The Journal of Applied Ecology* **10**:47–55.
- Davies MS, Snaydon RW. 1976. Rapid population differentiation in a mosaic environment. *Heredity* **36**:59–66.
- Davis MB, Shaw RG. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* **292**:673–679.
- De Frenne P, Rodríguez-Sánchez F, Coomes DA, Baeten L, Verstraeten G, Vellend M, Bernhardt-Römermann M, Brown CD, Brunet J, Cornelis J, Decocq GM, Dierschke H, Eriksson O, Gilliam FS, Hédli R, Heinken T, Hermy M, Hommel P, Jenkins MA, Kelly DL, Kirby KJ, Mitchell FJ, Naaf T, Newman M, Peterken G, Petrik P, Schultz J, Sonnier G, Van Calster H, Waller DM, Walther GR, White PS, Woods KD, Wulf M, Graae BJ, Verheyen K. 2013. Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America* **110**:18561–18565.
- de Lafontaine G, Amasifuen Guerra CA, Ducousso A, Petit RJ. 2014. Cryptic no more: soil macrofossils uncover Pleistocene forest microrefugia within a periglacial desert. *The New Phytologist* **204**:715–729.
- Dearborn KD, Danby RK. 2017. Aspect and slope influence plant community composition more than elevation across forest-tundra ecotones in subarctic Canada. *Journal of Vegetation Science* **28**:595–604.
- Delcourt HR, Delcourt PA. 1984. Ice-age haven for hardwoods. *Natural History* **93**:22–28.
- Delcourt PA, Delcourt HR, Brister RC, Lackey LE. 1980. Quaternary vegetation history of the Mississippi embayment. *Quaternary Research* **13**:111–132.
- Dittmar EL, Schemske DW. 2017. The edaphic environment mediates flowering-time differentiation between adjacent populations of *Leptosiphon parviflorus*. *The Journal of Heredity* **109**:90–99.
- Dobrowski SZ. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* **17**:1022–1035.
- Donelson JM, Salinas S, Munday PL, Shama LNS. 2018. Transgenerational plasticity and climate change experiments: where do we go from here? *Global Change Biology* **24**:13–34.
- Dore MH. 2005. Climate change and changes in global precipitation patterns: what do we know? *Environment International* **31**:1167–1181.
- Dudley SA, Schmitt J. 1996. Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *The American Naturalist* **147**:445–465.
- Dupont L. 2011. Orbital scale vegetation change in Africa. *Quaternary Science Reviews* **30**:3589–3602.
- Dusenge ME, Duarte AG, Way DA. 2019. Plant carbon metabolism and climate change: elevated CO<sub>2</sub> and temperature impacts on photosynthesis, photorespiration and respiration. *The New Phytologist* **221**:32–49.
- Ehleringer JR, Cooper TA. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* **76**:562–566.
- Eisenhauer N, Cesarz S, Koller R, Worm K, Reich PB. 2012. Global change belowground: impacts of elevated CO<sub>2</sub>, nitrogen, and summer drought on soil food webs and biodiversity. *Global Change Biology* **18**:435–447.
- Ellegren H. 2014. Genome sequencing and population genomics in non-model organisms. *Trends in Ecology & Evolution* **29**:51–63.
- Eller AS, McGuire KL, Sparks JP. 2011. Responses of sugar maple and hemlock seedlings to elevated carbon dioxide under altered above- and belowground nitrogen sources. *Tree Physiology* **31**:391–401.
- Engelbrecht BM, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* **447**:80–82.
- Fadrique B, Báez S, Duque Á, Malizia A, Blundo C, Carilla J, Osinaga-Acosta O, Malizia L, Silman M, Farfán-Ríos W, Malhi Y, Young KR, Cuesta CF, Homeier J, Peralvo M, Pinto E, Jadan O, Aguirre N, Aguirre Z, Feeley KJ. 2018. Widespread but heterogeneous responses of Andean forests to climate change. *Nature* **564**:207–212.
- Farooq M, Hussain M, Wahid A, Siddique KHM. 2012. Drought stress in plants: an overview. In: Aroca R, ed. *Plant responses to drought stress*. Berlin, Heidelberg: Springer, 1–33.
- Farquhar GD. 1997. Carbon dioxide and vegetation. *Science* **278**:1411–1411.
- Fawcett S, Sistla S, Dacosta-Calheiros M, Kahraman A, Reznicek AA, Rosenberg R, von Wettberg EJB. 2019. Tracking microhabitat temperature variation with iButton data loggers. *Applications in Plant Sciences* **7**:e01237–e01237.
- Feurdean A, Bhagwat SA, Willis KJ, Birks HJ, Lischke H, Hickler T. 2013. Tree migration-rates: narrowing the gap between inferred post-glacial rates and projected rates. *PLoS One* **8**:e71797.
- Ficklin DL, Novick KA. 2017. Historic and projected changes in vapor pressure deficit suggest a continental-scale drying of the United States atmosphere. *Journal of Geophysical Research-Atmospheres* **122**:2061–2079.
- Fisher RA. 1930. *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Flexas J, Loreto F, Medrano H, Flexas J, Loreto F, Medrano H. 2012. Terrestrial photosynthesis in a changing environment. In: Loreto F, Medrano H, Flexas J, eds. *Terrestrial photosynthesis in a changing environment*. Cambridge: Cambridge University Press, 1–6.
- Fos S, Laguna E, Jiménez J, Gómez-Serrano MÁ. 2017. Plant micro-reserves in Valencia (E. Spain): a model to preserve threatened flora in China? *Plant Diversity* **39**:383–389.
- Fox RJ, Donelson JM, Schunter C, Ravasi T, Gaitán-Espitia JD. 2019. Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **374**:20180174.
- Franco AC, Nobel PS. 1989. Effect of nurse plants on the microhabitat and growth of cacti. *Journal of Ecology* **77**:870–886.
- Franks SJ. 2011. Plasticity and evolution in drought avoidance and escape in the annual plant *Brassica rapa*. *The New Phytologist* **190**:249–257.
- Franks SJ, Avise JC, Bradshaw WE, Conner JK, Etterson JR, Mazer SJ, Shaw RG, Weis AE. 2008. The resurrection initiative: storing ancestral genotypes to capture evolution in action. *Bioscience* **58**:870–873.
- Franks SJ, Hamann E, Weis AE. 2018. Using the resurrection approach to understand contemporary evolution in changing environments. *Evolutionary Applications* **11**:17–28.
- Franks SJ, Sim S, Weis AE. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences of the United States of America* **104**:1278–1282.
- Fransen B, de Kroon H, Berendse F. 2001. Soil nutrient heterogeneity alters competition between two perennial grass species. *Ecology* **82**:2534–2546.

- Free CL, Baxter GS, Dickman CR, Leung LK. 2013. Resource pulses in desert river habitats: productivity-biodiversity hotspots, or mirages? *PLoS One* 8:e72690.
- Galen C. 2000. High and dry: drought stress, sex-allocation trade-offs, and selection on flower size in the alpine wildflower *Polemonium viscosum* (Polemoniaceae). *The American Naturalist* 156:72–83.
- Galloway L. 2004. Maternal effects provide phenotypic adaptation to local environmental conditions. *The New Phytologist* 166:93–99.
- Galloway LF, Etterson JR. 2007. Transgenerational plasticity is adaptive in the wild. *Science* 318:1134–1136.
- García-Palacios P, Maestre FT, Bardgett RD, de Kroon H. 2012. Plant responses to soil heterogeneity and global environmental change. *The Journal of Ecology* 100:1303–1314.
- Gavin DG, Fitzpatrick MC, Gugger PF, Heath KD, Rodríguez-Sánchez F, Dobrowski SZ, Hampe A, Hu FS, Ashcroft MB, Bartlein PJ, Blois JL, Carstens BC, Davis EB, de Lafontaine G, Edwards ME, Fernandez M, Henne PD, Herring EM, Holden ZA, Kong WS, Liu J, Magri D, Matzke NJ, McGlone MS, Saltré F, Stigall AL, Tsai YH, Williams JW. 2014. Climate refugia: joint inference from fossil records, species distribution models and phylogeography. *The New Phytologist* 204:37–54.
- Ghalambor CK, McKay JK, Carroll SP, Reznick DN. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology* 21:394–407.
- Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD. 2010. A framework for community interactions under climate change. *Trends in Ecology & Evolution* 25:325–331.
- Ginocchio R, Carvallo G, Toro I, Bustamante E, Silva Y, Sepúlveda N. 2004. Micro-spatial variation of soil metal pollution and plant recruitment near a copper smelter in Central Chile. *Environmental Pollution* 127:343–352.
- Gómez R, Méndez-Vigo B, Marcer A, Alonso-Blanco C, Picó FX. 2018. Quantifying temporal change in plant population attributes: insights from a resurrection approach. *AOB Plants* 10:ply063; doi:10.1093/aobpla/ply063.
- Gossmann TI, Shanmugasundram A, Börns S, Duvaux L, Lemaire C, Kuhl H, Klages S, Roberts LD, Schade S, Gostner JM, Hildebrand F, Vowinkel J, Bichet C, Müllerer M, Calvani E, Zelezniak A, Griffin JL, Bork P, Allaine D, Cohas A, Welch JJ, Timmermann B, Ralser M. 2019. Ice-age climate adaptations trap the alpine marmot in a state of low genetic diversity. *Current Biology* 29:1712–1720.e7.
- Gould BA, Chen Y, Lowry DB. 2018. Gene regulatory divergence between locally adapted ecotypes in their native habitats. *Molecular Ecology* 27:4174–4188.
- Grabherr G, Gottfried M, Paull H. 1994. Climate effects on mountain plants. *Nature* 369:448.
- Graham LJ, Spake R, Gillings S, Watts K, Eigenbrod F. 2019. Incorporating fine-scale environmental heterogeneity into broad-extent models. *Methods in Ecology and Evolution* 10:767–778.
- Guo Q. 1998. Microhabitat differentiation in Chihuahuan Desert plant communities. *Plant Ecology* 139:71–80.
- Hamann E, Weis AE, Franks SJ. 2018. Two decades of evolutionary changes in *Brassica rapa* in response to fluctuations in precipitation and severe drought. *Evolution* 72:2682–2696.
- Hamidov A, Helming K, Bellocchi G, Bojar W, Dalgaard T, Ghaley BB, Hoffmann C, Holman I, Holzkämper A, Krzeminska D, Kværnø SH, Lehtonen H, Niedrist G, Øygarden L, Reidsma P, Roggero PP, Rusu T, Santos C, Seddaiu G, Skarbøvik E, Ventrella D, Żarski J, Schönhart M. 2018. Impacts of climate change adaptation options on soil functions: a review of European case-studies. *Land Degradation & Development* 29:2378–2389.
- Hampe A, Jump AS. 2011. Climate relicts: past, present, future. *Annual Review of Ecology, Evolution, and Systematics* 42:313–333.
- Hannah L, Flint L, Syphard AD, Moritz MA, Buckley LB, McCullough IM. 2014. Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. *Trends in Ecology & Evolution* 29:390–397.
- Harrison S, Noss R. 2017. Endemism hotspots are linked to stable climatic refugia. *Annals of Botany* 119:207–214.
- Harrison SP, Yu G, Takahara H, Prentice IC. 2001. Palaeovegetation. Diversity of temperate plants in east Asia. *Nature* 413:129–130.
- Hatfield JL, Prueger JH. 2015. Temperature extremes: effect on plant growth and development. *Weather and Climate Extremes* 10:4–10.
- He Q, Edwards DL, Knowles LL. 2013. Integrative testing of how environments from the past to the present shape genetic structure across landscapes. *Evolution* 67:3386–3402.
- He Q, Prado JR, Knowles LL. 2017. Inferring the geographic origin of a range expansion: latitudinal and longitudinal coordinates inferred from genomic data in an ABC framework with the program x-origin. *Molecular Ecology* 26:6908–6920.
- Hegland SJ, Nielsen A, Lázaro A, Bjerknes AL, Totland Ø. 2009. How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12:184–195.
- Hendry AP, Schoen DJ, Wolak ME, Reid JM. 2018. The contemporary evolution of fitness. *Annual Review of Ecology, Evolution, and Systematics* 49:457–476.
- Hereford J. 2009. A quantitative survey of local adaptation and fitness trade-offs. *The American Naturalist* 173:579–588.
- Herrera CM, Bazaga P. 2016. Genetic and epigenetic divergence between disturbed and undisturbed subpopulations of a Mediterranean shrub: a 20-year field experiment. *Ecology and Evolution* 6:3832–3847.
- Hewitt GM. 1999. Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society* 68:87–112.
- Hewitt G. 2000. The genetic legacy of the Quaternary ice ages. *Nature* 405:907–913.
- Hoffmann AA, Hallas RJ, Dean JA, Schiffer M. 2003. Low potential for climatic stress adaptation in a rainforest *Drosophila* species. *Science* 301:100–102.
- Holeski LM, Jander G, Agrawal AA. 2012. Transgenerational defense induction and epigenetic inheritance in plants. *Trends in Ecology & Evolution* 27:618–626.
- Hughes AR, Inouye BD, Johnson MT, Underwood N, Vellend M. 2008. Ecological consequences of genetic diversity. *Ecology Letters* 11:609–623.
- Hylander K, Ehrlén J, Luoto M, Meineri E. 2015. Microrefugia: not for everyone. *Ambio* 44:S60–S68.
- Inouye DW. 2019. Effects of climate change on alpine plants and their pollinators. *Annals of the New York Academy of Sciences*. doi:10.1111/nyas.14104.
- Intergovernmental Panel on Climate C (IPCC). 2013. *Climate change 2013 - the physical science basis*. Cambridge, United Kingdom and New York: Cambridge University Press.
- Jackson ST, Webb RS, Anderson KH, Overpeck JT, Webb T III, Williams JW, Hansen BCS. 2000. Vegetation and environment in Eastern North America during the Last Glacial Maximum. *Quaternary Science Reviews* 19:489–508.
- Jarquín D, Crossa J, Lacaze X, Du Cheyron P, Daucourt J, Lorgeou J, Piraux F, Guerreiro L, Pérez P, Calus M, Burgueño J, de los Campos GJT, Genetics A. 2014. A reaction norm model for genomic selection using high-dimensional genomic and environmental data. *Theoretical and Applied Genetics* 127:595–607.
- Jump AS, Hunt JM, Martínez-Izquierdo JA, Peñuelas J. 2006. Natural selection and climate change: temperature-linked spatial and temporal trends in gene frequency in *Fagus sylvatica*. *Molecular Ecology* 15:3469–3480.
- Kaisermann A, de Vries FT, Griffiths RI, Bardgett RD. 2017. Legacy effects of drought on plant-soil feedbacks and plant-plant interactions. *The New Phytologist* 215:1413–1424.
- Karl TR, Kukla G, Razuvayev VN, Changery MJ, Quayle RG, Heim RR, Easterling DR, Fu CB. 1991. Global warming - evidence for asymmetric diurnal temperature-change. *Geophysical Research Letters* 18:2253–2256.
- Kay K, Ward K, Watt L, Schemske D. 2011. Plant speciation. In: Harrison S, Rajakaruna N, eds. *Serpentine: the evolution and ecology of a model system*. Berkeley, CA: University of California Press, 71–96.
- Kelly AE, Goulden ML. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America* 105:11823–11826.
- Kennedy CM. 2018. Conserving species in a fragmented world: the arising researcher. *The Bulletin of the Ecological Society of America* 99:166–167.
- Kirschbaum MUF, McMillan AMS. 2018. Warming and elevated CO<sub>2</sub> have opposing influences on transpiration. Which is more important? *Current Forestry Reports* 4:51–71.
- Kleynhans EJ, Otto SP, Reich PB, Vellend M. 2016. Adaptation to elevated CO<sub>2</sub> in different biodiversity contexts. *Nature Communications* 7:12358.



- Knapp AK, Hoover DL, Wilcox KR, Avolio ML, Koerner SE, La Pierre KJ, Loik ME, Luo Y, Sala OE, Smith MD. 2015. Characterizing differences in precipitation regimes of extreme wet and dry years: implications for climate change experiments. *Global Change Biology* 21:2624–2633.
- Kooyers NJ, Colicchio JM, Greenlee AB, Patterson E, Handloser NT, Blackman BK. 2019. Lagging adaptation to climate supersedes local adaptation to herbivory in an annual monkeyflower. *The American Naturalist* 194:541–557.
- Kooyers NJ, Greenlee AB, Colicchio JM, Oh M, Blackman BK. 2015. Replicate altitudinal clines reveal that evolutionary flexibility underlies adaptation to drought stress in annual *Mimulus guttatus*. *The New Phytologist* 206:152–165.
- Kossov O, Frenkel Z, Korol A, Nevo E. 2009. Genetic diversity and stress of *Ricotia lunaria* in “Evolution Canyon,” Israel. *The Journal of Heredity* 100:432–440.
- Kozłowski TT, Kramer PJ, Pallardy SG. 1991. Temperature. In: Kozłowski TT, Kramer PJ, Pallardy SG, eds. *The physiological ecology of woody plants*. San Diego, CA: Academic Press, 65.
- Krizek BA, Anderson JT. 2013. Control of flower size. *Journal of Experimental Botany* 64:1427–1437.
- Kruckeberg AR. 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. *American Journal of Botany* 38:408–419.
- Kumarathunge DP, Medlyn BE, Drake JE, Tjoelker MG, Aspinwall MJ, Battaglia M, Cano FJ, Carter KR, Cavaleri MA, Cernusak LA, Chambers JQ, Crous KY, De Kauwe MG, Dillaway DN, Dreyer E, Ellsworth DS, Ghanoum O, Han Q, Hikosaka K, Jensen AM, Kelly JW, Kruger EL, Mercado LM, Onoda Y, Reich PB, Rogers A, Slot M, Smith NG, Tervainen L, Tissue DT, Togashi HF, Tribuzy ES, Uddling J, Vårhammar A, Wallin G, Warren JM, Way DA. 2019. Acclimation and adaptation components of the temperature dependence of plant photosynthesis at the global scale. *The New Phytologist* 222:768–784.
- Laguna E, Deltoro VI, Perez-Botella J, Perez-Rovira P, Serra L, Olivares A, Fabregat C. 2004. The role of small reserves in plant conservation in a region of high diversity in eastern Spain. *Biological Conservation* 119:421–426.
- Lang B, Geiger A, Oyunbileg M, Ahlborn J, von Wehrden H, Wesche K, Oyuntsetseg B, Romermann C. 2019. Intraspecific trait variation patterns along a precipitation gradient in Mongolian rangelands. *Flora* 254:135–146.
- Langerhans RB, DeWitt TJ. 2002. Plasticity constrained: over-generalized induction cues cause maladaptive phenotypes. *Evolutionary Ecology Research* 4:857–870.
- Latimer CE, Zuckerberg B. 2017. Forest fragmentation alters winter microclimates and microrefugia in human-modified landscapes. *Ecography* 40:158–170.
- Lavi R, Sapir Y. 2015. Are pollinators the agents of selection for the extreme large size and dark color in *Oncocyclus* irises? *The New Phytologist* 205:369–377.
- Leal ME. 2001. Microrefugia, small scale ice age forest remnants. *Systematics and Geography of Plants* 71:1073–1077.
- Lechowicz MJ, Bell G. 1991. The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. *The Journal of Ecology*, 79:687–696.
- Leempoel K, Parisod C, Geiser C, Joost S. 2018. Multiscale landscape genomic models to detect signatures of selection in the alpine plant *Biscutella laevigata*. *Ecology and Evolution* 8:1794–1806.
- Leimu R, Fischer M. 2008. A meta-analysis of local adaptation in plants. *PLoS One* 3:e4010.
- Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768–1771.
- Lenoir J, Hattab T, Pierre G. 2017. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. *Ecography* 40:253–266.
- Linkosalo T, el-Khouri H, Mäkipää R, Pulkkinen P, Juurola E. 2016. Increased atmospheric CO<sub>2</sub> concentration enhances the development of photosynthetic capacity beyond the temperature effect for silver birch in simulated future climate. *Scandinavian Journal of Forest Research* 32:651–657.
- Liu Y, Reich PB, Li G, Sun S. 2011. Shifting phenology and abundance under experimental warming alters trophic relationships and plant reproductive capacity. *Ecology* 92:1201–1207.
- Liu M, Wang Z, Li S, Lü X, Wang X, Han X. 2017. Changes in specific leaf area of dominant plants in temperate grasslands along a 2500-km transect in northern China. *Scientific Reports* 7:10780.
- Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. 2009. The velocity of climate change. *Nature* 462:1052–1055.
- Lowry DB, Rockwood RC, Willis JH. 2008. Ecological reproductive isolation of coast and inland races of *Mimulus guttatus*. *Evolution* 62:2196–2214.
- Lüthi D, Le Floch M, Bereiter B, Blunier T, Barnola JM, Siegenthaler U, Raynaud D, Jouzel J, Fischer H, Kawamura K, Stocker TF. 2008. High-resolution carbon dioxide concentration record 650,000–800,000 years before present. *Nature* 453:379–382.
- Mandák B, Havrdová A, Krak K, Hadincová V, Vít P, Zákavský P, Douda J. 2016. Recent similarity in distribution ranges does not mean a similar postglacial history: a phylogeographical study of the boreal tree species *Alnus incana* based on microsatellite and chloroplast DNA variation. *The New Phytologist* 210:1395–1407.
- Manel S, Poncet BN, Legendre P, Gugerli F, Holderegger R. 2010. Common factors drive adaptive genetic variation at different spatial scales in *Arabidopsis alpestris*. *Molecular Ecology* 19:3824–3835.
- Massatti R, Knowles LL. 2016. Contrasting support for alternative models of genomic variation based on microhabitat preference: species-specific effects of climate change in alpine sedges. *Molecular Ecology* 25:3974–3986.
- Mathobho R, Marais D, Steyn JM. 2017. The effect of drought stress on yield, leaf gaseous exchange and chlorophyll fluorescence of dry beans (*Phaseolus vulgaris* L.). *Agricultural Water Management* 180:118–125.
- Matte D, Larsen MAD, Christensen OB, Christensen JH. 2019. Robustness and scalability of regional climate projections over Europe. *Frontiers in Environmental Science* 6:163.
- McLachlan JS, Clark JS, Manos PS. 2005. Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86:2088–2098.
- McLaughlin BC, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson SE. 2017. Hydrologic refugia, plants, and climate change. *Global Change Biology* 23:2941–2961.
- McNeilly T, Antonovics J. 1968. Evolution in closely adjacent plant populations IV. Barriers to gene flow. *Heredity* 23:205–218.
- Mee JA, Moore JS. 2014. The ecological and evolutionary implications of microrefugia. *Journal of Biogeography* 41:837–841.
- Mertes K, Jetz W. 2018. Disentangling scale dependencies in species environmental niches and distributions. *Ecography* 41:1604–1615.
- Meyer SE. 1986. The ecology of gypsophile endemism in the eastern Mojave Desert. *Ecology* 67:1303–1313.
- Misiewicz TM, Fine PV. 2014. Evidence for ecological divergence across a mosaic of soil types in an Amazonian tropical tree: *Protium subseriatum* (Burseraceae). *Molecular Ecology* 23:2543–2558.
- Misson L, Limousin JM, Rodriguez R, Letts MG. 2010. Leaf physiological responses to extreme droughts in Mediterranean *Quercus ilex* forest. *Plant, Cell & Environment* 33:1898–1910.
- Mitchell N, Whitney KD. 2018. Can plants evolve to meet a changing climate? The potential of field experimental evolution studies. *American Journal of Botany* 105:1613–1616.
- Monteverde E, Gutierrez L, Blanco P, Pérez de Vida F, Rosas JE, Bonnacarrère V, Quero G, McCouch S. 2019. Integrating molecular markers and environmental covariates to interpret genotype by environment interaction in rice (*Oryza sativa* L.) grown in subtropical areas. *G3 (Bethesda, Md.)* 9:1519–1531.
- Mooney KA, Agrawal AA. 2008. Phenotypic plasticity. In: Tilmon K, ed. *Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects*. Berkeley and Los Angeles, CA: University of California Press, 43–57.
- Moran NA. 1992. The evolutionary maintenance of alternative phenotypes. *The American Naturalist* 139:971–989.
- Morelli TL, Daly C, Dobrowski SZ, Dulen DM, Ebersole JL, Jackson ST, Lundquist JD, Millar CI, Maher SP, Monahan WB, Nydick KR, Redmond KT, Sawyer SC, Stock S, Beissinger SR. 2016. Managing climate change refugia for climate adaptation. *PLoS One* 11:e0159909.

- Morrison JIL, Lawlor DL. 1999. Interactions between increasing CO<sub>2</sub> concentration and temperature on plant growth. *Plant Cell Environ* 22:659–682.
- Mosblech NAS, Bush MB, van Woesik R. 2011. On metapopulations and microrefugia: palaeoecological insights. *Journal of Biogeography* 38:419–429.
- Munguía-Rosas MA, Ollerton J, Parra-Tabla V, De-Nova JA. 2011. Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favoured. *Ecology Letters* 14:511–521.
- Neilson RP, Pitelka LF, Solomon AM, Nathan R, Midgley GF, Fragoso JMV, Lischke H, Thompson K. 2005. Forecasting regional to global plant migration in response to climate change. *Bioscience* 55:749–759.
- Nevo E. 2012. “Evolution Canyon”, a potential microscale monitor of global warming across life. *Proceedings of the National Academy of Sciences of the United States of America* 109:2960–2965.
- Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F, van Kleunen M. 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* 15:684–692.
- Niskanen AKJ, Heikkinen RK, Mod HK, Väre H, Luoto M. 2016. Improving forecasts of arctic-alpine refugia persistence with landscape-scale variables. *Geografiska Annaler: Series A, Physical Geography* 99:2–14.
- Nussey DH, Postma E, Gienapp P, Visser ME. 2005. Selection on heritable phenotypic plasticity in a wild bird population. *Science* 310:304–306.
- Oldfather MF, Ackerly DD. 2019. Microclimate and demography interact to shape stable population dynamics across the range of an alpine plant. *The New Phytologist* 222:193–205.
- Olson D, DellaSala DA, Noss RF, Strittholt JR, Kass J, Koopman ME, Allnutt TF. 2012. Climate change refugia for biodiversity in the Klamath-Siskiyou ecoregion. *Natural Areas Journal* 32:65–74.
- Panetta AM, Stanton ML, Harte J. 2018. Climate warming drives local extinction: evidence from observation and experimentation. *Science Advances* 4:eaaq1819.
- Papadopoulou A, Knowles LL. 2016. Toward a paradigm shift in comparative phylogeography driven by trait-based hypotheses. *Proceedings of the National Academy of Sciences of the United States of America* 113:8018–8024.
- Parachnowitsch AL, Kessler A. 2010. Pollinators exert natural selection on flower size and floral display in *Penstemon digitalis*. *The New Phytologist* 188:393–402.
- Patsiou TS, Conti E, Zimmermann NE, Theodoridis S, Randin CF. 2014. Topo-climatic microrefugia explain the persistence of a rare endemic plant in the Alps during the last 21 millennia. *Global Change Biology* 20:2286–2300.
- Paz H. 2003. Root/shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats, and ecological groups. *Biotropica* 35:318–332.
- Paz-Kagan T, Brodrick PG, Vaughn NR, Das AJ, Stephenson NL, Nydick KR, Asner GP. 2017. What mediates tree mortality during drought in the southern Sierra Nevada? *Ecological Applications* 27:2443–2457.
- Pearce DW, Millard S, Bray DF, Rood SB. 2006. Stomatal characteristics of riparian poplar species in a semi-arid environment. *Tree Physiology* 26:211–218.
- Pearson RG, Phillips SJ, Loranty MM, Beck PSA, Damoulas T, Knight SJ, Goetz SJ. 2013. Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change* 3:673–677.
- Pereira A. 2016. Plant abiotic stress challenges from the changing environment. *Frontiers in Plant Science* 7:1123.
- Pérez-Sánchez RM, Flores J, Jurado E, Gonzalez-Salvatierra C. 2015. Growth and ecophysiology of succulent seedlings under the protection of nurse plants in the Southern Chihuahuan Desert. *Ecosphere* 6:art36.
- Pessarakli M. 2016. *Handbook of photosynthesis*. Boca Raton, FL: CRC Press.
- Pincebourde S, Murdock CC, Vickers M, Sears MW. 2016. Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. *Integrative and Comparative Biology* 56:45–61.
- Pradervand J-N, Dubuis A, Pellissier L, Guisan A, Randin C. 2013. Very high resolution environmental predictors in species distribution models. *Progress in Physical Geography: Earth and Environment* 38:79–96.
- Prentice HC, Li Y, Lönn M, Tunlid A, Ghatnekar L. 2015. A horizontally transferred nuclear gene is associated with microhabitat variation in a natural plant population. *Proceedings. Biological Sciences* 282:20152453.
- Prentice HC, Lonn M, Lefkovitch LP, Runyeon H. 1995. Associations between allele frequencies in *Festuca ovina* and habitat variation in the alvar grasslands on the Baltic Island of Oland. *Journal of Ecology* 83:391–402.
- Price DT, Alfaro RI, Brown KJ, Flannigan MD, Fleming RA, Hogg EH, Girardin MP, Lakusta T, Johnston M, McKenney DW, Pedlar JH, Stratton T, Sturrock RN, Thompson ID, Trofymow JA, Venier LA. 2013. Anticipating the consequences of climate change for Canada's boreal forest ecosystems. *Environmental Reviews* 21:322–365.
- Price N, Moyers BT, Lopez L, Lasky JR, Monroe JG, Mullen JL, Oakley CG, Lin J, Ågren J, Schrider DR, Kern AD, McKay JK. 2018. Combining population genomics and fitness QTLs to identify the genetics of local adaptation in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences of the United States of America* 115:5028–5033.
- Price TD, Qvarnström A, Irwin DE. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proceedings. Biological Sciences* 270:1433–1440.
- Provan J, Bennett KD. 2008. Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology & Evolution* 23:564–571.
- Pugnaire FI, Morillo JA, Penuelas J, Reich PB, Bardgett RD, Gaxiola A, Wardle DA, van der Putten WH. 2019. Climate change effects on plant-soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems. *Science Advances* 5:eaa21834.
- Qian C, Yan X, Yin H, Fan X, Yin X, Sun P, Li Z, Nevo E, Ma XF. 2018. Transcriptomes divergence of *Ricotta lunaria* between the two micro-climatic divergent slopes at “Evolution Canyon” I, Israel. *Frontiers in Genetics* 9:506.
- Qiu YX, Fu CX, Comes HP. 2011. Plant molecular phylogeography in China and adjacent regions: tracing the genetic imprints of Quaternary climate and environmental change in the world's most diverse temperate flora. *Molecular Phylogenetics and Evolution* 59:225–244.
- Rasmann S, Pellissier L, Defosse E, Jactel H, Kunstler G, Bailey JK. 2014. Climate-driven change in plant-insect interactions along elevation gradients. *Functional Ecology* 28:46–54.
- Ravenscroft CH, Whitlock R, Fridley JD. 2015. Rapid genetic divergence in response to 15 years of simulated climate change. *Global Change Biology* 21:4165–4176.
- Razgour O, Forester B, Taggart JB, Bekaert M, Juste J, Ibáñez C, Puechmille SJ, Novella-Fernandez R, Alberdi A, Manel S. 2019. Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. *Proceedings of the National Academy of Sciences of the United States of America* 116:10418–10423.
- Rehush N, Abegg M, Waser L, Brändli U-B. 2018. Identifying tree-related microhabitats in TLS point clouds using machine learning. *Remote Sensing* 10:1735.
- Relyea RA. 2005. The heritability of inducible defenses in tadpoles. *Journal of Evolutionary Biology* 18:856–866.
- Rengel Z. 2011. Soil pH, soil health and climate change. In: Singh B, Cowie A, Chan K, eds. *Soil health and climate change*. Soil Biology, Vol. 29. Berlin, Heidelberg: Springer, 69–85.
- Reside AE, Critchell K, Crayn DM, Goosem M, Goosem S, Hoskin CJ, Sydes T, Vanderduys EP, Pressey RL. 2019. Beyond the model: expert knowledge improves predictions of species' fates under climate change. *Ecological Applications* 29:e01824.
- Richards CL, Alonso C, Becker C, Bossdorf O, Bucher E, Colomé-Tatché M, Durka W, Engelhardt J, Gaspar B, Gogol-Döring A, Grosse I, van Gurp TP, Heer K, Kronholm I, Lampei C, Latzel V, Mirouze M, Opgenoorth L, Paun O, Prohaska SJ, Rensung SA, Stadler PF, Trucchi E, Ullrich K, Verhoeven KJF. 2017. Ecological plant epigenetics: evidence from model and non-model species, and the way forward. *Ecology Letters* 20:1576–1590.
- Richards CL, Schrey AW, Pigliucci M. 2012. Invasion of diverse habitats by few Japanese knotweed genotypes is correlated with epigenetic differentiation. *Ecology Letters* 15:1016–1025.
- Richards CL, White SN, McGuire MA, Franks SJ, Donovan LA, Mauricio R. 2010. Plasticity, not adaptation to salt level, explains variation along a salinity gradient in a salt marsh perennial. *Estuaries and Coasts* 33:840–852.
- Richardson JL, Urban MC, Bolnick DI, Skelly DK. 2014. Microgeographic adaptation and the spatial scale of evolution. *Trends in Ecology & Evolution* 29:165–176.
- Riddoch BJ. 1993. The adaptive significance of electrophoretic mobility in phosphoglucose isomerase (PGI). *Biological Journal of the Linnean Society* 50:1–17.

- Rincint R, Malosetti M, Ababaei B, Touzy G, Mini A, Bogard M, Martre P, Le Gouis J, van Eeuwijk F. 2019. Using crop growth model stress covariates and AMMI decomposition to better predict genotype-by-environment interactions. *Theoretical and Applied Genetics* 132:3399–3411.
- Robinson EA, Ryan GD, Newman JA. 2012. A meta-analytical review of the effects of elevated CO<sub>2</sub> on plant–arthropod interactions highlights the importance of interacting environmental and biological variables. *The New Phytologist* 194:321–336.
- Rossi G, Orsenigo S, Montagnani C, Fenu G, Gargano D, Peruzzi L, Wagensommer RP, Foggi B, Bacchetta G, Domina G, Conti F, Bartolucci F, Gennai M, Ravera S, Cogoni A, Magrini S, Gentili R, Castello M, Blasi C, Abeli T. 2015. Is legal protection sufficient to ensure plant conservation? The Italian Red List of policy species as a case study. *Oryx* 50:431–436.
- Rull V. 2009. Microrefugia. *Journal of Biogeography* 36:481–484.
- Rull V. 2014. Macrorefugia and microrefugia: a response to Tzedakis et al. *Trends in Ecology & Evolution* 29:243–244.
- Salmela MJ. 2014. Rethinking local adaptation: mind the environment! *Forest Ecology and Management* 312:271–281.
- Salmela MJ, Cavers S, Cottrell JE, Iason GR, Ennos RA. 2013. Spring phenology shows genetic variation among and within populations in seedlings of Scots pine (*Pinus sylvestris* L.) in the Scottish Highlands. *Plant Ecology & Diversity* 6:523–536.
- Salmela MJ, Ewers BE, Weing C. 2016. Natural quantitative genetic variance in plant growth differs in response to ecologically relevant temperature heterogeneity. *Ecology and Evolution* 6:7574–7585.
- Sandring S, Agren J. 2009. Pollinator-mediated selection on floral display and flowering time in the perennial herb *Arabidopsis lyrata*. *Evolution* 63:1292–1300.
- Scheiner SM. 2002. Selection experiments and the study of phenotypic plasticity. *Journal of Evolutionary Biology* 15:889–898.
- Scheiner SM, Lyman RF. 1989. The genetics of phenotypic plasticity I. Heritability. *Journal of Evolutionary Biology* 2:95–107.
- Schemske DW. 1984. Population structure and local selection in *Impatiens pallida* (Balsaminaceae), a selfing annual. *Evolution* 38:817–832.
- Scherrer D, Koerner C. 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology* 16:2602–2613.
- Schlichting CD. 1986. The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics* 17:667–693.
- Schmitt J, Dudley SA, Pigliucci M. 1999. Manipulative approaches to testing adaptive plasticity: phytochrome-mediated shade-avoidance responses in plants. *The American Naturalist* 154:S43–S54.
- Schmitt J, Gamble SE. 1990. The effect of distance from the parental site on offspring performance and inbreeding depression in *Impatiens capensis*: a test of the local adaptation hypothesis. *Evolution* 44:2022–2030.
- Schmitt T, Varga Z. 2012. Extra-Mediterranean refugia: the rule and not the exception? *Frontiers in Zoology* 9:22.
- Schwartz NB, Budsock AM, Uriarte M. 2019. Fragmentation, forest structure, and topography modulate impacts of drought in a tropical forest landscape. *Ecology* 100:e02677.
- Sexton JP, Hangartner SB, Hoffmann AA. 2013. Genetic isolation by environment or distance: which pattern of gene flow is most common? *Evolution* 68:1–15.
- Shaw RG, Etterson JR. 2012. Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. *The New Phytologist* 195:752–765.
- Sheik CS, Beasley WH, Elshahed MS, Zhou X, Luo Y, Krumholz LR. 2011. Effect of warming and drought on grassland microbial communities. *The ISME Journal* 5:1692–1700.
- Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Luo Y. 2007. Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences of the United States of America* 104:198–202.
- Sheth SN, Kulbaba MW, Pain RE, Shaw RG. 2018. Expression of additive genetic variance for fitness in a population of partridge pea in two field sites. *Evolution* 72:2537–2545.
- Siepielski AM, Morrissey MB, Buoro M, Carlson SM, Caruso CM, Clegg SM, Coulson T, DiBattista J, Gotanda KM, Francis CD, Hereford J, Kingsolver JG, Augustine KE, Kruuk LE, Martin RA, Sheldon BC, Sletvold N, Svensson EI, Wade MJ, MacColl AD. 2017. Precipitation drives global variation in natural selection. *Science* 355:959–962.
- Silva CE, Kellner JR, Clark DB, Clark DA. 2013. Response of an old-growth tropical rainforest to transient high temperature and drought. *Global Change Biology* 19:3423–3434.
- Silvertown J, Poulton P, Johnston E, Edwards G, Heard M, Biss PM. 2006. The Park Grass Experiment 1856–2006: its contribution to ecology. *Journal of Ecology* 94:801–814.
- Singhal S. 2013. De novo transcriptomic analyses for non-model organisms: an evaluation of methods across a multi-species data set. *Molecular Ecology Resources* 13:403–416.
- Smith DS, Schweitzer JA, Turk P, Bailey JK, Hart SC, Shuster SM, Whitham TG. 2011. Soil-mediated local adaptation alters seedling survival and performance. *Plant and Soil* 352:243–251.
- Soliveres S, Eldridge DJ, Maestre FT, Bowker MA, Tighe M, Escudero A. 2015. Microhabitat amelioration and reduced competition among understory plants as drivers of facilitation across environmental gradients: towards a unifying framework. *Perspectives in Plant Ecology, Evolution and Systematics* 13:247–258.
- Soltis DE, Morris AB, McLachlan JS, Manos PS, Soltis PS. 2006. Comparative phylogeography of unglaciated eastern North America. *Molecular Ecology* 15:4261–4293.
- Sork VL. 2017. Genomic studies of local adaptation in natural plant populations. *The Journal of Heredity* 109:3–15.
- Stein A, Gerstner K, Kreft H. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters* 17:866–880.
- Steinbauer MJ, Grytnes JA, Jurasinski G, Kulonen A, Lenoir J, Pauli H, Rixen C, Winkler M, Bardy-Durchhalter M, Barni E, Björkman AD, Breiner FT, Burg S, Czortek P, Dawes MA, Delimat A, Dullinger S, Erschbamer B, Felde VA, Fernández-Arberas O, Fossheim KF, Gómez-García D, Georges D, Grindrud ET, Haider S, Haugum SV, Henriksen H, Herreros MJ, Jaroszewicz B, Jaroszynska F, Kanka R, Kapfer J, Klanderud K, Kühn I, Lamprecht A, Matteodo M, di Cella UM, Normand S, Odland A, Olsen SL, Palacio S, Petey M, Piscová V, Sedlakova B, Steinbauer K, Stöckli V, Svenning JC, Teppa G, Theurillat JP, Vittoz P, Woodin SJ, Zimmermann NE, Wipf S. 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* 556:231–234.
- Steiner KC, Berrang PC. 1990. Microgeographic adaptation to temperature in pitch pine progenies. *American Midland Naturalist* 123:292–300.
- Steinger T, Roy BA, Stanton ML. 2003. Evolution in stressful environments II: adaptive value and costs of plasticity in response to low light in *Sinapis arvensis*. *Journal of Evolutionary Biology* 16:313–323.
- Stewart JR. 2009. The evolutionary consequence of the individualistic response to climate change. *Journal of Evolutionary Biology* 22:2363–2375.
- Stewart JR, Lister AM. 2001. Cryptic northern refugia and the origins of the modern biota. *Trends in Ecology & Evolution* 16:608–613.
- Stewart JR, Lister AM, Barnes I, Dalén L. 2010. Refugia revisited: individualistic responses of species in space and time. *Proceedings. Biological Sciences* 277:661–671.
- Stratton DA, Bennington CC. 1998. Fine-grained spatial and temporal variation in selection does not maintain genetic variation in *Erigeron annuus*. *Evolution* 52:678–691.
- Sultan SE. 1987. Evolutionary implications of phenotypic plasticity in plants. In: Hecht MK, Wallace B, Prance GT, eds. *Evolutionary biology: volume 21*. Boston, MA: Springer US, 127–178.
- Tang CQ, Matsui T, Ohashi H, Dong YF, Momohara A, Herrando-Moraira S, Qian S, Yang Y, Ohsawa M, Luu HT, Grote PJ, Krestov PV, Ben LePage, Werger M, Robertson K, Hobohm C, Wang CY, Peng MC, Chen X, Wang HC, Su WH, Zhou R, Li S, He LY, Yan K, Zhu MY, Hu J, Yang RH, Li WJ, Tomita M, Wu ZL, Yan HZ, Zhang GF, He H, Yi SR, Gong H, Song K, Song D, Li XS, Zhang ZY, Han PB, Shen LQ, Huang DS, Luo K, López-Pujol J. 2018. Identifying long-term stable refugia for relict plant species in East Asia. *Nature Communications* 9:4488.
- Tezara W, Mitchell VJ, Driscoll SD, Lawlor DW. 1999. Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. *Nature* 401:914–917.
- Thuiller W, Albert C, Araújo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgley GF, Paterson J, Schurr FM, Sykes MT, Zimmermann NE. 2008. Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* 9:137–152.



- Tomiolo S, Van der Putten WH, Tielbörger K. 2015. Separating the role of biotic interactions and climate in determining adaptive response of plants to climate change. *Ecology* 96:1298–1308.
- Trenberth KE. 2011. Changes in precipitation with climate change. *Climate Research* 47:123–138.
- Tripathi AM, Singh A, Singh R, Verma AK, Roy S. 2019. Modulation of miRNA expression in natural populations of *A. thaliana* along a wide altitudinal gradient of Indian Himalayas. *Scientific Reports* 9:441.
- Turner RM, Alcorn SM, Olin G, Booth JA. 1966. The influence of shade, soil, and water on saguaro seedling establishment. *Botanical Gazette* 127:95–102.
- Tymen B, Vincent G, Courtois EA, Heurtebize J, Dauzat J, Marechaux I, Chave J. 2017. Quantifying micro-environmental variation in tropical rainforest understory at landscape scale by combining airborne LiDAR scanning and a sensor network. *Annals of Forest Science* 74:32.
- Tzedakis PC, Emerson BC, Hewitt GM. 2013. Cryptic or mystic? Glacial tree refugia in northern Europe. *Trends in Ecology & Evolution* 28:696–704.
- Urban MC, Tewksbury JJ, Sheldon KS. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings. Biological Sciences* 279:2072–2080.
- Uriarte M, Muscarella R, Zimmerman JK. 2018. Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. *Global Change Biology* 24:e692–e704.
- Väliranta M, Kaakinen A, Kuhry P, Kultti S, Salonen JS, Seppä H. 2011. Scattered late-glacial and early Holocene tree populations as dispersal nuclei for forest development in north-eastern European Russia. *Journal of Biogeography* 38:922–932.
- Vallenback P, Bengtsson BO, Ghatnekar L. 2010a. Geographic and molecular variation in a natural plant transgene. *Genetica* 138:355–362.
- Vallenback P, Ghatnekar L, Bengtsson BO. 2010b. Structure of the natural transgene PgiC2 in the common grass *Festuca ovina*. *PLoS One* 5:e13529.
- Vallenback P, Jaarola M, Ghatnekar L, Bengtsson BO. 2008. Origin and timing of the horizontal transfer of a PgiC gene from *Poa* to *Festuca ovina*. *Molecular Phylogenetics and Evolution* 46:890–896.
- van der Hammen T, Hooghiemstra H. 2000. Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia. *Quaternary Science Reviews* 19:725–742.
- Van der Putten WH, Macel M, Visser ME. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 365:2025–2034.
- Via S, Lande R. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39:505–522.
- Visser ME. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings. Biological Sciences* 275:649–659.
- Wadgymar SM, Daws SC, Anderson JT. 2017a. Integrating viability and fecundity selection to illuminate the adaptive nature of genetic clines. *Evolution Letters* 1:26–39.
- Wadgymar SM, Lowry DB, Gould BA, Byron CN, Mactavish RM, Anderson JT, Stinchcombe J. 2017b. Identifying targets and agents of selection: innovative methods to evaluate the processes that contribute to local adaptation. *Methods in Ecology and Evolution* 8:738–749.
- Wadgymar SM, Mactavish RM, Anderson JT. 2018a. Transgenerational and within-generation plasticity in response to climate change: insights from a manipulative field experiment across an elevational gradient. *The American Naturalist* 192:698–714.
- Wadgymar SM, Ogilvie JE, Inouye DW, Weis AE, Anderson JT. 2018b. Phenological responses to multiple environmental drivers under climate change: insights from a long-term observational study and a manipulative field experiment. *The New Phytologist* 218:517–529.
- Wagner DN, Baris TZ, Dayan DI, Du X, Oleksiak MF, Crawford DL. 2017. Fine-scale genetic structure due to adaptive divergence among microhabitats. *Heredity* 118:594–604.
- Wahid A, Gelani S, Ashraf M, Foolad MR. 2007. Heat tolerance in plants: an overview. *Environmental and Experimental Botany* 61:199–223.
- Walker BJ, Busch FA, Driever SM, Kromdijk J, Lawson T. 2018. Survey of tools for measuring in vivo photosynthesis. In: Covshoff S, ed. *Photosynthesis. Methods in molecular biology*, Vol. 1770. New York, NY: Humana Press, 3–24.
- Wang JJ, Bradburd GS. 2014. Isolation by environment. *Molecular Ecology* 23:5649–5662.
- Warren JM, Norby RJ, Wullschlegel SD. 2011. Elevated CO<sub>2</sub> enhances leaf senescence during extreme drought in a temperate forest. *Tree Physiology* 31:117–130.
- Weinig C. 2000. Differing selection in alternative competitive environments: shade-avoidance responses and germination timing. *Evolution* 54:124–136.
- Weinig C, Delph LF. 2001. Phenotypic plasticity early in life constrains developmental responses later. *Evolution* 55:930–936.
- Weis AE, Wadgymar SM, Sekor M, Franks SJ. 2014. The shape of selection: using alternative fitness functions to test predictions for selection on flowering time. *Evolutionary Ecology* 28:885–904.
- Wilczek AM, Cooper MD, Korves TM, Schmitt J. 2014. Lagging adaptation to warming climate in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences of the United States of America* 111:7906–7913.
- Willis KJ, van Andel TH. 2004. Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quaternary Science Reviews* 23:2369–2387.
- Wintle BA, Kujala H, Whitehead A, Cameron A, Veloz S, Kukkala A, Moilanen A, Gordon A, Lentini PE, Cadenhead NCR, Bekessy SA. 2019. Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* 116:909–914.
- Wolf JB, Wade MJ. 2009. What are maternal effects (and what are they not)? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364:1107–1115.
- Wright JP, Jones CG, Flecker AS. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96–101.
- Xu Z, Jiang Y, Jia B, Zhou G. 2016. Elevated-CO<sub>2</sub> response of stomata and its dependence on environmental factors. *Frontiers in Plant Science* 7:657.
- Xu ZZ, Shimizu H, Yagasaki Y, Ito S, Zheng YR, Zhou GS. 2013. Interactive effects of elevated CO<sub>2</sub>, drought, and warming on plants. *Journal of Plant Growth Regulation* 32:692–707.
- Yeaman S, Hodgins KA, Lotterhos KE, Suren H, Nadeau S, Degner JC, Nurkowski KA, Smets P, Wang T, Gray LK, Liepe KJ, Hamann A, Holliday JA, Whitlock MC, Rieseberg LH, Aitken SN. 2016. Convergent local adaptation to climate in distantly related conifers. *Science* 353:1431–1433.
- Zandalinas SI, Mittler R, Balfagón D, Arbona V, Gómez-Cadenas A. 2018. Plant adaptations to the combination of drought and high temperatures. *Physiologia Plantarum* 162:2–12.
- Zellweger F, De Frenne P, Lenoir J, Rocchini D, Coomes D. 2019. Advances in microclimate ecology arising from remote sensing. *Trends in Ecology & Evolution* 34:327–341.
- Zhang H, Wang E, Zhou D, Luo Z, Zhang Z. 2016. Rising soil temperature in China and its potential ecological impact. *Scientific Reports* 6:35530.
- Zhang YY, Fischer M, Colot V, Bossdorf O. 2013. Epigenetic variation creates potential for evolution of plant phenotypic plasticity. *The New Phytologist* 197:314–322.
- Żróbek-Sokolnik A. 2012. Temperature stress and responses of plants. In: Ahmad P, Prasad MNV, eds. *Environmental adaptations and stress tolerance of plants in the era of climate change*. New York, NY: Springer New York.