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Globally important plant functional traits for coping with climate change

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Abstract

The last decade has seen a proliferation of studies that use plant functional traits to assess how plants respond to climate change. However, it remains unclear whether there is a global set of traits that can predict plants' ability to cope or even thrive when exposed to varying manifestations of climate change. We conducted a systematic global review which identified 148 studies to assess whether there is a set of common traits across biomes that best predict positive plant responses in performance and fitness, to multiple climate changes and associated environmental changes.

Eight key traits appear to best predict positive plant responses to multiple climate/environmental changes across biomes: lower or higher specific leaf area (SLA), lower or higher plant height, greater water-use efficiency (WUE), greater resprouting ability, lower relative growth rate, greater clonality/bud banks/below-ground storage, higher wood density, and greater rooting depth. Trait attributes associated with positive responses appear relatively consistent within biomes and climate/environmental changes, except for SLA and plant height, where both lower and higher trait attributes are associated with a positive response depending on the biome and climate/environmental change considered. Overall, our findings illustrate important and general trait-climate responses within and between biomes that help us understand which plant phenotypes may cope with or thrive under current and future climate change.

Highlights

- Our research identifies a set of key traits that best predict positive plant responses to multiple climate/ environmental changes across biomes: lower or higher specific leaf area (SLA), lower or higher plant height, greater water-use efficiency (WUE), greater resprouting ability, lower relative growth rate, greater clonality/bud banks/below-ground storage, higher wood density, and greater rooting depth.

- We find consistence in the trait attributes (values/ states of traits) associated with positive responses for most of our key traits.

- There is a) an overrepresentation of studies focusing on leaf traits, although other traits are more consistently linked to positive responses, b) an overrepresentation of studies on decreased precipitation/drought compared to other changes c) an underrepresentation of studies in Deserts in relation to their global coverage, and an underrepresentation of studies in the Tundra biome in relation to expected climate changes.

- Our research supports that there are general trait-climate responses within and between biomes.

- Our results take us a step closer to understanding which plants can cope or thrive under climate change because of their trait makeup.

Introduction

Plant functional traits are heritable characteristics of morphology, physiology or phenology that influence individual performance and fitness and ultimately the responses of species to changes in the environment (Violle et al. 2007, Pérez-Harguindeguy et al. 2013, Garnier et al. 2016). The development of trait-based ecology has relied on the working hypothesis that there are general trait-environment relationships that can predict how biodiversity responds to climate

(Enquist et al. 2015). Some studies have focused on quantifying variation within specific individual traits along environmental gradients (Moles et al. 2009, Wright et al. 2017, Boonman et al. 2020), whereas others have focused on identifying coordination and trade-offs between different traits across species and landscapes (Díaz et al. 2016). Understanding both the type and consequences of trait variation is critical to determining species response to climate change, because a suite of traits can directly affect ecological tolerance, diversity and distribution of species (Díaz et al. 2016, Wright et al. 2017, Feng et al. 2018, Rueda et al. 2018). Whilst many studies have focused on those trait attributes that may restrict a species' ability to cope with environmental change, leading to vulnerability (Foden et al. 2008, Williams et al. 2008, Dawson et al. 2011, González-Suárez et al. 2013), less focus has been placed on those trait attributes that may enhance a species' ability to withstand climate and associated environmental change.

Climate change is one of the largest threats to current and future biodiversity (Sala et al. 2000, Bellard et al. 2012, Urban 2015, IPBES 2019). Future earth system projections indicate a suite of climatic and associated environmental changes with projections indicating: increases in atmospheric CO_2; an increase in global surface temperature by more than 2°C (under all but one emission scenarios); more frequent hot and fewer cold temperature extremes; more intense and frequent extreme precipitation events; a rise in sea-level; and an increased frequency and intensity of wildfires by the end of the 21st century (IPCC 2015). Additionally, indirect effects of climate change are suggested to have an impact on ecosystems such as subarctic peatlands where increased temperatures are predicted to enhance permafrost thaw, which in turn increases available nitrogen (Keuper et al. 2012).

Evidence from palaeoecological, present-day and modelling studies shows that species can have different responses to climate changes. These include adaptation, migration, extinction, or persistence (i.e., tolerance) (Aitken et al. 2008, Dawson et al. 2011, Willis and MacDonald 2011, IPCC 2015). All these responses are thought to be closely linked to the presence (or absence) of certain functional traits or specifically, trait attributes (value or state of a trait in a given location at a given time (Garnier et al. 2016)) (e.g. Estrada et al. 2016). Thus, having 'favourable' traits or trait attributes can allow a species to cope with a changing climate, whereas a lack of these can result in population decline or local extinctions.

Both empirical and theoretical work indicate that there should be a general subset of traits that best predict plant responses to global change (Lavorel and Garnier 2002, Moles et al. 2014, Michaletz et al. 2015). Recent theoretical advances have identified subsets of traits that are more central to how plants respond to drought (O'Brien et al. 2017, Powell et al. 2017, Feng et al. 2018, Brodribb et al. 2020) and temperature (Michaletz et al. 2015, Wright et al. 2017). Nonetheless, most studies indicating support for a general set of trait responses are empirical and comparative in approach

(Wright et al. 2010, Paine et al. 2015). For example, a global meta-analysis that explored plant recovery performance from water stress found that trade-offs of specific traits, mainly related to plant hydraulic architecture, leaf anatomy and physiology, affect plant recovery (Yin and Bauerle 2017). Similarly, a recent study in the Neotropics highlighted wood density and vessel size as important traits to help trees withstand drought (Esquivel-Muelbert et al. 2017).

Other studies have examined which specific trait attributes might be more favourable to tolerate climate change. For example, denser wood, lower specific leaf area and deeper roots have been found to be associated with lower tree mortality in the face of drought (Greenwood et al. 2017, O'Brien et al. 2017). However, to date, there has been no global study that assesses whether there is a general set of functional traits across global biomes that will allow plants to cope with, or even thrive under, multiple manifestations of climate change (i.e. a positive response).

In this study, we aimed to examine whether current studies indicate a general set of trait-environment relationships that underlie positive plant responses to climate change. Specifically, we undertook a systematic review process of the literature to identify 148 studies which analysed responses of plants with different traits to climate and associated environmental changes (hereafter climate/environmental changes). We used biomes as the units of analysis to determine whether positive trait–environment relationships are generalizable globally, irrespective of a region's history or differences in species assemblages (e.g. see Van Bodegom *et al.* 2012; Sandel *et al.* 2016).

Methods

Biome map and estimation of projected changes in temperature and precipitation

We used a modified version of the biome map of Dinerstein and colleagues (2017) (see Appendix S1, Supplementary Material) and reconstructed expected mean annual temperature and total annual precipitation projected for each biome for year 2050 (CMIP5 data) (IPCC 2015) RCP 6.0). This involved downloading model outputs from Worldclim v1.4 (Hijmans et al. 2005) at 30 arc-seconds pixel resolution together with the baseline maps (climate representing 1960-1990) (Hijmans et al. 2005). Then, for each climatic variable we summarized the mean value per biome per future climate model and calculated the absolute change in temperature and the relative change in precipitation in comparison to the mean value per biome of the baseline maps.

Systematic literature survey

We conducted a systematic survey to identify published studies in international journals spanning the years 2007-2017 that focused on traits which are associated with positive plant responses to climate/environmental change. In our study, positive responses

include both coping (e.g. survival) and thriving/ enhanced fitness (e.g. increased vegetative biomass) despite climate/environmental change. The search was conducted per biome, therefore constituting a global analysis.

In our search, conducted in SCOPUS, we used a combination of search terms including "plant", "climate", "change", "functional", "trait", and the name of each of the 12 selected biomes. This initial survey returned 1589 studies from which we selected 148 studies which met our criterion, that is: identifying a plant trait attribute that mediated a positive plant response to a simulated or observed climate/ environmental change (see Appendix S2, Table S1 for the list of studies and Appendix S1, Supplementary Material for further methods). We classified the positive response data into three fitness categories (after Violle et al. (2007), see Appendix S2, Table S2): plant survival (e.g. delayed mortality, stress tolerance, survival), reproductive output (e.g. enhanced reproductive effort, seed germination, recruitment) and vegetative biomass (e.g. abundance, biomass, community dominant trait).

We extracted all records of traits that were either associated with a positive response (positive record), or not associated with a response (referred to as null records) to climate/environmental changes (see Appendix S1, Supplementary Material and Fig. S1). In this way, we obtained a total of 598 records (446 positive responses and 152 null responses) from the 148 studies (see Appendix S2, Table S1).

All 101 traits were standardized and grouped into the five categories proposed by Pérez-Harguindeguy and colleagues (2013) (see, Appendix S1, Supplementary Material and Appendix S2, Table S3): below-ground, leaf, stem, regenerative and whole-plant traits. We also kept a few traits with a low number of records under the group category of "others".

Data synthesis

We summarized the data from the 148 studies using the records as a unit of analysis (since some studies contained several records) (see Appendix S1, Supplementary Material and Fig. S1).

In order to identify the most consistently important traits across biomes, we scored all traits reported in our selected studies according to their representation across biomes (proportion out of 12 total biomes) and climate/environmental changes (proportion out of six total changes – see below). These were weighted by the proportion of positive records out of total records (positive plus null records) to provide a level of confidence in that trait being consistently associated with a positive response to climate/environmental change. This scoring was calculated by the following equation, where Pr=proportion of positive records, Pc=proportion of positive records per climate/ environmental change and Pb=proportion of positive records per biome:

$$\text{Score} = \text{Pr}(\text{Pc}+\text{Pb})/2. \qquad (1)$$

Using this approach, the scores ranged from 0 to 1 and higher scoring traits (values closer to 1) thus representing those traits that are associated with multiple biomes and climate/environmental changes, according to our systematic survey. Once the globally important traits were identified, we extracted the information of their trait attributes per biome and climate/environmental change. Lastly, we analysed plant traits for each of the top three studied climate/ environmental changes and the associated attributes to analyse how consistent an attribute was within traits.

Results

Future projected climate change per biome

IPCC projections show that all biomes will experience an increase in temperature that ranges from 1 to 5 degrees ($^{\circ}$ C). The Tundra and Boreal Forests are projected to undergo the highest increase, while Tropical Forests biomes and Mangroves are expected to see the least increase in temperature (Fig. 1c). Projections of relative change in precipitation indicate that both the Mediterranean and the Mangrove biomes are projected to have a decrease in relative precipitation while Tundra and Boreal Forests are expected to have an increase in total annual precipitation (Fig. 1c). Additionally, precipitation shows variability in the direction of the trend (positive vs. negative). There is thus considerable variability in the projected trends, even at the coarse resolution of biomes.

Synthesis of studies

There has been an increase in the number of studies focusing on plant trait attributes associated with a positive response under climate change over the past ten years (see Appendix S1, Fig. S2). We found that the highest number of relevant studies and records have taken place in Mediterranean Forests, Woodlands and Scrubs (Fig. 1b and see Appendix S1, Fig. S3), while the lowest number of studies have occurred in Mangroves and Coniferous Forest. In addition, the Desert biome and Tropical Grasslands and Savannas, the two largest in aerial extent, are among the biomes with the lowest number of records found by our data-synthesis (Fig. 1b). The peer-reviewed studies found in our systematic search have an uneven geographic cover. Countries with the highest number of publications are USA, China and France (see Appendix S1, Fig. S4a), whereas the highest density of studies are concentrated in Europe and a few countries in South and Central America (see Appendix S1, Fig. S4b). The African continent has the poorest coverage of records (see Appendix S1, Fig. S4).

Plant responses to decreased precipitation were the most studied (Fig. 1d and see Appendix S1, Fig S5) but other climate/environmental changes studied included: increased temperature, frequency/intensity of fires, Nitrogen deposition, CO_2 and sea-level rise. We identified 101 traits in the analysed studies (see Appendix S2, Table S3) that were linked to a positive
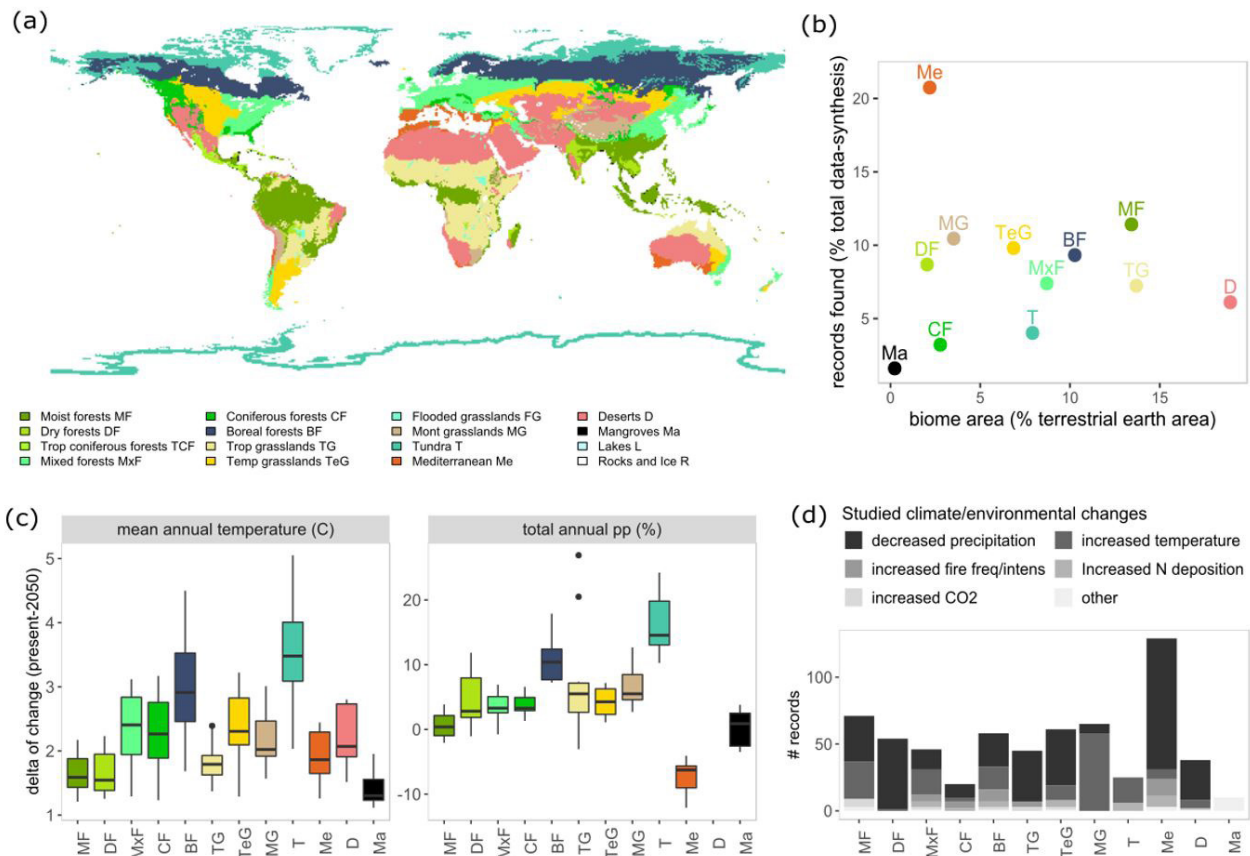
Figure 1. a) Biomes map (based on Dinerstein et al. (2017)), b) Percentage of records found per biome in our data-synthesis in comparison to each biome area, c) box plots of projected future change in temperature and precipitation (present – 2050) under scenario RCP 6.0 per biome, d) Number of records found in our data-synthesis per climate/environmental change for each biome. Abbreviations follow those in 1a. The number of studies increased over time 2007-2017 (Appendix S1, Fig. S2) and employed a range of methods (Appendix S1, Fig. S7).

plant response (see Appendix S2, Table S2) to a specific climate/environmental change. Of these, 34 are leaf traits, 19 are whole-plant traits, 17 are below-ground traits, 11 are regenerative traits, 8 are stem traits, 7 are flowering traits and 5 are classified as "others".

The traits with the highest number of total records (weighted by the proportion of positive records) were specific leaf area (SLA), followed by plant height, water-use efficiency (WUE), root depth and wood density (see Appendix S1, Fig. S5a). Leaf traits were by far the most recorded (see Appendix S1, Fig. S5b), however all, but one, of the other trait groups had a higher proportion of positive records than leaf traits (67%). Notably high proportions of positive records were seen in regenerative (84%), whole-plant (82%) and below-ground traits (82%) (see Appendix S2, Table S4).

Globally important trait attributes

Our data-synthesis indicates that overall, lower or higher SLA, better water-use efficiency, lower relative growth rate, greater or smaller plant height, and higher wood density are traits consistently linked to a

positive response across most biomes (Fig. 2a, Fig. 3). When looking across the suite of different climate/environmental changes, in addition to higher or lower SLA and higher or lower plant height, clonality/bud banks/larger below-ground storage, greater resprouting ability and greater rooting depth also appear to be traits linked to a positive response across the different climate/environmental changes (Fig. 2b, Fig. 4). By combining all traits in a biplot (Fig. 2c) and the associated combined score (see Appendix S2, Table S5), we identified eight traits as the "top" traits related to positive responses for both multiple climate/environmental changes and multiple biomes. Each of these top traits had a proportion of >0.4 along both axes. The "top" traits emerging as globally important are higher or lower SLA, higher or lower plant height, greater water-use efficiency, greater resprouting ability, lower relative growth rate, greater clonality/bud banks/below-ground storage, higher wood density and greater rooting depth (Figs. 2-4).

Although most of the trait's attributes were consistent across biomes, we found two (SLA and plant
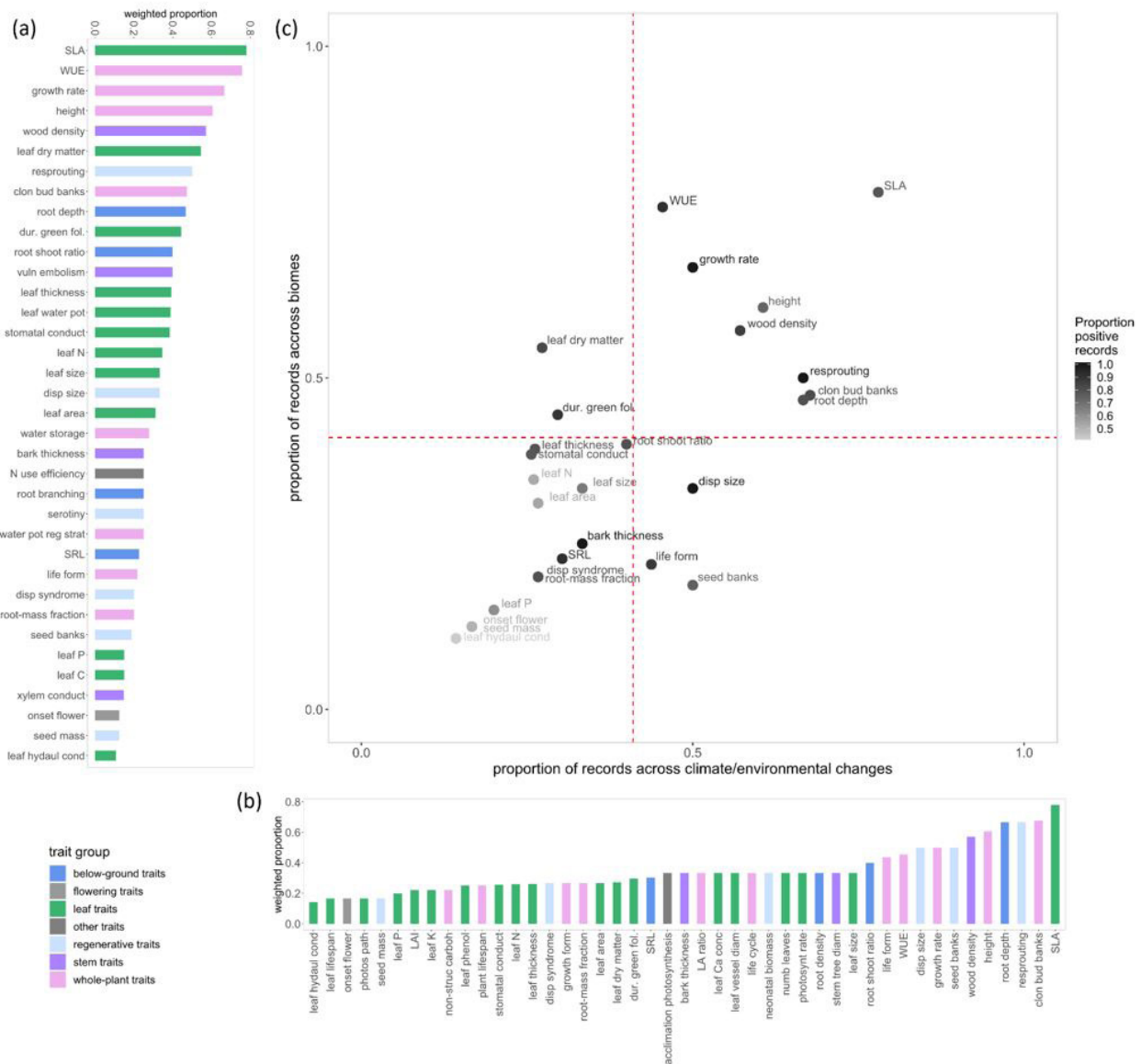
Figure 2. Scoring of traits that are linked to a positive response to climate and associated environmental change. The y-axis (a) represents the scoring of traits across biomes weighted by the confidence in the trait mediating a positive plant response (proportion of positive records out of all records including null), where higher values (closer to 1) are given to traits that are recorded as important for plant performance and fitness in a higher number of biomes while lower values (closer to 0) are for traits limited to a lower number of biomes. The x-axis (b) represents the scoring of traits across climate/environmental changes (see Fig. 1d) weighted by the confidence in the trait being associated with a positive response (proportion of positive records), where higher values (closer to 1) are assigned to traits that are linked to multiple climate/environmental changes while lower values (closer to 0) are linked to only few climate/environmental changes. Overall scores represented in (c) were determined by combining positive records of traits reported in our selected studies according to their representation across biomes and climate/environmental changes, weighted by the proportion of positive records out of total records (see methods for further details). Traits included in this figure were those with proportion of biomes and proportion of climate/environmental changes greater than 0.2 for enhanced clarity. Dotted red lines represent the cut-off for top traits at 0.4 proportion for each axis. Top traits are therefore those in the top right section of the figure. Full traits names in Appendix S2, Table S1.

height), where both lower and higher attributes were found to be important for plant performance and fitness under climate change across different biomes (Fig. 3).

The top five trait attributes that emerged for coping with decreased precipitation are lower SLA, higher WUE, higher wood density, deeper roots and smaller
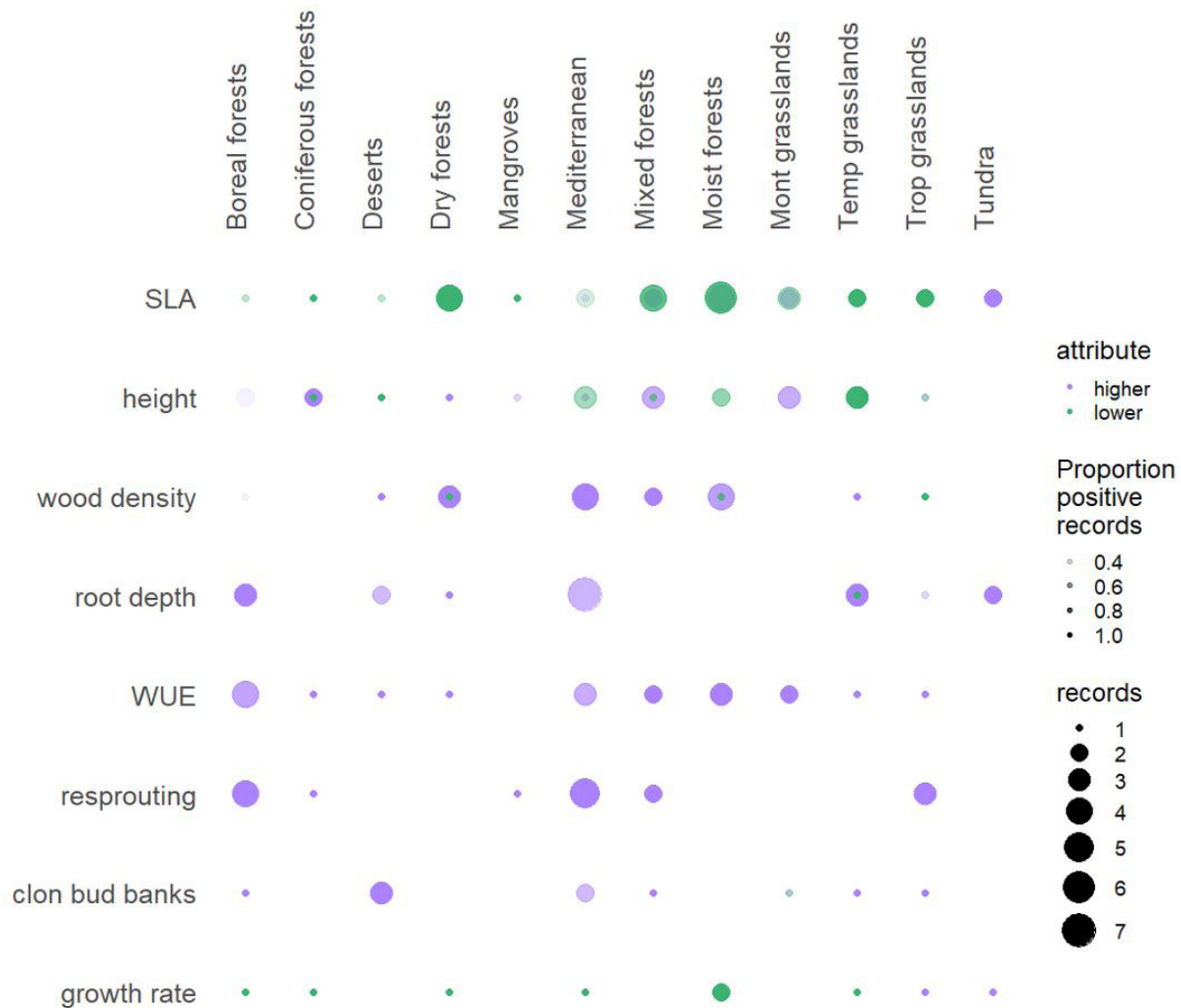
Figure 3. Top eight traits identified by this data-synthesis as important for plants to withstand climate change showing their trait attributes ("attribute"), support in number of records ("records") and the confidence in the observed records ("proportion of positive records" out of total number records). Where there are both higher and lower attributes, circles overlap and therefore the total number of records is a sum of both circle sizes.

plant height (Fig. 4a). The top trait attributes for coping with increased temperature are both lower and higher SLA, and greater plant height. Other attributes with less support in terms of number of records but which may also facilitate positive plant responses under increased temperatures, include having higher or lower leaf dry matter content, deciduous or evergreen foliage, higher WUE and higher relative growth rate (Fig. 4b). The top trait attributes to cope with fires are greater resprouting ability, greater clonality/bud banks/below-ground storage, greater serotiny, deeper roots and thicker bark. In general, there seems to be consistency in the trait attributes that are favourable to cope with fires (Fig. 4c). Not enough records on trait attributes were available for the remaining climate/environmental changes to make any significant inferences on these changes.

Discussion

Globally important traits and associated attributes for coping with climate change

Our data-synthesis identified eight main traits that are important for plants across biomes in coping with, or thriving under climate change (decreased precipitation, increased temperature, increased CO_2) and associated environmental changes (increased frequency and intensity of fires, increased nitrogen deposition and others (see Appendix S1, Fig. S6) (Fig. 2c). These are higher or lower SLA, higher or lower plant height, greater water-use efficiency, greater resprouting ability, lower relative growth rate, greater clonality/bud banks/below-ground storage, higher wood density and greater rooting depth. In
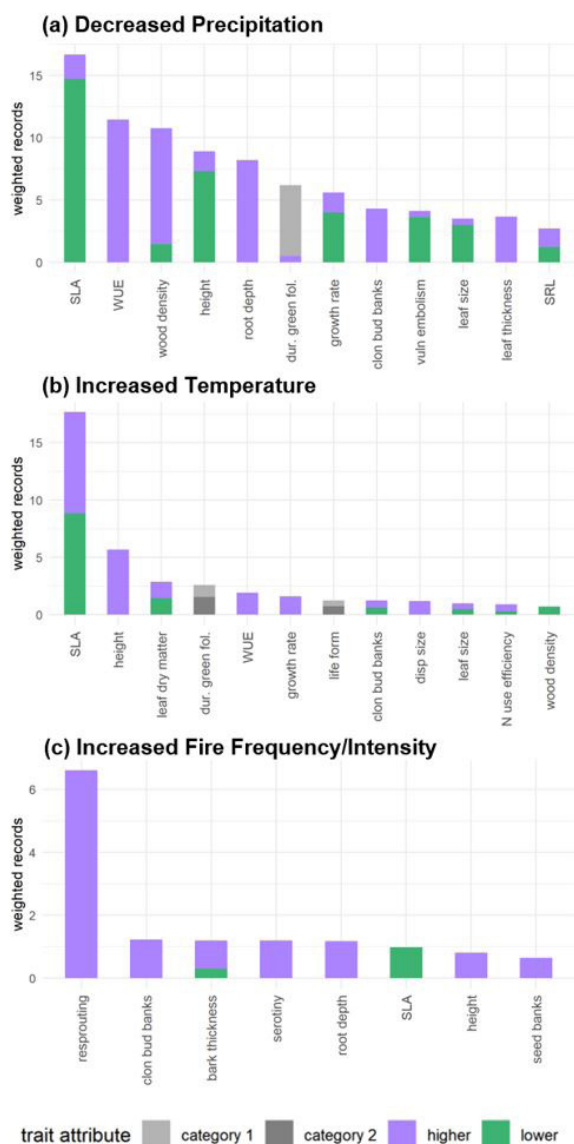
(a) Decreased Precipitation

(b) Increased Temperature

(c) Increased Fire Frequency/Intensity

trait attribute   category 1   category 2   higher   lower

Figure 4. Number of records weighted by the proportion of positive records out of total records that were found in our literature survey that support each trait as important for a plant to cope with climate/environmental change for a) decreased precipitation, b) increased temperature, c) increased fire frequency/intensity. Traits included were the top up to 12 for each climate/environmental change. Colours indicate the different trait attributes recorded by the studies. "Lower" and "higher" indicate attributes for quantitative traits. "Category 1" and "Category 2" indicate attributes of qualitative traits. Full traits names in Appendix S2, Table S1.

comparison with the largest existing trait database (TRY Kattge et al. (2011)), our top traits do not meaningfully match those that are most often measured, with only plant height and wood density falling within the top 10 most sampled traits and with most of our traits falling outside the top 100 sampled traits (see Appendix S2,

Table S6). This, along with accounting for the instances where traits were not associated with a response to climate/environmental change (null records), suggest that our presented traits are not merely those most sampled. Below we describe each of the globally important top traits we identified, together with how the trait attributes are related to climate changes and associated environmental changes in different biomes.

Specific leaf area (SLA)

Specific leaf area, defined as "one-sided area of a fresh leaf divided by its oven-dry mass" (Pérez-Harguindeguy et al. 2013), reflects a trade-off between leaf construction costs and carbon assimilation rates (Díaz et al. 2016). Previous work has identified that SLA positively scales with leaf nitrogen concentration and carbon assimilation rate and negatively with leaf life span (Reich et al. 1997, Blonder et al. 2011).

Our data-synthesis shows that in nine out of the twelve biomes, lower SLA is important for plant performance and fitness under *decreased precipitation* (Fig. 3, 4). For example, in Moist forests of Costa Rica, modelling and plot data indicate that species with lower SLA will better survive drought conditions and become dominant (Uriarte et al. 2016). The authors attribute this to smaller exposed leaf surfaces reducing water loss through evapotranspiration. The same pattern was also found in the Deserts of Australia (Baruch et al. 2017), the Savannas of Brazil (Ribeiro et al. 2016), the Ecuadorian (Chirino et al. 2017) and Bolivian Dry Forests (Markesteijn and Poorter 2009), where plants with lower SLA showed greater persistence under decreased precipitation. In these latter studies, lower SLA was also related to higher sclerophylly, suggesting that plants invested more resources in building robust leaves (lower SLA = more mass per unit of area) and thus adopted a conservative water use strategy (Chirino et al. 2017).

In contrast, studies focusing on plant responses to increased temperature found less consistent responses in SLA, in that both higher and lower values could result in positive responses, depending on the biome (Fig. 3, 4). For instance, in the Montane Grassland biome in Chongqing, China (Song et al. 2012) and in southern Norway (Guittar et al. 2016), species with higher SLA are more abundant in warmer temperatures at lower elevations. However, in Montane Grasslands of North-western Caucasus in Russia (Soudzilovskaia et al. 2013), species with lower SLA are more abundant in warmer climates. Similarly, in Temperate forests across Europe, some herbaceous species show decreasing SLA, together with smaller and thicker leaves, is linked to reduced evapotranspiration under warming, while other herbaceous species of these same biomes show increasing SLA under warmer climates (Lemke et al. 2015).

Plant height

Plant height is the distance from the ground level to the upper boundary of the main photosynthetic tissues of a plant at maturity, often expressed as maximum height (Pérez-Harguindeguy et al. 2013,

Díaz et al. 2016) and is the most common measure of whole plant size (Díaz et al. 2016). Plant height is associated with competition for light resources (Moles et al. 2009), where taller plants are able to display their leaves above others. This, however, trades off against the construction costs that come with growing taller (Poorter et al. 2008). Plant height is considered relevant for carbon storage capacity (Moles et al. 2009, Kattge et al. 2011) and is associated with and influenced by growth form, potential lifespan, competitiveness and other size-related traits (Pérez-Harguindeguy et al. 2013).

In our data-synthesis, plant height emerged as an important trait for plant performance and fitness in response to multiple climate/environmental changes across biomes. We found that for climatic warming, the attributes reported for this trait, i.e. being taller or shorter, differed across biomes. For example, greater grass height was associated with positive plant responses in two grassland biomes, in the Montane Grasslands of France (de Bello et al. 2013) and Norway (Guittar et al. 2016) and in Temperate Grasslands of California, USA (Sandel and Dangremond 2012). In the Boreal Forest, however, shorter trees seem to have higher growth rates than taller trees (Ratcliffe et al. 2016).

Under high water stress, plant height is generally an important trait, where shorter statured plants coped better across biomes (Fig. 3, 4). For instance in the Moist Broadleaf Forests of the Dinghushan Biosphere Reserve of China, the abundance of shorter-stature species increased in response to decreased precipitation (Zhou et al. 2013). Another example is found in Temperate Grasslands of California (USA), where shorter plants were more stress tolerant to decreased precipitation than taller plants (Fernandez-Going et al. 2012).

Water-use efficiency

Unlike SLA and plant height, water-use efficiency is a complex trait as it is determined by a number of different variables including but not limited to carbon gain per unit of water lost (Pérez-Harguindeguy et al. 2013), water transport features (Holloway-Phillips and Brodribb 2011), stomatal traits (Lawson and Blatt 2014) and leaf (Brodribb et al. 2007) and root architecture (White and Snow 2012). Despite this, our analysis indicates high coherency in results which indicate that across biomes and 3 climate/environmental changes, higher water-use efficiency is found to be positive for plant performance and fitness. Examples from the drier biomes indicate that greater WUE enabled Mediterranean trees in Sardinia (Italy) to cope better with drought stress (Altieri et al. 2015) and it was also a trait found to be more prevalent among shrubs in the drier sites of the Balearic Islands (Spain) (Lazaro-Nogal et al. 2013).

In Deserts of Arizona (USA), Huang *et al.* (2016) found that seedlings of herbaceous plants with greater WUE had higher stress tolerance and thus seedling survival in drought conditions. Similarly, examples from drier forested biomes such as the Boreal Forests of

Canada showed that higher WUE in trembling aspen enhanced the cavitation resistance and thus survival of these plants in drought (Schreiber et al. 2011), and in Dry Forests of Bolivia higher WUE enhanced drought tolerance of trees (Slot and Poorter 2007).

In wetter biomes, trait attributes were consistent i.e. higher WUE was important for plant performance and fitness under a variety of climate/environmental changes. For example, higher WUE was important under drought conditions for Moist Forest tree species in Bolivia (Slot and Poorter 2007). Under increased CO_2 conditions (measured experimentally), higher WUE was also associated with positive plant responses for coniferous trees of the Moist Forests in Panama (Dalling et al. 2016). Finally, field studies in Montane Grasslands of China indicate that under increased temperature, grasses with higher WUE had greater vegetative biomass and thus higher plant performance (Song et al. 2012, Li and Wu 2016).

Resprouting

Resprouting capacity can broadly be defined as the ability of plants to grow new shoots after destruction of above-ground biomass using below-ground and basal (Pérez-Harguindeguy et al. 2013) resources or sometimes, if the entire shoot is not damaged, from aerial resources (Clarke et al. 2013). Another important trait identified by our analysis is that of the presence of bud banks, which is a key determinant of resprouting ability (see further details below). The ability to resprout is important for plants to persist after disturbances such as fires, wind, mechanical removal, drought, frost, grazing and erosion events (Clarke et al. 2013, Pérez-Harguindeguy et al. 2013). In fire-driven systems, resprouting is often traded off against serotiny as a regenerative strategy which involves seeds being protected by seed capsules during fire and then released after fire.

Our study indicated that in biomes with and without a natural fire regime, resprouting was an important trait to cope with fire. However, the studies considered suggest that the benefit of resprouting vs. serotiny depends on the severity (Hollingsworth et al. 2013) and frequency of the fire (Buma et al. 2013) and on the stage of the post-fire cycle (Tavşanoğlu and Gürkan 2014).

In the Boreal Forest, being able to resprout was important after lower severity fires (Hollingsworth et al. 2013) and more frequent fires (Buma et al. 2013). In the Mediterranean biome, resprouting was important in conditions of increased fire frequency in SW Australia (Enright et al. 2014), however the study noted that seedling recruitment was additionally important in maintaining these resprouting species. In Turkey, resprouting species appeared to recover better over the longer term than reseeder species in post-fire recovery (Tavşanoğlu and Gürkan 2014). The ability to resprout epicormically was identified as important under increased fire frequency in Eucalypt trees in the Australian savanna (Clarke et al. 2015). In Mixed Forests, resprouting enhanced the population recovery after fire in the central Yunnan plateau

(China) (Su et al. 2015) and in Coniferous Forests of New Mexico and Arizona (USA) (Haire and McGarigal 2008). Furthermore, resprouting has also been found to be important under conditions of drought and wind in Mediterranean systems (Sánchez-Pinillos et al. 2016, Parra and Moreno 2017).

Relative growth rate

Relative growth rate (RGR) is defined as the increase in size of the plant relative to its initial size over a given time. It is different from the response variables "enhanced growth" or "biomass accumulation" used in this study as it is an inherent trait that is a time-associated variable (i.e. a rate with plants having faster or slower RGRs). Relative growth rate is a good indicator of plant productivity related to environmental stress and disturbance regimes (Pérez-Harguindeguy et al. 2013). Our data-synthesis shows that a high number of studies have demonstrated that under decreased precipitation conditions a lower relative growth rate is important for plant performance and fitness (Figs. 3, 4). These include studies in Temperate Coniferous Forests in Oregon, USA (Kerr et al. 2015) and Moist Broadleaf Forests species of Ecuador (Chirino et al. 2017), which link lower RGR with greater resistance to drought and extreme temperatures. However, in Moist Forests of Costa Rica, higher growth in the previous year allowed for greater survival in drought conditions (Uriarte et al. 2016). Also, Mediterranean grass species from California (USA) with greater summer dormancy, predominantly characterised by higher spring growth rate, had enhanced dehydration tolerance (Balachowski et al. 2016).

Several studies have also indicated that a faster RGR is an advantage with increased atmospheric CO_2 concentration. In Savannas of South Africa, woody species taking advantage of the CO_2 fertilisation effect, and thus able to grow faster, could escape the 'fire-trap', i.e. grow to a large enough stature to survive a surface fire (Bond and Midgley 2012). In experiments conducted on Moist Forest species of Panama, conifers with inherently slower growth rates benefitted more than angiosperms from the increase in atmospheric CO_2 because it stimulated enhanced growth (Dalling et al. 2016), a trend that could influence the composition in these forests.

Clonality, bud banks and below-ground storage organs

Clonality, the ability to reproduce vegetatively, allows plants to form bud banks, which enhances ability to recover and persist after disturbance through branching, shoot replacement and regrowth after severe seasons or injury (Pérez-Harguindeguy et al. 2013). Below-ground clonal organs can also serve as carbohydrate carbon storage, which provides resource for growth in future years (Soudzilovskaia et al. 2013).

Outputs from our data-synthesis show that reproducing clonally and/or increasing investment in bud banks and/or below-ground storage, has

been found to be important by different studies across biomes and multiple climate/environmental changes. For instance, studies in the warmer and drier Desert and Mediterranean biomes report that species with greater biomass allocation to roots (Tian et al. 2014, Tardella et al. 2016), greater carbohydrate reserves (Volaire et al. 2014) and below ground storage (Evans et al. 2014) showed enhanced drought tolerance, survival and post-drought recovery. In another study in the cooler biome of Temperate Grasslands and Savannas, species with bud banks had greater drought resistance in tall prairie grasslands of Kansas, USA, which ultimately lead to a shift in species composition (VanderWeide et al. 2014). In the even cooler forests of Boreal and Temperate Broadleaf and Mixed Forests biomes, the ability to reproduce vegetatively after severe dieback, enhanced drought tolerance and recovery at the population and individual level (Aubin et al. 2016).

In conditions of increased temperature these traits also proved important: greater investment in below-ground storage to support the following year's buds was the best predictor of species abundance of grasses in Montane Grasslands along a gradient of increasing temperature (Soudzilovskaia et al. 2013). Further, increased biomass allocation to roots was also associated with enhanced post-fire recovery in the Boreal Forest biome (Aubin et al. 2016).

Wood/stem-specific density

Wood density and stem-specific density (SSD) are used interchangeably with the distinction being that SSD can be measured for non-woody species (herbaceous) and that it includes the stem bark. This trait is calculated as dry mass per unit of fresh volume of a stem and is linked to the stability, hydraulics, growth, defence and architecture of plants (Pérez-Harguindeguy et al. 2013, Garnier et al. 2016). As a result, this trait is a central component of the "wood economic spectrum", which aims to describe functional trade-offs in woody plants (Chave et al. 2009). Species with higher wood density have enhanced resistance to hydraulic cavitation and physical damage/disease, but tissue costs associated with denser wood impose a limit on this.

Our analysis indicates that, across eight biomes, higher wood density was important for plant performance and fitness under decreased precipitation. For example, in Dry Forests of Bolivia seedlings with greater wood density had a reduced risk of cavitation during drought (Markesteijn and Poorter 2009) and in adult trees growth was less sensitive to reduced water availability for species with denser wood (Mendivelso et al. 2013). Similar trends were noticed in Moist Forests of M'Baïki (Central African Republic) (Ouédraogo et al. 2013), the Caribbean lowlands of Costa Rica (Uriarte et al. 2016) and Ecuador (Sakschewski et al. 2016), where studies combining monitoring and modelling indicated that under increased aridity or drought, trees found to be more resilient in terms of lower growth/biomass reduction and greater survival had greater wood

density. In Mediterranean environments, modelled plant community structure indicated that woodier species would be more prevalent under conditions of increased aridity (Frenette-Dussault et al. 2013). However, in Tropical Grasslands there seems to be a trade-off: in the Cerrado (Brazil), high wood density was found to be important as it prevents cavitation in stems, but low wood density allowed for higher water storage capacity (Hao et al. 2008).

Rooting depth

The root system of plants is the primary organ for water and nutrient uptake and is also responsible for resource transfer from the soil to above-ground parts of the plant. Rooting depth is an important morphological trait which determines from where in the soil profile the plant can acquire water and nutrients (Pérez-Harguindeguy et al. 2013). Plants with deep roots contribute disproportionally to the water and carbon balance of dry systems (Oliveira et al. 2005) and have an important role in ecosystem functioning under variable or decreasing precipitation (Maeght et al. 2013). Plant rooting depth therefore has an influence on ecosystem resilience during environmental stress such as drought, when deeper-rooted plants can tap groundwater more efficiently (Fan et al. 2017). Rooting depth is a trait rarely measured despite its perceived representation of hydraulic regulating strategies due to the difficulty of obtaining these data, which often involves labour-intensive root excavation (Iversen et al. 2017). Despite this, rooting depth was consistently identified as an important trait in our data-synthesis, across climate/environmental changes as well as biomes. The clearest trend that emerged from the studies we analysed associated with roots was that deeper roots were important for plant performance and fitness in drought conditions or in drier climates (Fig. 3). For example, reports from experiments on grassland species of the Temperate Grassland and Mediterranean biomes indicated that deeper roots enhanced potential depth of water uptake, which avoided dehydration and thus increased plant survival and recovery (Zwicke et al. 2015, Barkaoui et al. 2016). Additionally, deeper rooting was found to be important for fire survival by a number of studies, particularly for high-severity fires in trees of Boreal Forests, whereby deeper roots are protected from the lethal temperatures associated with fire (Aubin et al. 2016), potentially resulting in higher species abundances for those possessing these traits (Hollingsworth et al. 2013).

Implications and future directions

Future changes in the climate system will lead to regional key risks where some regions are projected to be more vulnerable to decreased precipitation and/or increased temperature than others (IPCC 2015, Fig. 1c). Our data-synthesis identified plant traits that enable species to cope with, or thrive under, specific climate/environmental changes (Fig. 4). The consistency observed in trait attributes within climate/environmental changes suggests generalizable response to climate change exists, and thus provides insights on key trait attributes for regions where these environmental changes are projected. In this way, we provide information that could be useful for prediction, management and/or restoration actions.

Our data synthesis also informs which traits can be focused on going forward in climate change studies. For example, less focus on those commonly sampled leaf traits that are not consistently associated with positive responses and more focus instead on other whole plant, regenerative and below-ground traits (See Appendix S2, Table S5 and S1, Fig S6) may be preferable when prioritising which traits to measure in the field. Furthermore, a greater focus on climate/environmental changes that remain relatively unstudied, but which are predicted to be significant in the future such as increased CO_2 and increased nitrogen deposition, would provide an enhanced understanding of plant responses to the full suite of factors associated with climate change. Finally, there should be enhanced effort to study plant traits in relation to climate change in Deserts, Temperate grasslands and Tundra as they remain under-sampled relative to their extent and perceived climate change vulnerability (Fig. 1b) (however see recent efforts to advance the literature on traits in the Tundra (Bjorkman et al. 2018a, Bjorkman et al. 2018b, Myers-Smith et al. 2019, Thomas et al. 2020).

There are several layers that need to be combined to have a complete picture of how the potential plant responses to climate changes are mediated by traits. There is a body of work focusing on responses at the molecular level that are related to individual phenotypic plasticity, showing that changes in trait attributes within individuals occur in response to environmental changes (Nicotra et al. 2010, Anderson 2016). This is a key point that is not addressed by our analysis but should be considered in future research as it may alter the relative abilities of different species responding positively to climate change where some species benefit from changing their traits (plasticity) (Nicotra et al. 2010), and some cannot but benefit from resource conservatism (bet-hedging) (Power et al. 2019). Another important consideration for future studies which is gaining momentum in the functional ecology community is that of intraspecific variation in traits. Although most trait studies use the mean trait value/attribute per species, intraspecific variation can contribute significantly to overall trait variation and should therefore not be overlooked (Albert et al. 2010, Mitchell et al. 2018). Explicitly analysing these elements requires detailed analysis of a) the change in trait attributes in response to environmental change (plasticity), (as above) and b) the variation in trait attributes both between and within species (intraspecific variation). This level of analysis is not yet widely available (Kattge et al. 2020) and remains an important future direction of study.

Conclusions

Although climate change has contributed to shaping plant form and function over millions of years,

the speed at which current climate change is being observed is unprecedented. We focused on identifying whether there are general patterns of plant functional traits that are associated with positive plant responses (ability to cope or thrive) under predicted climate and associated environmental changes, across biomes. Our data-synthesis identified a subset of top traits and their associated attributes namely higher or lower specific leaf area, higher or lower plant height, greater water-use efficiency, greater resprouting ability, lower relative growth rate, greater clonality/bud banks/below-ground storage, higher wood density, and greater rooting depth. Significantly, these findings do not merely reflect traits highly sampled. We found that trait attributes are quite consistent across the globe for the top traits that help plants to cope with decreased precipitation (i.e. higher wood density, lower SLA, higher WUE, deeper roots). Although more data are required to sufficiently compare other climate/environmental changes, both higher and lower SLA are reported to be important under increased temperature, and resprouting ability is reported to be important under increased frequency or intensity of fire.

Knowledge of which plant traits and attributes are important under different climate and associated environmental changes is key when developing a range of management decisions. For instance, it could help breeding programmes select species or varieties with key traits and trait attributes. It could also help conservation and restoration actions identify species that are resistant vs. vulnerable to climatic changes. Further, our analysis has implications for which ecosystem services will be more resilient to climate change, as many are linked to specific traits (e.g. the size and architecture of root and shoot systems regulate climate, water, and soils of ecosystems, Garnier et al. (2016)). More effort is needed to overcome the knowledge gaps we identified, such as which traits and climate/environmental changes future studies should focus on and which biomes these studies should target.

Acknowledgements

Supplementary Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
Appendix S1, Supplementary details on the biome selection and systematic literature review for this study
Appendix S1, Figure S1. Approach to record data extracted from each publication identifying traits that mediate positive responses to climate change

Appendix S1, Figure S2. Number of publications by publication year (2007-2017) from our data-synthesis identifying traits that mediate positive responses to climate change
Appendix S1, Figure S3. Number of publications per biome from our data-synthesis identifying traits that mediate positive responses to climate change
Appendix S1, Figure S4. Maps summarising the geographic coverage and abundance of literature by country and in relation to the area of each country
Appendix S1, Figure S5. Graph summarising the number of records for each of the traits and trait groups that mediated a positive or null response to climate change
Appendix S1, Figure S6. Graph summarising the number of records for each of the climate/environmental changes analysed in this data-synthesis identifying traits mediating positive responses to climate change
Appendix S1, Figure S7. Graph summarising the number of both publications and records for each of the methods used in this data-synthesis identifying traits mediating positive responses to climate change
Appendix S2, Table S1. List of the studies used for this data-synthesis based on the global systematic review of literature identifying traits that mediate positive responses to climate change.
Appendix S2, Table S2. List of positive plant responses to climate/environmental change mediated by traits found in our data synthesis based on a global systematic review of literature
Appendix S2, Table S3. List of traits identified by our data synthesis that were found to mediate positive plant responses to climate change.
Appendix S2, Table S4. Proportion of the positive records out of the total number of records for each trait group considered in the data-synthesis identifying traits that mediate positive responses to climate change
Appendix S2, Table S5. Traits identified by our data-synthesis listed by their score of importance calculated from the proportions of biomes and climate/environmental changes and weighted by the proportion of positive records
Appendix S2, Table S6. Comparison of global trait observations and ranking of the top 8 traits identified by our data-synthesis in terms of total trait observations and number of species with trait observations.

Author Contributions

KJW, NK and CT conceived the study and designed the approach, NK, JC and CT collected the data, NK and CT performed the data-synthesis, all authors substantially contributed to discussion of results, NK and CT wrote the first draft and received substantial contribution from other authors.

Data Accessibility

We do not have new data but have synthesized information from published papers that are listed in Appendix S2 Table S1.

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