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; microenvrionment; microhabitat; paleorefugia; 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
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 (Kooiers 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 Dizzo 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 (Ty men 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).
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 (Zróbek-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 (Kozlowski 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 (Jarquin 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 [CO₂],
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 CO₂ can induce
higher photosynthetic rates (Farquhar 1997; Ainsworth and
Rogers 2007; Bagley et al. 2015; Dusenge et al. 2019), and reduced

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.
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 [CO2] 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 CO2 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 (Tomiloi 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
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 [CO₂] 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. 2018; Tripathi 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; Wadgymar 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 Leptosipon parviflorus (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 Riccia lunaria (Brassicaceae) populations inhabiting contrasting microsites within the Evolution Canyon model system in Lower Nahal Oren, Mount Carmel, Israel (Kossover 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                                                                 |
|-------------------------|---------------------------------------------------------------------------|---------------------------------------------------------------------------|
| **Abiotic**             |                                                                           |                                                                           |
| [CO₂]                   | Increased: CO₂ 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. | Hartfield 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)                                        |
| **Biotic**              |                                                                           |                                                                           |
| 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). Ricota 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. parviflorus 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; Mungua-Rosas et al. 2013; Anderson et al. 2012; Bemmels and Anderson 2019). As a result, populations of A. odoratum, L. parviflorus, 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 (Poaeeae), which may help them adapt to micro-environmental variation in pH and soil moisture (Vallenback et al. 2008, 2010a, b; Prentice et al. 2015). PGIIC 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 Wadgymar 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 (Poeaeae) 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 Wadgymar 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 Etterton 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; Wadgymar et al. 2012b; 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
by analysing fitness data. For example, in the annual forb, *Arabidopsis thaliana* (Brassicaceae), Price et al. (2018) identified specific genes responsible for genetic trade-offs and described signatures of divergent evolutionary trajectories by combining information on QTLs (quantitative trait loci) previously mapped for fitness with population genomic methods (Price et al. 2018). Reciprocal transplant experiments for studying local adaptation can be conducted in conjunction with genomic scans that employ fine-scale population sampling, an assessment of microhabitat environmental heterogeneity, estimates of gene flow among microhabitats and knowledge of variation in functional traits. This research programme would provide a comprehensive picture of a population’s genetic potential to adapt to climate change conditions and the extent to which microsites facilitate the maintenance of adaptive genetic variation within populations.

**Phenotypic plasticity**

In addition to adapting to novel conditions via genetic changes in trait means across generations, populations respond to climate change through phenotypic plasticity (Nicotra et al. 2010). Many plant species have evolved plasticity in one or more traits, such that families with high levels of plasticity readily shift their phenotypes in response to the environment they encounter (Bradshaw 1965; Via and Lande 1985; Schlitching 1986; Sultan 1987; Mooney and Agrawal 2008). Adaptive plasticity is a strategy that maximizes fitness across habitat types and environmental gradients. Fine-grained spatial and temporal heterogeneity in the environment can favour the evolution of phenotypic plasticity if individuals experience multiple abiotic or biotic conditions across their lifespans or if their offspring disperse into distinct microhabitats (Moran 1992; Stratton and Bennington 1998; Alpert and Simms 2002). Micro-environmental variation increases the degree of selection for phenotypic plasticity in a population, and therefore the ability of plasticity to contribute to population persistence under climate change. One example where microhabitats have been linked to the evolution of plasticity is in the annual plant *Erodium cicutarium* (Geraniaceae), which inhabits both serpentine and non-serpentine soils in California (USA) (Baythavong and Stanton 2010; Baythavong 2011). The serpentine microhabitats of *E. cicutarium* consist of heterogeneous micro-environments located well within typical dispersal distances of one another, whereas the non-serpentine soils are more consistent in edaphic conditions and feature fewer distinct microsites (Baythavong and Stanton 2010; Baythavong 2011). Divergent selection favours increased plasticity in the serpentine soils and reduced plasticity in the non-serpentine, producing patterns of genetic differentiation in this system (Baythavong and Stanton 2010; Baythavong 2011). Micro-environmental variation can thus favour the evolution of adaptive plasticity, which could allow populations to respond rapidly to future climates if those axes of environmental variation currently exist within microhabitats.

Phenotypic plasticity itself is a trait under genetic control and can evolve in response to selection (Schlichting 1986; Sultan 1987; Mooney and Agrawal 2008; Baythavong and Stanton 2010). Several studies have quantified heritability in plasticity by evaluating genotype-by-environment interactions in key functional traits (Scheiner and Lyman 1989; Scheiner 2002; Nussey et al. 2005; Relyea 2005; Visser 2008; Anderson and Gezon 2015). For example, the subalpine forb *Boechera stricta* (Brassicaceae) maintains significant heritability in plasticity of phenological and morphological traits (Anderson and Gezon 2015). Through calculating the heritability of traits and plasticity, it is possible to make predictions about the extent to which populations will respond to novel selection imposed by climate change, and whether plasticity has the potential to evolve.

Adaptive plasticity could buffer populations from the effects of climate change in the short term (Chevin and Lande 2010; Chevin et al. 2010; Nicotra et al. 2010). Populations have already shifted their geographic distributions in response to climate change (e.g. Grabherr et al. 1994; Kelly and Goulden 2008; Lenoir et al. 2008; Chen et al. 2011; Fadrique et al. 2018; Steinbauer et al. 2018). However, climate change could rapidly outpace the adaptive and migratory potential of most species (Billington and Pelham 1991; Hoffmann et al. 2003; Loarie et al. 2009; Bellard et al. 2012; Wilczek et al. 2014; Gossmann et al. 2019). Plasticity could prevent short-term population declines if individuals can shift their trait values in response to novel climates until migration or adaptation can occur (Nicotra et al. 2010; Fox et al. 2019). Microhabitat variation thus has the potential to contribute to persistence in rapidly changing conditions through favouring the evolution of plasticity.

Populations that have historically been exposed to high microhabitat heterogeneity may have evolved higher

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**Figure 3.** Rare genotypes can display a fitness advantage over common genotypes in future conditions. Panels show fitness reaction norms of common and rare genotypes in contemporary and future conditions. Solid lines with circles refer to fitness values of common genotypes and dashed lines with triangles represent the fitness values of rare genotypes. Common and rare genotypes display higher fitness in their relative microhabitats under contemporary conditions (panel A). In future conditions, rare genotypes can have a fitness advantage through ‘pre-adaptation’ to stressful conditions by harbouring unique adaptive alleles (panel B). Rare and common genotypes can also decline in fitness overall in future conditions due to factors such as elevated temperatures, increased drought, increased herbivory and habitat fragmentation.
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; Weining 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 (Weining 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 heterogenous environments with high levels of gene flow, which can hinder local adaptation (Sclhichting 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 (Wadgymar 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; Holeiski 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; Wadgymar 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 (Wadgymar 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 population-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 (Välimarinta et al. 2011) and tropical biomes (Leaf 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 Fisher 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 Fisher 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).

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 ecologic insights into the roles of microrefugia. For example, modelling methodologies that incorporate genetic, climatological, spatial and ecologic 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 CO₂ 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 (Ackery 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. 2019).
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 relic 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

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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.
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 microrefugia, 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 microrefugia 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 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 [CO2]: 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, Soucemanianadin 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 (Itta virginica; Itacaceae). 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, Warrener 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 Impatiens capensis. Evolution 45:178–189.

Arnold PA, Kruuk LEJ, 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, Ashcroft MB. 2010. Identifying refugia from climate change. Journal of Biogeography 37:1407–1413.

Baker BH, Sultan SE, Lopez-Chichakwa 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, McNemey FA, Blyth C, Caddy-Retalic S, Christmas MJ, Gellie NJC, Lowe AJ, Martin-Fores I, Nielsen KE, Breed MF. 2018. Functional acclimation across microgeographic scales in Diodosia vissoria. AoB Plants 10:pyo292; doi:10.1093/aobpla/pyo292.

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 LT. 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.

Bennett 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.

Bennett 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.

Bennett 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, Eggleton S, Schmitt J, Neubauer-Ahles C, Stocker TF, Fischer H, Kipfstuhl S, Chappellaz J. 2015. Revision of the EPICA Dome C CO2 record from 800 to 600 kyr before present. Geophysical Research Letters 42:542–549.

Bertioli 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.

Bhatnagar JK, Schmitt J. 2008. Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? Journal of Biogeography 35:464–482.

Biliingston 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 PF. 2002. Are competitive interactions influenced by spatial nutrient heterogeneity and root foraging behaviour? The New Phytologist 154:809–817.

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 guineense (Caesalpiniaeae) 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 224:1435–1441.

Brashad AD. 1965. Evolutionary significance of phenotypic plasticity in plants. In: Caspari EW, Thoday JM, eds. Advances in genetics. Cambridge, MA: Academic Press, 115–155.

Braudwood 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 5:1700512.

Byers DL, Chang SM. 2017. Studying plant-pollinator interactions facing climate change and changing environments. Applications in Plant Sciences 5:app.1700502.

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 J. 2007. Translocations, conservation, and climate change: use of restoration sites as protorefuges and protorefugia. Restoration Ecology 15:239–264.

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.
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 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 Galapagos 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, 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.

Dai A. 2013. Increasing drought under global warming in observations and model simulations. Science Advances 4:eaaat2380.

Chiang F, Mazzuysani O, AghaKouchak A. 2018. Amplified warming of droughts in southern United States in observations and model simulations. Science Advances 4:eaaat2380.

Doré 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 parviflora. The American Naturalist 147:445–465.

Dupont L. 2011. Orbital scale vegetation change in Africa. Quaternary Science Reviews 30:3589–3602.

Duseenge ME, Duarte AG, Way DA. 2019. Plant carbon metabolism and climate change: elevated CO₂ 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, Wunn K, Reich PB. 2012. Global change belowground: impacts of elevated CO₂, 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, Bézé S, Duque Á, Malizia A, Blundo C, Carilla J, Osinaga Acosta O, Malizia L, Siliman M, Farfán-Ríos W, Malhi Y, Young KR, Cuesta CF, Homeier J, Perlino M, Pinto E, Jadan O, Aguirre N, Aguirre T, 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: Arora 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, Silsila S, Dacosta-Calheiros M, Kuhlman A, Renz ice AA, Rosenberg R, von Wettberg EJB. 2019. Tracking microhabitat temperature variation with iButton data loggers. Applications in Plant Sciences 7:e01237–e01237.

Ferdaun 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.

Fleischer K,壹分钟洛雷托 F, Medrano H, Flechas J, Loreto F, Medrano H. 2012. Terrestrial photosynthesis in a changing environment. In: Loreto F, Medrano H, Flechas J, ed.s. Terrestrial photosynthesis in a changing environment. Cambridge: Cambridge University Press, 1–6.

Fox S, Lagana E, Jiménez J, Gómez-Serrano MA. 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, Nobis 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 104:1278–1283.

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. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF, Etterson JR. 2007. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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 LF. 2004. Transgenerational plasticity is adaptive in new environments. Functional Ecology 21:394–407.

Galin 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.
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.

Lambeck K, Luyendyk B, Markwick A, van de Graaff M. 2014. Replicate postglacial refugia for the New Zealand takahe (Himantopus Novaezelandiae) under climate change. Proceedings of the National Academy of Sciences USA 111:8391–8396.

Leino MR. 2001. Microrefugia, small scale ice age forest remnants. Systematics and Geogrphy 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 New Phytologist 120:408–419.

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. Ecology 98:1580–1590.

Lavoie MB, Joly P, Massot M, Andrieu C, Marsden EA. 2015. The role of small reserves in plant conservation in the western United States. Biological Conservation 187:97–108.

Leamy LE, Coen E, Shenk TJ. 2001. Root phenology impacts on soil nitrogen availability. Nature 409:1056–1059.

Lev-Yadun S, Sileshi G, Brown J, Zhang L, Zhang J, Zhou Q, Tian L. 2020. The role of microrefugia in climate change adaptation: A meta-analysis. Scientific Reports 10:12013.

Lev-Yadun S, Sileshi G, Brown J, Zhang L, Zhang J, Zhou Q, Tian L. 2020. The role of microrefugia in climate change adaptation: A meta-analysis. Scientific Reports 10:12013.

Liaw KY, Liu T, Kuo K, Lin YB, Chou T. 2015. Climate change and the distribution of primeval forests in Taiwan. Forests 6:314.

Locke JA, Varner RE, Bazzaz FA, Apps MJ, Barfield WM, Estrella TP, et al. 2015. Trends and drivers of forest response to climate change: a synthesis of long-term forest response experiments. Global Change Biology 21:3579–3594.

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, Liu 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 coastal 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, Přikryl P, Zákřovský P, Doudua 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.

Mansfield DL, Cavender-Bares J. 2012. The role of microrefugia in forest responses to climate change. Forest Ecology and Management 268:86–96.

Marchetti JK, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson SE. 2015. The role of microrefugia in forest responses to climate change. Forest Ecology and Management 344:110–120.

Marchetti JK, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson SE. 2015. The role of microrefugia in forest responses to climate change. Forest Ecology and Management 344:110–120.

Mandák B, Havrdová A, Krak K, Hadincová V, Přikryl P, Zákřovský P, Doudua 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.

Mansfield DL, Cavender-Bares J. 2012. The role of microrefugia in forest responses to climate change. Forest Ecology and Management 268:86–96.

Mandák B, Havrdová A, Krak K, Hadincová V, Přikryl P, Zákřovský P, Doudua 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.

Mansfield DL, Cavender-Bares J. 2012. The role of microrefugia in forest responses to climate change. Forest Ecology and Management 268:86–96.

Mandák B, Havrdová A, Krak K, Hadincová V, Přikryl P, Zákřovský P, Doudua 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.

Mansfield DL, Cavender-Bares J. 2012. The role of microrefugia in forest responses to climate change. Forest Ecology and Management 268:86–96.

Marchetti JK, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson SE. 2015. The role of microrefugia in forest responses to climate change. Forest Ecology and Management 344:110–120.

Marchetti JK, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson SE. 2015. The role of microrefugia in forest responses to climate change. Forest Ecology and Management 344:110–120.

Marchetti JK, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson SE. 2015. The role of microrefugia in forest responses to climate change. Forest Ecology and Management 344:110–120.

Marchetti JK, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson SE. 2015. The role of microrefugia in forest responses to climate change. Forest Ecology and Management 344:110–120.
Morrison JL, Lawlor DL. 1999. Interactions between increasing CO2 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.

Munguia-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, Postma E, Cianci B, Vissier ME. 2005. Selection on inheritable phenotypic plasticity in a wild bird population. Science 310:304–306.

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, Mathiesius 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, Vissier ME. 2005. Selection on inheritable phenotypic plasticity in a wild bird population. Science 310:304–306.

Oldfather MF, Ackerly DD. 2003. Root/shoot allocation and root architecture in seedlings: evidence from observation and experimentiation. Science Advances 4:eaag1819.

Papadopoulou A, Knowles LL. 2016. Toward a paradigm shift in comparative geography 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 flower size and floral display in a natural plant population. Proceedings. Biological Sciences 282:20152453.

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:eart36.

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 Ecological 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.
Alexa E. Robinson, Ryan CB, Newman JA. 2012. A meta-analytical review of the effects of elevated CO2 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 RF, Fogg B, Bacchetta G, Domina G, Conti F, Bartolucci F, Gennai M, Ravera S, Cogoni A, Magrini S, Gentili R, Castello M, Blasi C, Abeil T. 2015. Is legal protection sufficient to ensure plant conservation? The Italian Red List of policy species as a case study. Oryx 59:431–436.

Rull V. 2005. Microrefugia. Journal of Biogeography 32:481–484.

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! 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 IR. 2011. Effect of warming and drought on grassland microbial communities. The ISME Journal 5:1690–1700.

Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schimel DS, Verburg PS, Wallace LL, Sherry RA, Zhou X, Gu S, Arnone JA 3rd, Schime...
Tomlin S, Van der Putten WH, Tielbörker 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 sugarcane 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 forest 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.

Van MC, Tewksbury JJ, Sheldon KS. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinguitions 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.

Vallinara M, Kaakinen A, Kuhry P, Kuiti S, Salonen JS, Seppa 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, Hoogemstra 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 1:39–39.

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 61:159–223.

Walker RJ, 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 JI, Bradburd GS. 2014. Isolation by environment. Molecular Ecology 23:5649–5662.

Warren JM, Norby RJ, Wullschleger SD. 2011. Elevated CO2 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 creates developmental responses later. Evolution 55:930–936.

Wei S, 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.

Wójcicki AM, Cooper MD, Korves TM, Schmitt J. 2014. Logging 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 FE, Cadenhead NCR, Bekesyy 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-CO2 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 CO2, drought, and warming on plants. Journal of Plant Growth Regulation 32:692–707.

Yeeam S, Hodgins KA, Lotterhos KE, Suren H, Degner JC, Morkowski KA, Smets F, Wang T, Gray LK, Liese KJ, Hamann A, Holliday JA, Whitlock MC, Rieseberg LH, Atken SN. 2016. Convergent local adaptation to climate in distantly related conifers. Science 353:1431–1433.

Zandalinas SI, Mütter R, BallaÅ iÅ d N, 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 197:316–322.

Zróbek-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.